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OSTRACODA FROM THE SUTTERBY MARL (U. APTIAN) OF SOUTH LINCOLNSHIRE

by P. KAYE and D. BARKER

ABSTRACT. The ostracod fauna of the Sutterby Marl at its type locality is described and contrasted with faunas of other British Lower Cretaceous horizons. Twenty-five species and subspecies have been found, of which two species and two subspecies are considered new.

THE basal member of what Swinnerton (1935) has called the Langton Series is a marl which forms a prominent springline in the area around Spilsby. This, the Sutterby Marl, can be seen in the edge of a field near Sutterby (Grid. Ref. TF 726391) where ploughing has cut into a bluff formed by the overlying Carstone. The field has many specimens of the belemnite *Neohibolites ewaldi* scattered over it.

Whilst mapping the area in 1963, J. Newton-Smith, of Leicester University, dug a pit towards the bottom of the field and exposed a mottled yellow-brown marl containing many *N. ewaldi*. There was a line of phosphatic nodules towards the base. A stiff grey marl which underlay the nodules yielded no fossils, but the upper marls contained ostracoda when washed down. Samples were also obtained from a pit, higher up the field, dug in April 1964 by a party consisting of Newton-Smith, Kaye, Barker, and others. These later samples have produced the richest Aptian fauna yet found in Britain which is described below.

The original sample taken by Newton-Smith is equivalent to the lower of two samples collected in the later excavation. Twenty-five species and subspecies of ostracoda were recorded from the Sutterby Marl, of which two species and two subspecies are considered new.

Acknowledgements. The authors are most grateful to Mr. J. Newton-Smith for bringing the project to their notice and for his help in the field work. We are also grateful to certain members of Leicester and Reading University Geology Departments for help in the collecting of the samples. The photographs used in the plates were taken by Mr. J. L. Watkins and text-fig. 1 was drawn by Mrs. J. Lees, both of Reading University Department to whom we are greatly indebted. Thanks are also due to Mrs. M. Kaye who typed the manuscript of this paper.

SYSTEMATIC DESCRIPTIONS

Order PODOCOPIA

Suborder PODOCOPINA

Superfamily CYPRIDACEA

Family CYPRIDIDAE

Subfamily MACROCYPRIDINAE

Genus MACROCYPRIS Brady 1868

Macrocypris parva Kaye 1965a

1965a *Macrocypris parva* Kaye, p. 75, pl. 5, figs. 1, 2.

[Palaeontology, Vol. 8, Part 3, 1965, pp. 375-90, pls. 48-50.]

Material. Three carapaces, BM Io 2712 from the Sutterby Marl, Sutterby, Lincs.

Remarks. The Sutterby findings extend the range of this species to the Upper Aptian. It has previously been recorded from the Hauterivian/Barremian of Speeton.

Family INCERTAE SEDIS
Genus KRAUSELLA Ulrich 1894

Krausella minuta Triebel 1936

Plate 48, figs. 12, 14

- 1936 *Krausella minuta* Triebel in Veen, p. 46, pl. 10, figs. 7-15.
1940 *Krausella minuta* Triebel; Bonnema, p. 115, pl. 3, figs. 32-34.
? 1946 *Krausella minuta* Triebel; Bold, p. 67, pl. 2, figs. 7a, b.

Material. Five carapaces and a single left valve from the Sutterby Marl, Sutterby, Lincs. BM Io 2694-6.

Measurements.

	Length	Height
Carapace Io 2694	0.50 mm.	0.30 mm.
Left valve Io 2695	0.45 mm.	0.28 mm.

Remarks. This small, distinctive species was first described by Triebel from the Lower Cretaceous of Germany, and later by Bonnema (1940) from the Upper Chalk. The valves are small and smooth with the left valve being much larger than the right. Hingement appears to be by simple overlap rather than by a definite tooth arrangement.

Family BAIRDIIDAE
Genus PONTOCYPRELLA Mandelstam 1956

Pontocyprrella rara Kaye 1965a

Plate 49, figs. 6-12

1965a *Pontocyprrella rara* Kaye, p. 74, pl. 5, fig. 14.

Material. Eighteen specimens from the upper sample and thirteen specimens from the lower sample BM Io 2662-9. Sutterby Marl, U. Aptian, Sutterby.

Measurements.

	Length	Height
L.V. Io 2662	0.85 mm.	0.45 mm.
R.V. Io 2665	0.85 mm.	0.40 mm.

Remarks. *Pontocyprrella rara* has only been found before as a few specimens in the basal Lower Aptian (*bodei* zone) at Speeton, Yorkshire (Kaye 1965a). It is, however, one of the most abundant species in both of the Sutterby Marl samples. The Sutterby specimens are larger than the Speeton forms and the measurements of the latter approximate to those of the penultimate instars at Sutterby. Full details of the adults of the species can now therefore be given. The major distinguishing features are the median position of the greatest height and greatest width, and the angular posterior end. The ventral margin is straight in the left valves and concave in the right valves. The prolongation of the antero-dorsal margin so characteristic of the genus is well marked. Internally the most prominent features are the wide anterior and narrow posterior vestibules. Normal pore canals are small but rather abundant and well scattered over the lateral surface. The hinge consists of a long narrow bar in the right valves which

fit into a long smooth groove in the left valves. Above the bar in the right valve there is a narrow marginal shelf. The muscle scars form a small rosette below the centre of the valve. They consist of four scars, two elongate anterior scars with two oval scars, one postero-dorsal, and the other posterior of them.

Superfamily CYTHERACEA

Family CYTHERIDEIDAE

Subfamily SCHULERIDEINAE

Genus SCHULERIDEA Swartz and Swain 1946

Schuleridea derooi Damotte and Grosdidier 1963

Plate 49, figs. 16, 19-21

1963 *Schuleridea derooi* Damotte and Grosdidier, p. 154, pl. 1, figs. 4a-i.

Material. Thirty specimens from the Sutterby Marl, U. Aptian of Sutterby, BM Io 2673-7.

Remarks. This species is abundant throughout the Sutterby Marl and has been recorded from the Lower and Upper Aptian of the Isle of Wight and the Lower Aptian of the Paris Basin.

Genus DOLOCYTHERIDEA Triebel 1938

Dolocytheridea minuta Kaye 1963

Plate 48, figs. 15-17

1963c *Dolocytheridea minuta* Kaye, p. 34, pl. 1, figs. 4-5.

1965b *Dolocytheridea minuta* Kaye; Kaye, p. 37.

Material. Six specimens from the lower sample, Sutterby Marl, Sutterby BM Io 2697-9.

Remarks. This species though originally described from the Upper Hauterivian and Lower Barremian at Speeton has also been recorded from the Lower and Upper Aptian of the Isle of Wight and the Lower Aptian of the Paris Basin. It also occurs quite abundantly in the Gault Clay, Middle and Upper Albian, of southern England.

Family CYTHERURIDAE

Genus CYTHERURA Sars 1866

Cytherura reticulosa (Chapman 1894)

1894 *Cytheropteron reticulosum* Chapman, p. 692, pl. 33, figs. 6a-c.

1964b *Cytherura reticulosa* (Chapman); Kaye, p. 318, pl. 55, figs. 7, 9.

Remarks. This form occurs only rarely at Sutterby but is one of the most characteristic species of lower horizons in the Lincolnshire Lower Cretaceous.

Genus DOLOCYTHERE Mertens 1956

Dolocythere rara Mertens 1956

1956 *Dolocythere rara* Mertens, p. 192, pl. 10, figs. 33-37; pl. 13, figs. 91-93.

1964b *Dolocythere rara* Mertens; Kaye, p. 322, pl. 55, figs. 12, 14, 15.

Remarks. This species occurs rarely in the upper sample of the Sutterby Marl.

Genus ACROCYTHERE Neale 1960

Acrocythere haueriviana (Bartenstein) 19561956 *Orthonotacythere haueriviana* Bartenstein, p. 532, pl. 3, figs. 80, 81.1960 *Acrocythere haueriviana* Bartenstein; Neale, p. 213, pl. 3, figs. 7a-b, pl. 4, figs. 10, 14.

Remarks. *A. haueriviana* has only been found rarely in the Sutterby Marl. It is extremely abundant at lower horizons in the 'Boreal' Lower Cretaceous of northern England.

Genus EUCYTHERURA Muller 1894

Eucytherura ornata Kaye 1964a

Plate 48, fig. 11

1964a *Eucytherura ornata* Kaye, p. 100, pl. 4, figs. 11-12.

Material. Two valves BM Io 2692-3 from the lower sample, Sutterby Marl, Sutterby, Lincs.

Measurements.

	<i>Length</i>	<i>Height</i>
L.V. Io 2692	0.32 mm.	0.17 mm.
R.V. Io 2693	0.32 mm.	0.17 mm.

Remarks. This species was only represented before by a single valve from the Barremian at Speeton. Its highly distinctive ornament is not comparable to any other species of this, or related, genera.

Genus CYTHEROPTERON Sars 1866

Subgenus CYTHEROPTERON Sars 1866

Cytheropteron (*C.*) cf. *inaequivalve* Bonnema 1941

Plate 48, figs. 8-10, 13

1941 *Cytheropteron inaequivalve* Bonnema, p. 27, pl. 6, figs. 24-28.

EXPLANATION OF PLATE 48

All figs. $\times 66$.

Figs. 1-4. *Cytheropteron* (*Infracytheropteron*) *lindumensis* sp. nov. 1. L.V. (Holotype) lateral view, Io 2678. 2. R.V. (Paratype) lateral view, Io 2679. 3. R.V. (Paratype) lateral view, Io 2680. 4. L.V. (Paratype) lateral view, Io 2681.

Figs. 5, 7. *Cytheropteron* (*Eocytheropteron*) *nova reticulata* ssp. nov. 5. R.V. (Paratype) lateral view, Io 2683. 7. L.V. (Holotype) lateral view, Io 2684.

Fig. 6. *Cytheropteron* (*C.*) *rugosa* Kaye. 6. R.V. lateral view, Io 2686.

Figs. 8-10, 13. *Cytheropteron* (*C.*) *inaequivalve* Bonnema. 8. R.V. lateral view, Io 2687. 9. L.V. lateral view, Io 2688. 10. L.V. lateral view, Io 2689. 13. Carapace dorsal view, Io 2690.

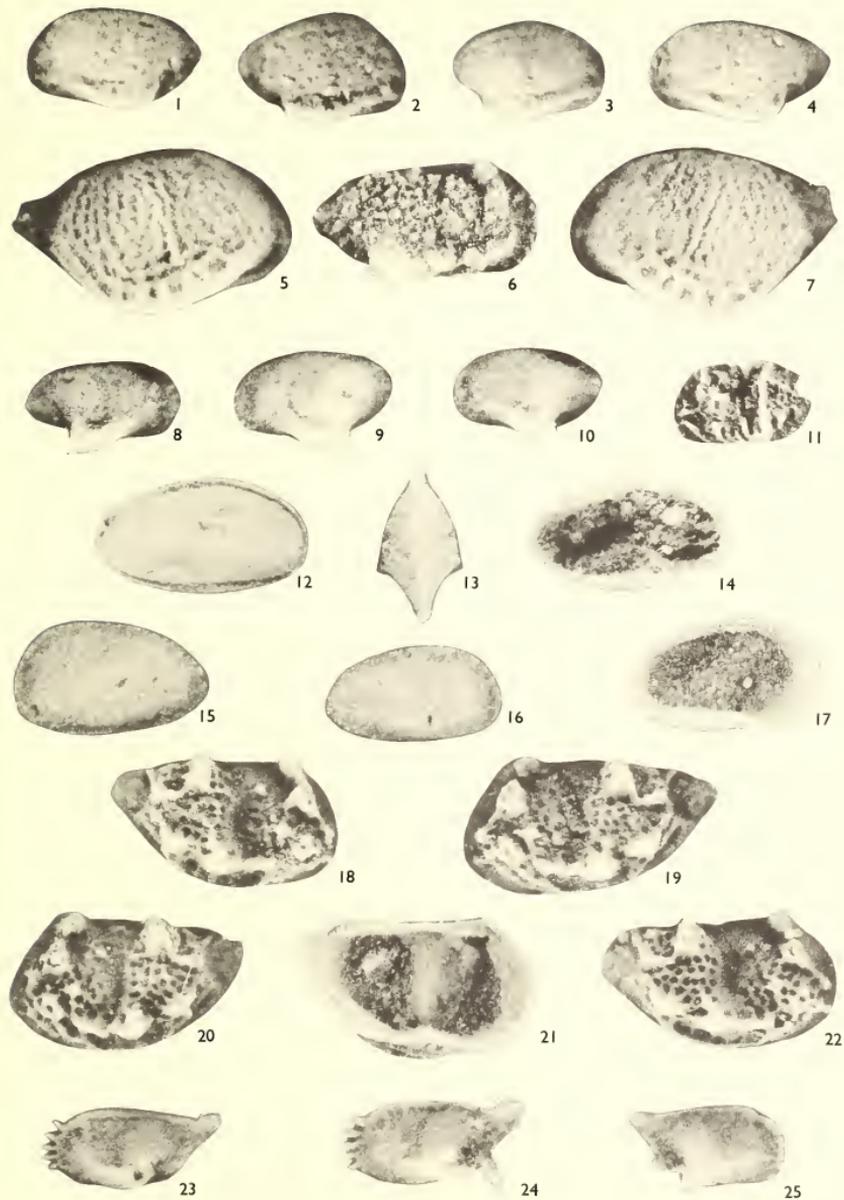
Fig. 11. *Eucytherura ornata* Kaye. 11. L.V. lateral view, Io 2692.

Figs. 12, 14. *Krausella minuta* Triebel. 12. Carapace from right, Io 2694. 14. L.V. internal view, Io 2695.

Figs. 15-17. *Dolocytheridea minuta* Kaye. 15. L.V. lateral view, Io 2697. 16. R.V. lateral view, Io 2698. 17. L.V. internal view, Io 2699.

Figs. 18-22. *Orthonotacythere inversa tuberculata* Kaye. 18. R.V. lateral view, Io 2701. 19. L.V. lateral view, Io 2702. 20. L.V. lateral view, Io 2703. 21. L.V. internal view, Io 2704. 22. R.V. lateral view, Io 2705.

Figs. 23-25. ?*Stillina* cf. *fluitans* Bonnema. 23. L.V. lateral view, Io 2707. 24. L.V. lateral view, Io 2708. 25. R.V. lateral view, Io 2709.



Material. Eleven valves and one carapace BM Io 2687-91 from the Sutterby Marl, Sutterby, Lincs.

Measurements.

	<i>Length</i>	<i>Height</i>
L.V. Io 2688	0.37 mm.	0.23 mm.
R.V. Io 2687	0.37 mm.	0.23 mm.

Description. Valves small, elongate; dorsal margin arched in left valves but with weak cardinal angles in the right valves. Anterior margin broadly rounded, posterior margin angled at mid-height. A broad-based ventral alate expansion occurs directed posteriorly and tipped with a small spine. Lateral surface smooth. Duplicature moderately broad, crossed by few thick, straight radial pore canals. Normal pore canals not abundant, well scattered. Hinge crenulate, merodont.

Remarks. The Sutterby specimens are almost identical to the Chalk form *C. inaequivalve* Bonnema (1941) differing in the broad base of the alae. This feature gives the alae a more triangular appearance when viewed dorsally. *C. (C.) inaequivalve* differs from *C. v.-scriptum* Veen (1936), *C. nannisimum* Damotte and Grosdidier (1963), *C. reightonensis* Kaye (1964a) and other Cretaceous species in the lack of surface ornament and the type of alae.

Cytheropteron (C.) rugosa Kaye 1965b

Plate 48, fig. 6

1965b *Cytheropteron (C.) rugosa* Kaye, p. 38, pl. 8, figs. 4-5.

Material. One right valve BM Io 2686 from the upper sample, Sutterby Marl, U. Aptian, Lincs.

Remarks. This species is abundant in the Upper Aptian of the Isle of Wight and the Hauterivian and Barremian of Lincolnshire. The Sutterby specimen is identical in all its features.

Subgenus EOCYTHEROPTERON Alexander 1933

Cytheropteron (Eocytheropteron) nova Kaye 1964a ssp. *reticulata* ssp. nov.

Plate 48, figs. 5, 7

Holotype. A left valve BM Io 2684 from the Sutterby Marl, U. Aptian, Sutterby, Lincs.

Paratypes. Six specimens BM Io 2683-5 from the same sample.

Diagnosis. A subspecies of *C. (Eo.) nova* Kaye with a row of prominent square reticulations along the crest of the alae.

Measurements.

	<i>Length</i>	<i>Height</i>
L.V. Io 2684 (holotype)	0.62 mm.	0.37 mm.
R.V. Io 2683 (paratype)	0.62 mm.	0.37 mm.

Description. This subspecies is almost identical with *C. (Eo.) nova* s.str. from the Hauterivian and Barremian at Speeton (Kaye 1964a) differing principally in having a prominent row of large square reticulations along the crest of the ventral alate expansion. The Sutterby subspecies is a little larger and has the alate expansion rather more drawn out and not quite as symmetrically rounded. They are almost certainly derived from *C. (Eo.) nova* s.s.

Subgenus INFRACYTHEROPTERON Kaye 1964

Cytheropteron (Infracytheropteron) exquisita Kaye 19641964a *Cytheropteron (Infracytheropteron) exquisita* Kaye, p. 105, pl. 5, figs. 9-10.*Material.* Two carapaces BM Io 2711 from the Sutterby Marl, Sutterby, Lincs.*Cytheropteron (Infracytheropteron) lindumensis* sp. nov.

Plate 48, figs. 1-4

Holotype. A left valve BM Io 2678 from the Upper Aptian, Sutterby Marl, Sutterby, Lincs.*Paratypes.* Six adult valves and one juvenile BM Io 2679-81 from the same sample.*Diagnosis.* A small smooth species of *Cytheropteron (Infracytheropteron)* with a strongly arched dorsal margin in the right valve and an asymmetrical lateral alate expansion.*Measurements.*

	Length	Height
Holotype L.V. Io 2678	0.41 mm.	0.25 mm.
Paratype R.V. Io 2679	0.42 mm.	0.25 mm.

Description. Valves small, laterally compressed. Dorsal margin strongly arched in the right valves, weakly arched in the left valves. Greatest height at one-third length. Anterior margin broadly rounded, posterior margin angled at mid height. Lateral surface smooth, inflated with an alate expansion ventro-laterally. No median sulcus. Alate expansion low, asymmetrical, and weakly directed postero-ventrally. Ventral surface smooth. Duplicature fairly broad, crossed by few straight thick radial pore canals, six anteriorly, three posteriorly. Normal pore canals not abundant, concentrated along the crest of the ala. The hinge in the left valve consists of a broad marginal bar which fits into a prominent open-ended furrow in the right valve. Above the median furrow in the right valve is a strong curved marginal bar which fits above the bar of the left valve. The median bar of the left valve has terminal gaps to accommodate the margin of the right valve.

Remarks. This species differs from the only other member of the subgenus, *C. (I.) exquisita* Kaye (1964a), in being larger and having a smooth lateral surface. The hinge, inflation, shape of the dorsal margin and relative inflation of the lateral surface above the alae are the easiest distinguishing features of the species from members of related subgenera.

Genus STILLINA Laurencich 1957

? *Stillina* cf. *fluitans* (Bonnema) 1941

Plate 48, figs. 23-25

1941 *Cytheropteron fluitans* Bonnema, p. 27, pl. 6, figs. 29-36.*Material.* Eleven somewhat fragmentary valves BM Io 2707-9 from the Sutterby Marl, Sutterby, Lincs.*Measurements.*

	Length	Height
L.V. Io 2707	0.42 mm.	0.22 mm.

Description. This small highly distinctive species has previously only been recorded from

the Upper Chalk but one of us (P.K.) has found it abundantly throughout the Gault Clay (M. and U. Albian) of southern England.

The valves are very strongly compressed laterally and have a spine-like ventral ala. Posterior to the ala there is a prominent spine lying somewhat beyond the inflated area on the valve margin. It tends to be directed ventrally rather than ventro-laterally as in the case of the ala. The posterior is drawn out into a long upturned caudal process; the anterior margin is strongly denticulate.

The duplicature is broad and crossed by few straight radial pore canals. There is in most Chalk and Albian specimens a prominent eye tubercle and keel-like ridge along the dorsal margin. These features tend to be absent in the Aptian specimens and in certain specimens from the higher horizons but may be a dimorphic characteristic. The hinge is merodont to weakly amphidont in the Aptian specimens but is more strongly amphidont in later forms. The anterior tooth in the right valve is knob-like whilst the median elements are not strongly divided. Though the external features are identical the hinge differs from that of true *Stillina*. As, however, the specimens do not fit into any other described genus they are left tentatively in that genus. Fuller description of the more abundant Albian material may finally resolve the difficulties.

Genus ORTHONOTACYTHERE Alexander 1933

Orthonotacythere inversa tuberculata Kaye 1963

Plate 48, figs. 18–22

1963e *Orthonotacythere inversa tuberculata* Kaye, p. 436, pl. 61, figs. 11, 15, 16.

Material. Fifteen specimens from the Sutterby Marl, U. Aptian, Sutterby. BM Io 2701–6.

Remarks. This form is the youngest member of a morphological sequence of subspecies of *Orthonotacythere inversa* (Cornuel) 1846 found in the Speeton clay. It occurs in the Upper Barremian at Speeton and its range is extended by the Sutterby findings into the Upper Aptian. The dominant ornamental features of the subspecies are the pronounced ventral longitudinal ribbing and tuberculation, differing from the other subspecies of *O. inversa* in the lack of vertical costation on the lateral surface. *O. inversa tuberculata* differs from the species of *Orthonotacythere* found in the Aptian of the Isle of Wight such as *O. atypica* Kaye (1965b) and *O. catalaunica* Damotte and Grosdidier (1963) in details of the ornament, particularly the costation.

Orthonotacythere sp. B

Plate 49, figs. 17, 18

Material. Six valves and fragments from the Sutterby Marl, Upper Aptian, at Sutterby, Lincs. BM. Io 2670–2.

Measurements.

	<i>Length</i>	<i>Height</i>
L.V. Io 2670	at least 0.70 mm.	0.45 mm.

Description. A species of *Orthonotacythere* with a deep vertical median sulcus and a pronounced ventral longitudinal ridge. The valves are rather large and are devoid of reticulation. A weak swelling occurs in the antero-dorsal region, probably representing

the eye tubercle and associated tubercle but the rest of the lateral surface is smooth. The ventral longitudinal ridge is high and keel-like. It is ventrally arcuate and is thickened in places giving a somewhat fluted effect. It is not tuberculate. Two short, slightly oblique longitudinal ridges run below the major rib on the ventral undersurface. The internal features are identical to other members of the genus.

Remarks. This species though represented by few generally broken specimens and therefore not completely described or named is undoubtedly distinct. It shows considerable similarities to *O. inornata* Kaye (1965*b*) from the Upper Aptian of the Isle of Wight but differs in the keel-like nature of the ventral rib and the antero-dorsal tuberculation. The lack of reticulation and poor tuberculation distinguish it from all other described species of the genus.

Family BYTHOCYATHERIDAE
Genus MONOCERATINA Roth 1928

Monoceratina tricuspidata (Jones and Hinde) 1890

Plate 48, fig. 13

- 1890 *Cytheropteron cuspidatum tricuspidata* Jones and Hinde, p. 38, pl. 3, figs. 6, 7.
1936 *Monoceratina tricuspidata* (Jones and Hinde); Veen, pp. 42, 43, pl. 2, figs. 4–11.
1940 *Monoceratina tricuspidata* (Jones and Hinde); Bonnema, p. 40, pl. 6, figs. 77–80.
1941 *Monoceratina tricuspidata* (Jones and Hinde); Triebel, p. 353.
1964*c* *Monoceratina tricuspidata* (Jones and Hinde); Kaye, p. 56, pl. 3, figs. 7, 8.

Material. Eight specimens and fragments from the Sutterby Marl, U. Aptian, Sutterby, Lincs. BM Io 2657–8.

Measurements.

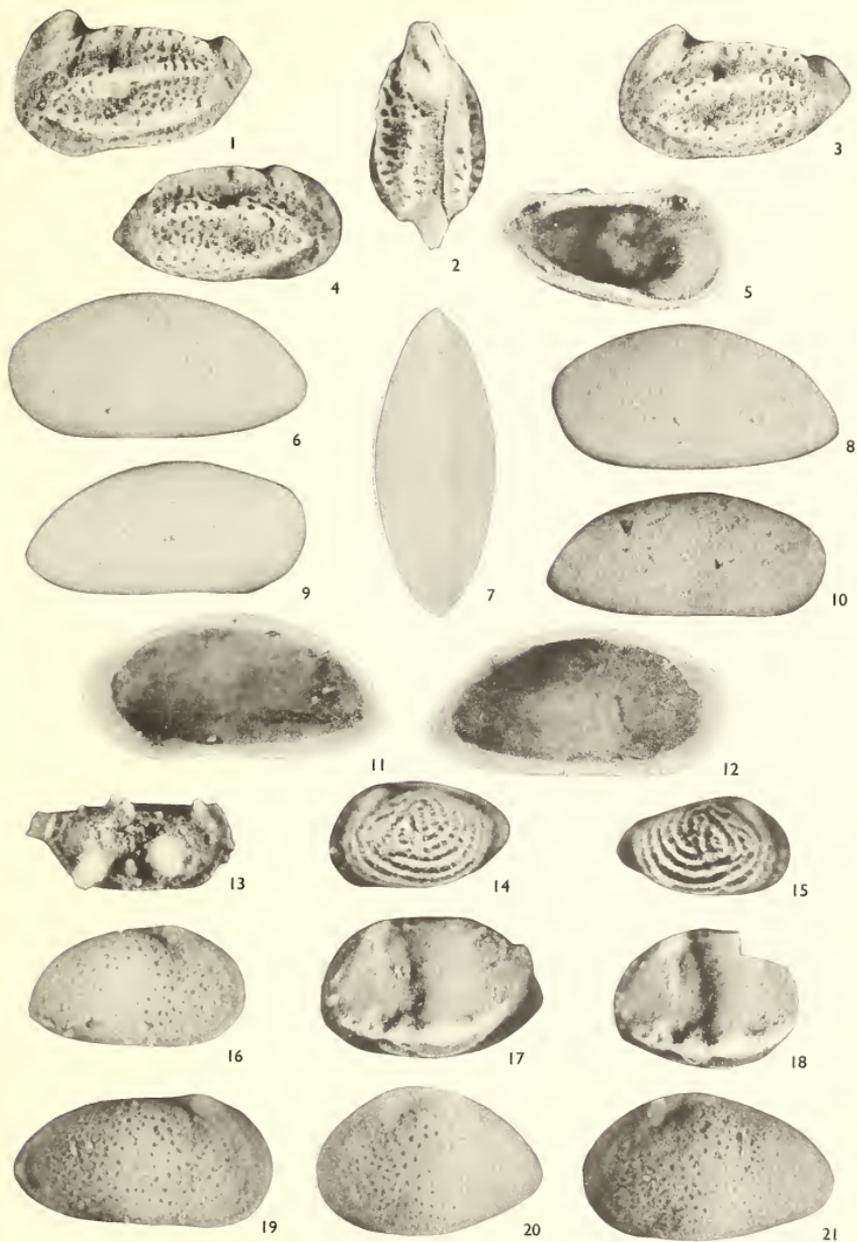
	Length	Height
R.V. Io 2657	0.62 mm.	0.27 mm.

Remarks. This species has previously been recorded only from the Upper Chalk and its range is therefore considerably extended. One of us (P.K.) has, however, specimens of this species from the Cambridge Greensand (U. Albion) in his collections. The Sutterby specimens match the ornament and other features of the Chalk forms exactly.

EXPLANATION OF PLATE 49

All figs. $\times 50$.

- Figs. 1–5. *Protocythere mertensi langtonensis* ssp. nov. 1. L.V. (Holotype) lateral view, Io 2651. 2. Carapace (Paratype) dorsal view, Io 2652. 3. L.V. (Paratype) lateral view, Io 2653. 4. R.V. (Paratype) lateral view, Io 2654. 5. L.V. (Paratype) internal view, Io 2655.
Figs. 6–12. *Pontocyprilla rara* Kaye. 6. L.V. lateral view, Io 2662. 7. Carapace dorsal view, Io 2663. 8. L.V. lateral view, Io 2664. 9. R.V. lateral view, Io 2665. 10. R.V. lateral view, Io 2666. 11. R.V. internal view, Io 2667. 12. L.V. internal view, Io 2668.
Fig. 13. *Monoceratina tricuspidata* (Jones and Hinde). 13. R.V. lateral view, Io 2657.
Figs. 14, 15. *Neocythere (Physocythere)* cf. *bordeti* Damotte and Grosdidier. 14. L.V. lateral view, Io 2659. 15. R.V. lateral view, Io 2660.
Figs. 16, 19–21. *Schuleridea derooi* Damotte and Grosdidier. 16. Female R.V. lateral view, Io 2673. 19. Male R.V. lateral view, Io 2674. 20. Female L.V. lateral view, Io 2675. 21. Male L.V. lateral view, Io 2676.
Figs. 17, 18. *Orthonotacythere* sp. B. 17. R.V. lateral view, Io 2670. 18. R.V. lateral view, Io 2671.





Family PROGONOCYTHERIDAE
 Subfamily PROGONOCYTHERINAE
 Genus NEOCYTHERE Mertens 1956
 Subgenus PHYSCYTHERE Kaye 1963a

Neocythere (Physocythere) cf. bordeti (Damotte and Grosdidier) 1963

Plate 49, figs. 14, 15

1963 *Centrocythere bordeti* Damotte and Grosdidier, pp. 156-7, pl. 2, figs. 8a-h.

Material. Fifteen specimens from the Sutterby Marl, U. Aptian, Sutterby, Lincs. BM Io 2659-61.

<i>Measurements.</i>	<i>Length</i>	<i>Height</i>
Male L.V. BM Io 2659	0.57 mm.	0.35 mm.

Remarks. The Sutterby specimens agree well with Damotte and Grosdidier (1963) forms from the Lower Aptian of the Paris Basin in all details but hingement. The latter authors state that the species has a characteristic *Centrocythere* type hinge which from Mertens's (1956) description of the type species should be amphidont with a high step-like anterior tooth and a divided posterior tooth separated by a weakly crenulate furrow in the right valves, a broad accommodation groove being present above the median element in the left valves.

In the Sutterby specimens the hinge is merodont with a strongly crenulate median element in the left valve and a wide marginal shelf. The anterior and posterior teeth in the right valve are both strongly subdivided. On this basis the specimens fall better within the subgenus *Physocythere* than in *Centrocythere*.

Subfamily PROTOCYTHERINAE
 Genus PROTOCYTHERE Triebel 1938

Protocythere derooi Oertli 1958

Plate 50, figs. 6, 8, 9, 11

1958 *Protocythere derooi* Oertli, p. 1509, pl. 6, figs. 129-43.

1965b *Protocythere derooi* Oertli; Kaye, p. 44, pl. 6, fig. 10.

Material. Six specimens from the lower sample, Sutterby Marl, U. Aptian, Sutterby, Lincs. BM Io 2637-41.

<i>Measurements.</i>	<i>Length</i>	<i>Height</i>
Female L.V. Io 2633	0.67 mm.	0.39 mm.
Female R.V. Io 2632	0.61 mm.	0.33 mm.

Remarks. This species, first recorded from the Upper Aptian of SE. France, has also been found in the Upper Aptian of the Isle of Wight. Its most diagnostic feature is the cross-rib joining the median and dorsal longitudinal ribs posteriorly.

Protocythere mertensi Kaye 1963d ssp. *langtonensis* ssp. nov.

Plate 49, figs. 1-5

Holotype. A left valve BM Io 2651 from the upper sample of the Sutterby Marl, Sutterby, Lincs.

Paratypes. Seven valves and one carapace BM Io 2652-6 from the same sample.

Diagnosis. A subspecies of *Protocythere mertensi* being much smaller in size and having a less well developed muscle node than the species sensu stricto.

Measurements.

	<i>Length</i>	<i>Height</i>
L.V. Holotype Io 2651	0.75 mm.	0.42 mm.
R.V. Paratype Io 2654	0.73 mm.	0.35 mm.

Description. The specimens of this subspecies are closely similar to *P. mertensi* s.s. Kaye (1963*d*) but are smaller and differ in minor features of the ornament. The muscle node is poorly developed in *P. mertensi langtonensis* whilst the reticulate ornament runs uninterrupted across the crests of the longitudinal ribs. The ventral rib is less inflated and the ventral margin is longer and straighter than in *P. mertensi* s.s. The dorsal rib is also less convex and the eye tubercle less well developed than in the latter subspecies.

Internally the major difference is the small number of radial pore canals (8-9 anteriorly) in *P. mertensi langtonensis* compared with the large number (twenty anteriorly) characteristic of *P. mertensi* s.s.

Remarks. This species is obviously very closely related to *P. mertensi* s.s. which occurs in the Lower Albian (*ewaldi* Marl) at Speeton and is presumably ancestral to it.

It is also closely similar to the Apto/Albian form *P. gaultina* Kaye (1963*d*) but lacks the characteristic anterior marginal ridge. From *P. tricostata* Triebel (1940) it differs in the smaller size and in the junction of the median and ventral ridges anteriorly.

Family TRACHYLEBERIDIDAE
Subfamily TRACHYLEBERIDINAE
Genus CYTHEREIS Jones 1849

Cythereis bekumensis Triebel 1940

Plate 50, figs. 13-16

1940 *Cythereis bekumensis* Triebel, p. 188, pl. 4, figs. 45-46, pl. 10, fig. 107.
non 1956 *Cythereis* aff. *bekumensis* Triebel; Deroo, p. 1518, pl. 4, fig. 58.

Material. Six specimens BM Io 2646-50 from the lower sample, Sutterby Marl, Sutterby, Lincs.

Measurements.

	<i>Length</i>	<i>Height</i>
Male L.V. Io 2649	0.95 mm.	0.50 mm.
Female L.V. Io 2648	0.87 mm.	0.50 mm.
Female R.V. Io 2646	0.87 mm.	0.46 mm.

EXPLANATION OF PLATE 50

All figs. $\times 50$.

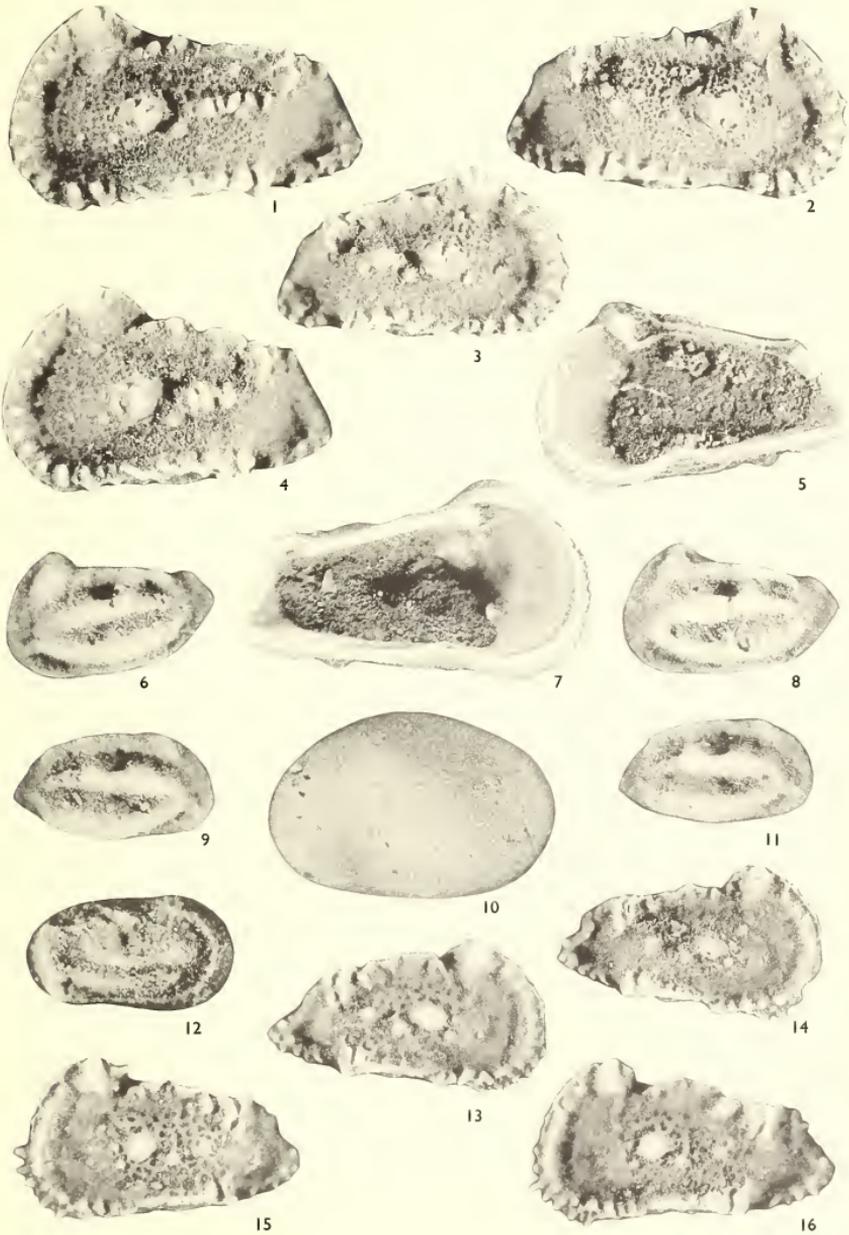
Figs. 1-5, 7. *Cythereis sutterbyensis* sp. nov. 1. Male L.V. (Holotype) lateral view, Io 2630. 2. Male R.V. (Paratype) lateral view, Io 2631. 3. Female R.V. (Paratype) lateral view, Io 2632. 4. Female L.V. (Paratype) lateral view, Io 2633. 5. Male R.V. (Paratype) internal view, Io 2634. 7. Male L.V. (Paratype) internal view, Io 2635.

Figs. 6, 8, 9, 11. *Protocythere derooi* Oertli. 6. L.V. lateral view, Io 2637. 8. L.V. lateral view, Io 2638. 9. R.V. lateral view, Io 2639. 11. R.V. lateral view, Io 2640.

Fig. 10. *Cytherella ovata* (Roemer). 10. R.V. lateral view, Io 2642.

Fig. 12. *Cytherelloidea* cf. *ovata* Weber. 12. R.V. lateral view, Io 2644.

Figs. 13-16. *Cythereis bekumensis* Triebel. 13. R.V. lateral view, Io 2646. 14. R.V. lateral view, Io 2647. 15. L.V. lateral view, Io 2648. 16. L.V. lateral view, Io 2649.



Remarks. The major distinguishing features of this species are the strong lateral compression, the prominent muscle node and short weak median rib. The intercostal areas are weakly reticulate whilst the anterior marginal rib is well marked. The dorsal and ventral longitudinal ribs are keel-like, but postero-ventral inflation is very weak.

C. bekumensis is similar to *C. bartensteini* Oertli (1958) but is larger and less inflated and not as strongly ornamented. It differs from *C. geometrica* s.s. Damotte and Grosdidier (1963) in being larger, reticulate, and having the ribs keel-like rather than rounded.

Cythereis sutterbyensis sp. nov.

Plate 50, figs. 1-5, 7

Holotype. A male left valve BM Io 2630 from the upper sample, Sutterby Marl, U. Aptian, Sutterby, Lincs.

Paratypes. Five valves and one carapace BM Io 2631-6 from the same sample.

Diagnosis. A large species of *Cythereis* with heavily calcified valves. Median rib short, spined, separated from the prominent muscle node. Lateral surface weakly reticulate.

Measurements.

	Length	Height
Holotype male L.V. Io 2630	1.12 mm.	0.60 mm.
Paratype female L.V. Io 2633	1.05 mm.	0.64 mm.
Paratype male R.V. Io 2634	1.07 mm.	0.59 mm.
Paratype female R.V. Io 2632	1.00 mm.	0.59 mm.

Description. Valves large, very strongly built. Dorsal and ventral margins straight converging posteriorly. Cardinal angles well marked, greatest height at a quarter length. Anterior margin broadly rounded; posterior triangular, angled ventrally. Lateral surface moderately inflated and weakly reticulate. Dorsal and ventral ridges prominent and wrinkled. Median ridge very short with a series of spines on its crest, separated anteriorly from the high, ridged muscle node. Anterior and posterior marginal ridges well marked and bearing small tubercles. Eye tubercle prominent, anterior margin denticulate.

Interior of valves characteristic of genus. Hinge strongly developed, terminal teeth in right valve, high with subdivisions on crest.

Remarks. The most obvious characteristics of this species are its large size and strong build. It is closest in arrangement of the ornament to *C. geometrica fittoni* Kaye (1965*b*) differing principally in the greater prominence of the ribs and reticulation.

Suborder PLATYCOPINA

Family CYTHERELLIDAE

Genus CYTHERELLA Jones 1849

Cytherella ovata (Roemer) 1840

Plate 50, fig. 10

- 1840 *Cytherina ovata* Roemer, p. 104, pl. 16, fig. 21.
 1849 *Cytherella ovata* (Roemer); Jones, p. 28, pl. 7, figs. 24*a-g*.
 1890 *Cytherella ovata* (Roemer); Jones and Hinde, p. 44, pl. 3, figs. 48-54.
 1956 *Cytherella ovata* (Roemer); Deroo, pp. 1508, 1523, pl. 1, figs. 4-6.
 1958 *Cytherella ovata* (Roemer); Oertli, p. 1502, pl. 1, figs. 10-29.

Material. Twenty-three specimens from the lower sample, Sutterby Marl, Sutterby, Lincs. BM Io 2642-3.

Measurements.

	<i>Length</i>	<i>Height</i>
R.V. Io 2642	0.90 mm.	0.57 mm.

Remarks. This well-known Aptian/Albian species is particularly abundant in the lower sample at Sutterby but is rather rare in the upper one. The specimens correspond exactly with those found in the Albian both at Speeton and in southern England.

Genus CYTHERELLOIDEA Alexander 1929

Cytherelloidea cf. *ovata* Weber 1934

Plate 50, fig. 12

1963b *Cytherelloidea* cf. *ovata* Weber; Kaye, p. 116.

Material. Two pre-adult specimens from the upper sample, Sutterby Marl. BM Io 2644-5.

Remarks. These two juvenile specimens are undoubtedly identical to the forms described as *C.* cf. *ovata* from the basal Aptian at Speeton. They have a weaker dorsal rib, and a more arcuate median rib than true *C. ovata* Weber (1934) and also have the ventral rib poorly connected posteriorly.

CONCLUSIONS

The Sutterby Marl is quite rich in ostracoda, twenty-five species and subspecies being represented. Twenty of these species have been recorded in the Cretaceous elsewhere in the British Isles, two species and two subspecies being new, one species being left unnamed. The Sutterby fauna is closely similar to the pre-Aptian 'Boreal province' faunas found at Speeton, Yorkshire and from Lincolnshire. Of the twenty known species in the Sutterby Marl, twelve are known from these 'Boreal' pre-Aptian deposits. Similarities to the top Barremian and basal Aptian faunas at Speeton are very close with characteristic species such as *O. inversa tuberculata* and *Pontocyprilla rara* being particularly well represented. A correlation between faunas in the 'Boreal' province is only to be expected but more striking is the dissimilarity between the fauna of the Sutterby Marl and the *ewaldi* Marl (L. Albian at Speeton). No species are common to these two units which have been regarded as equivalent by previous authors. Geographical considerations could perhaps account for this but the close similarities between the Sutterby and earlier Speeton faunas seems to discount it. Ecological differences are possible but again unlikely between two very similar clay horizons. A time as well as space difference seems the most likely explanation plus perhaps uplift along the Market Weighton axis in Aptian times (see Kaye 1964d).

Though having essentially a 'Boreal' fauna the Sutterby Marl shows some similarities to the Aptian of southern England. Eight species recorded at Sutterby are also present in the U. Aptian of southern England; three of these being found in the Bargate Beds near Guildford and six in the Upper Aptian of the Isle of Wight.

These similarities add weight to the theory of connexion of the 'Tethyan' and 'Boreal' seas during the Aptian through the English Midlands (Kaye 1964b, 1965b). The three species common to the Sutterby Marl and Bargate Beds of Surrey, *Cytherura reticulosa*

(Chapman), *Dolocythere rara* Mertens, and *Acrocythere haueriviana* (Bartenstein) are all well-known 'Boreal' forms and seem to indicate a southward migration in Upper Aptian times. The Isle of Wight Aptian has six species in common with the Sutterby Marl. The three species found in the Lower Aptian are also found in the Upper Aptian in the island and there is therefore no evidence of a Lower Aptian connexion of the two seas. Three of the six U. Aptian species, common to both the Isle of Wight and Sutterby: i.e. *Schuleridea derooi*, *Neocythere* (*Ph.*) *bordeti*, and *Protocythere derooi*, are 'Tethyan' forms well known from the Aptian of the Paris Basin and indicate northward migration whilst the remaining three species *Dolocytheridea minuta*, *Dolocythere rara*, and *Cytheropteron* (*C.*) *rugosa* are 'Boreal' species and indicate southward migration. *Dolocytheridea minuta* is somewhat anomalous for though being a characteristic Hauterivian and Barremian 'Boreal' form it is also known from the Lower Aptian of the Isle of Wight and the Paris Basin. Some migration route must therefore have been open to it in Lower Aptian times, presumably through S. Germany. Interchange of species does seem conclusive in the Upper Aptian but full mixing of the faunas is not likely, only a few forms having penetrated from one province to another. Ecological considerations and relative competition can perhaps account for this.

The Sutterby fauna does not persist into the Gault seas, only five Sutterby species being found in the Albian. Five species are also common to the Sutterby Marl and the Chalk. Three of these species *Cytheropteron* (*C.*) *inaequivalve*, *?Stillina* cf. *fluitans* and *Monoceratina tricuspida* are characteristic Chalk forms though the latter two have been recently found by one of the authors (Kaye) in the Gault clay. This great extension of the range of these species is rather striking but the alate nature of all three may point to some ecological factor. Alate or ventrally expanded species are very common in the Sutterby Marl, with members of genera such as *Cytheropteron*, *Monoceratina*, *Orthonotacythere*, and *Cythereis* being particularly prominent. They also form a large proportion of Chalk ostracod fauna.

Slight differences do occur between the two samples taken in the Sutterby Marl. The upper sample is richer in species and numbers than the lower one and in general most of the species found rarely in the lower one are more abundant in the upper one. The most distinctive differences between the two samples are the great abundance of *Cytherella ovata* in the lower sample when it is rare in the upper sample and also the absence of *Cythereis bekumensis* and *Protocythere derooi* from the upper sample. The latter two species seem to be replaced at the higher horizon by *Cythereis sutterbyensis* and *Protocythere mertensi langtonensis* which are absent from the lower sample.

Correlation of the Sutterby Marl with other Cretaceous horizons in Britain is difficult and its exact zonal horizon is not clear. The bulk of the Marl is Upper Aptian whilst the phosphate nodule bed contains ammonites indicating many Lower Aptian horizons (Casey 1961, pp. 570-1). The Marls above contain ammonites of the genus *Colombiceras*, only known elsewhere in this country from the Aptian of Upware which is itself of questionable horizon. It is likely that the basal Upper Aptian in southern England is the time equivalent of the Sutterby but the difference in lithology and difference in faunal province make exact correlation difficult. The Aptian in Yorkshire is very thin and the greatest similarities are between the Sutterby Marl and the pre-Aptian (plus basal Aptian *bodei* zone) at Speeton, rather than with the *ewaldi* Marl. The latter deposit has, however, only proved fossiliferous in its upper few feet where a lower Albian microfauna quite

SPECIES	UPPER APTIAN SUTTERBY, Lincs	UPPER APTIAN SURREY	LOWER APTIAN ISLE OF WIGHT	UPPER APTIAN ISLE OF WIGHT	PRE APTIAN N. ENGLAND	ALBIAN ENGLAND	POST ALBIAN BRITISH ISLES
<i>Cytherella avata</i> (Raemer)	X					X	X
<i>Cytherelloidea cf. ovata</i> Weber	X				X		
<i>Macrocypris parva</i> Kaye	X				X		
<i>Pantacyprilla rara</i> Kaye	X				X		
<i>Krausella minuta</i> Triebel	X				X		X
<i>Schuleridea deraai</i> D.B.G.	X		X	X			
<i>Dalacytheridea minuta</i> Kaye	X		X	X	X	X	
<i>Cytherura reticulata</i> (Chapman)	X	X			X		
<i>Eucytherura ornata</i> Kaye	X				X		
<i>Cytherapteran</i> (C) <i>inaequivalve</i> Bonnema	X						X
<i>Cytherapteran</i> (C) <i>rugosa</i> Kaye	X			X	X		
<i>C</i> (<i>Eacytherapteran</i>) <i>nava reticulata</i> sp. nov.	X						
<i>C</i> (<i>Infracytherapteran</i>) <i>exquisita</i> Kaye	X				X		
<i>C</i> (<i>Infracytherapteran</i>) <i>lindumensis</i> sp. nov.	X						
? <i>Stillina cf. fluitans</i> Bonnema	X					X	X
<i>Dalacythere rara</i> Mertens	X	X		X		X	
<i>O. inversa tuberculata</i> Kaye	X				X		
<i>Orthonotacythere</i> sp. B.	X						
<i>Manacratina tricuspidata</i> (Jones & Hinde)	X					X	X
<i>Neocythere</i> (Ph) <i>cf. bardeti</i> (D.B.G.)	X		X	X			
<i>Acrarythere hauteriviana</i> (Bartenstein)	X	X			X		
<i>Pratacythere deraai</i> Oertli	X			X			
<i>Pratacythere mertensi langtonensis</i> sp. nov.	X						
<i>Cythereis bekumensis</i> Triebel	X				X		
<i>Cythereis sutterbyensis</i> sp. nov.	X						

Known distribution of species of Ostracoda found in the Sutterby Marl

TEXT-FIG. 1.

unlike the Sutterby one is found. The Sutterby Marl is, therefore, either absent at Speeton or represented in the barren lower layer of the *ewaldi* Marl. *Neohibolites ewaldi* though giving its name to the lithological unit is never common at Speeton but is very abundant at Sutterby and it is by no means certain that the specimens found at the two localities are conspecific. The absence of the Carstone at Speeton and its prominence overlying the Sutterby Marl in Lincolnshire may indicate geographical separation of the two areas possibly due to uplift along the Market Weighton axis. The relationship of the *ewaldi* Marl to the Carstone is problematical, particularly as the Carstone itself is diachronous and it is likely that the upper fossiliferous portion of the *ewaldi* Marl is equivalent to part of the Carstone. The Carstone has, however, yielded a Middle Albian ostracod fauna at Melton in South Yorkshire and may be represented in part by the 'Greensand Streak' at Speeton and basal sands at West Heslerton (see Kaye 1964*d*). The absence of the Gault and the thin Red Chalk in Lincolnshire may bear out this suggestion.

The distribution and range of the ostracoda found at Sutterby are shown on text-fig. 1.

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UPPER JURASSIC AND LOWER CRETACEOUS MICROFOSSILS FROM THE HAUTES-ALPES

by JUDITH TURNER

ABSTRACT. Common pelagic (Tethyan) microfossils from the Upper Jurassic and Berriasian rocks of La Faurie, Hautes-Alpes, France, are described and illustrated, and their stratigraphical distribution compared with that of similar assemblages elsewhere. The fossils include crinoids, tintinnids, radiolarians, and *incertae sedis* such as *Globochaete*, *Cadosina*, and *Stomiosphaera*. *Lombardia* Brönnimann is considered to be a synonym of *Saccocoma* Agassiz.

IN the department of the Hautes-Alpes, in south-eastern France, near the village of La Faurie, the Kimmeridgian, Tithonian and Berriasian stages are represented by fine-grained calcareous rocks varying from pure limestones to marls (text-fig. 1). Coccoliths may form a large part of the ground-mass of the rock. In the Kimmeridgian the *pseudomutabilis* Zone and the basal part of the *beckeri* Zone consist of dark marls up to 200 m. thick. Above are up to 100 m. of marly limestone and limestones, with occasional chert nodules, forming the main part of the *beckeri* Zone and of the Tithonian. Conglomerates, probably originating as the result of movement of unconsolidated sediments in mudflows, are common in the Lower Tithonian, and are of extremely variable thickness; they usually give rise to prominent topographic features. The Berriasian is formed of alternating marls and marly limestones.

The beds are sporadically rich in ammonites, including aptychi, and belemnites and brachiopods may occur. The marls below the marly limestones of the *beckeri* Zone and the Lower Tithonian are particularly poor in macrofossils. Microfossils, however, are common in most beds, and various assemblages occur which can be used for correlation locally and which may eventually prove to be useful over a wide area of Southern Europe. References to the forms which occur are widely scattered and illustrations sometimes inadequate so that it has been thought useful to bring them together in one article.

The commonest microfossils are: plates of small crinoids of the family Saccocomidae recovered from washings from marls of the Kimmeridgian and, seen in thin section only, tintinnids such as *Calpionella* and *Tintinnopsella*, radiolarians, and various *incertae sedis* such as *Globochaete*, *Cadosina*, and *Stomiosphaera*.

The specimens figured are deposited in the Hunterian Museum, Glasgow.

Phylum ECHINODERMATA

Class CRINOIDEA

Order ROVEACRINIDA Sieverts-Doreck 1953

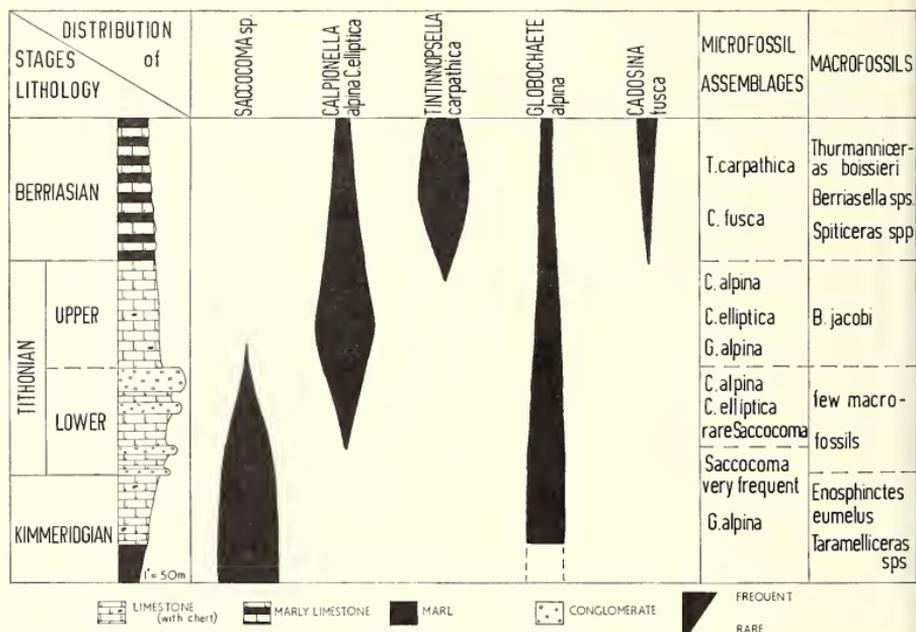
Family SACCOCOMIDAE d'Orbigny 1852

Genus SACCOCOMA Agassiz 1835 [= *Lombardia* Brönnimann 1955]

Description. Angular, usually bilaterally symmetrical shapes between 50μ and 150μ in length and formed of a single calcite crystal, occur in large numbers in thin sections of the Kimmeridgian and the lowermost Tithonian (Pl. 51, fig. 2). There is now no doubt,

[*Palaentology*, Vol. 8, Part 3, 1965, pp. 391-6, pls. 51-52.]

since the work of Verniory (1954, p. 327), that these are random sections through the brachial plates of small, pelagic crinoids of the family Saccocomidae, although they have been described as various other echinoderm fragments, algae or sponge spicules (Lombard 1938, 1945; Brönnimann 1955). Various types of brachial plates are found in washings of the Kimmeridgian marls which correspond exactly to the description of *Saccocoma* given by Jaekel (1892).



TEXT-FIG. 1. Stratigraphical distribution of microfossils in the Upper Jurassic and Lower Cretaceous of the Hautes-Alpes, France. Specimen numbers refer to catalogue of the Hunterian Museum, Glasgow.

These plates include the first primibrachial, identified by its horizontal proximal facet and strongly oblique distal facet (Pl. 52, figs. 16, 17). This distal facet is joined to the oblique proximal facet of the first secundibrachial, an axillary brachial easily identified by its double distal surfaces (Pl. 52, figs. 20–23). Other plates include unbranched secundibrachials with or without large, delicate, wing-like extensions (Pl. 52, fig. 18). Distal, unwinged brachials of the arms and pinnuli also occur in large numbers (Pl. 52, figs. 24, 25). It is possible to distinguish on some of the brachials the lateral facet from which branched the pinnuli (Pl. 52, figs. 26, 27). Some spined fragments also occur (Pl. 52, fig. 19) very similar to parts of radial plates as described by Verniory (1961, p. 316). All the specimens show a ventral canal and a coarsely reticulate surface.

In 1955 Brönnimann erected the genus *Lombardia*, with three 'species', *arachnoidea*,

perplexa, and *angulata*, for various forms found in thin sections in Cuban material. These three 'species' are, as Verniory (1956a, p. 86, see also Dufaure 1958, pl. 6, figs. 1-6) has shown, winged brachials of *Saccocoma* viewed obliquely (Pl. 52, figs. 3, 9) and vertically (Pl. 52, fig. 10) and distal (non-winged) brachials viewed vertically (Pl. 52, figs. 1, 2). *Lombardia* is, therefore, a junior synonym of *Saccocoma*.

Sieverts-Doreck subdivided *Saccocoma* into three morphological groups (1955, p. 119) without giving any new specific names. These groups were characterized by having I. Unspined radial plates, calyx margin straight, proximal brachials without extensions for muscle attachment. II. Spined radial plates, calyx margin straight, with dense or sieve-like plates for muscle attachment. III. Unspined radial plates, calyx margin incurved to cover part of the oral cavity, including *S. tenella* from the upper part of the Upper Jurassic.

She then says that the new species will be described at a later date, but this description does not yet seem to have appeared. Verniory, however, has described one of the forms, with a diagnosis communicated verbally to him by Sieverts-Doreck. He presumably uses the abbreviation *in coll.* (= *in colloquio*) to mean 'in verbal communication'. *S. quenstedti* Sieverts-Doreck *in* Verniory, 1961, is a spined form and thus belongs to Group II. It may be noted here that Verniory's drawing (pl. 1, fig. 7) described as a secundibrachial, is in reality a 1st primibrachial. He also mentions (1962a, p. 390; 1962b, p. 394) a 'groupe *S. schattenbergi* Sieverts-Doreck (*in coll.*)' presumably to include Group I of Sieverts-Doreck, many of the specimens of which are found in the Schattenberg collection, and a *S. feifeli* Sieverts-Doreck (*in coll.*). Characters are given to differentiate these forms from *S. quenstedti*. ICZN Article 13 (p. 13) states that for a name to be available it must be 'accompanied by a statement that purports to give characters differentiating the taxon'. The names *S. schattenbergi* and *S. feifeli* therefore appear to be available, *S. schattenbergi* for a form with thicker radials with long oral projections and *S. feifeli* for a small form with its calyx very flattened axially. It is to be hoped that Sieverts-Doreck's further paper mentioned on p. 119 in her 1955 article will expand these diagnoses and compare these species with other ones previously described.

Phylum PROTOZOA

Class CILIATA

Order SPIROTRICHIDA Bütschli 1889

Suborder TINTINNINA Claparède and Lachmann 1858

Description. The essential details of the structure and stratigraphical distribution of the tintinnids of the Upper Jurassic and the Cretaceous remain as they were described by Colom (1948, p. 251).

In the La Faurie region *Calpionella alpina* Lorenz and *C. elliptica* Cadisch (Pl. 52, figs. 5, 7) appear in the Lower Tithonian, in beds still containing fragments of *Saccocoma*. They do not, however, become very abundant until the upper part of the Tithonian, where they occur in swarms. The two species continue, with decreasing numbers, into the Berriasian, where they are accompanied by numerous *Tintinnopsella carpathica* Murgeanu and Filipescu (Pl. 52, figs. 4, 8). This form is now known to occur in uppermost Tithonian beds (Colom *et al.* 1954), though its presence in large numbers is usually regarded as diagnostic of the Lower Cretaceous.

Other tintinnids also occur, some of which are of stratigraphical importance, like *Stenosemellopsis hispanica* (Colom) which is frequent, although not confined to the Berriasian, but most of them are rare and therefore of less general use for stratigraphical purposes.

Class ACTINOPODA
Subclass RADIOLARIA

Large numbers of radiolaria occur at all horizons. The silica of which they were originally formed has very largely been replaced by calcite, but many still retain the form of the porous skeleton and delicate spines of the original structure (Pl. 52, figs. 13, 14, 15).

INCERTAE SEDIS

Genus *GLOBOCHAETE* Lombard 1945

Globochaete alpina Lombard 1945

Discussion. *Globochaete alpina* (the 'organisme D' of Joukowsky and Favre 1913) is a

EXPLANATION OF PLATE 51

Thin sections photographed in ordinary light.

Fig. 1. *Calpionella* limestone, with *C. alpina* Lorenz (a), *C. elliptica* Cadisch (b); Uppermost Lower Tithonian, Veynes; $\times 60$.

Fig. 2. Limestone with *Saccocoma*: sections through winged secundibrachial (c) and distal (unwinged) brachials (d); Lower Tithonian, La Faurie; $\times 60$.

Fig. 3. Limestone with *Cadosina fusca* (e) and *Tintinnopsella* sp. (f); Berriasian, La Faurie; $\times 120$.

Fig. 4. *Stomiosphaera minutissima* (Colom); Upper Tithonian, St. Julien, X308; $\times 750$.

Fig. 5. *Cadosina fusca* Wanner; Berriasian, Veynes, X309; $\times 750$.

EXPLANATION OF PLATE 52

Figs. 1, 2, 3, 9, 10. *Saccocoma* sp., $\times 150$. 1-2, Vertical sections through distal brachials, 'Lombardia angulata' Brönnimann; E3657/1, 2. 3, 9, Horizontal sections through winged brachials, fig. 3 showing the central canal, 'L. arachnoidea' Brönnimann; E3657/3, 4. 10, Vertical section through winged brachial, 'L. perplexa' Brönnimann; Lower Tithonian, E3657/5. (Figs. 1, 3, 9, 10, La Faurie, fig. 2, St. Julien).

Figs. 4, 8. *Tintinnopsella carpathica* Murgeanu and Filipescu; Berriasian, La Faurie, P409/1, 2. $\times 300$. 4, showing caudal elongation.

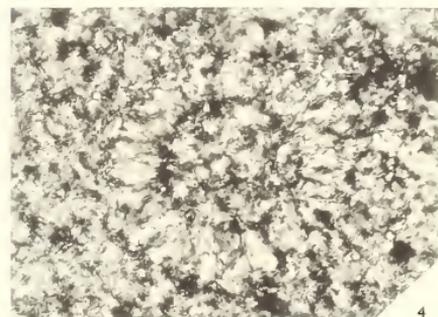
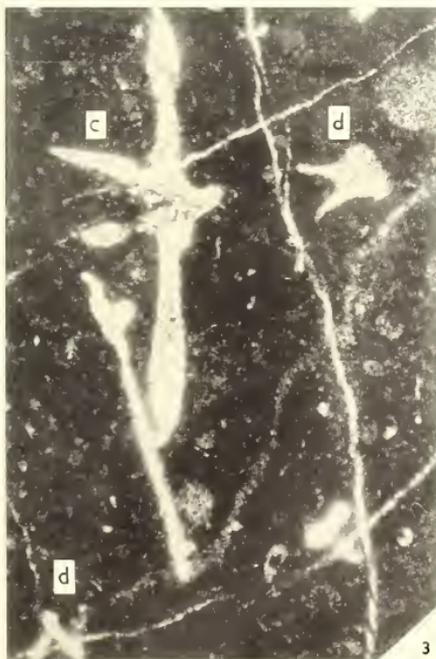
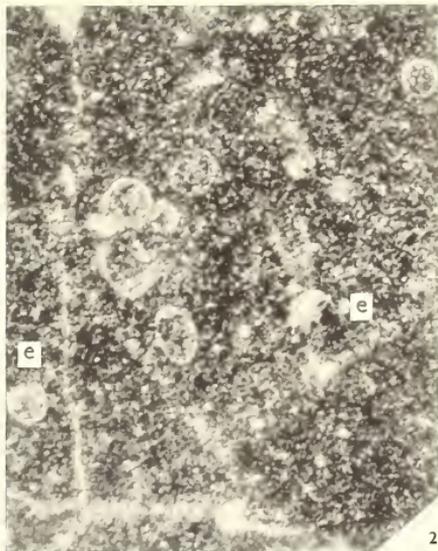
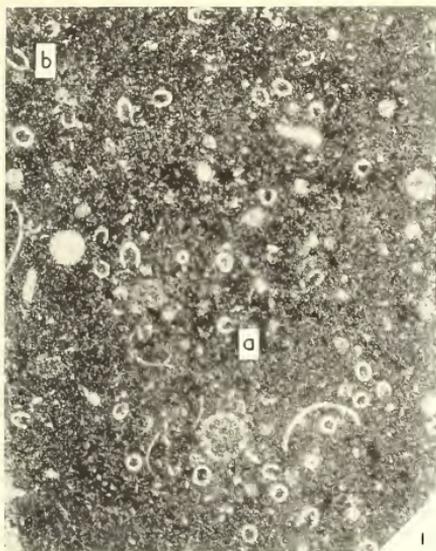
Fig. 5. *Calpionella alpina* Lorenz; Upper Tithonian, La Faurie, P410; $\times 300$.

Figs. 6, 11, 12. *Globochaete alpina* Lombard; Tithonian, La Faurie; X300. 6, irregular form, X310. 11, quadrilobate form, (a) ordinary light, (b) under crossed nicols to show extinction cross, X311. 12, bilobate form, X312.

Fig. 7. *Calpionella elliptica* Cadisch; Upper Tithonian, La Faurie, P411; $\times 300$.

Figs. 13-15. Radiolaria; Berriasian, La Faurie, P1101-3; $\times 150$.

Figs. 16-27. *Saccocoma* spp.; Kimmeridgian, beckeri Zone, Vaunièrette, St. Julien; $\times 50$. 16-17, *Saccocoma* sp., primibrachials. 16, ventral surface showing ventral canal and horizontal proximal facet where the brachial joined the radial plate, E3654/1. 17, oblique view of dorsal surface showing oblique distal facet, E3654/2. 18, *Saccocoma* sp., secundibrachial, ventral view with broken bases of wing-like extensions, E3654/3. 19, *Saccocoma quenstedti* Sieverts-Doreck in Verniory, spined fragment of radial, E3655. 20-21. *Saccocoma* sp., axillary secundibrachials. 20, dorsal view showing coarse reticulate surface and double distal facets, E3654/4. 21, ventral view showing oblique proximal facet and double distal facets, E3654/5. 22-23. *Saccocoma tenella* (Goldfuss), axillary brachials showing wing-like, reticulate extensions. 22, dorsal surface E3656/1. 23, ventral surface E3656/2. 24-27, *Saccocoma* sp., distal brachials. 24, dorsal view, E3654/6. 25, ventral view with ventral canal E3654/7. 26, dorsal view of brachial with base for pinnule, E3654/8. 27, ventral view of brachial with base for pinnule, E3654/9.







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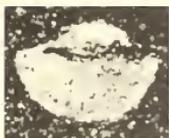
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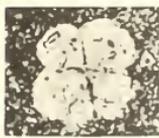
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11a



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11b



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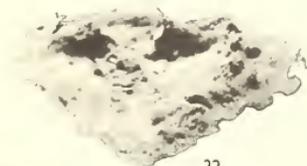
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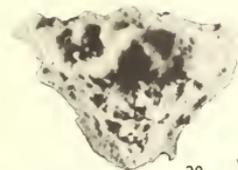
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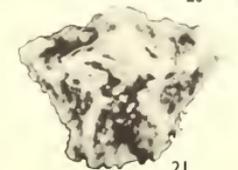
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spherical, bi- or quadri-lobate organism 50 μ to 80 μ in diameter, formed of radial fibrous calcite (Pl. 52, figs. 6, 11, 12). It may occur at all horizons but is more common in the Jurassic (Durand-Delga 1956, pp. 143-53).

The systematic position of this organism is not known, although it has been suggested (Lombard 1945, pp. 167-8) that it is the zoospore of a calcareous alga.

Genus CADOSINA Wanner 1940

Cadosina fusca Wanner 1940

Description. *Cadosina fusca* is a small (50 μ) spherical body of light-brown porcellaneous calcite, with a wall 10 μ to 15 μ thick around a centre of fine calcite (Pl. 51, fig. 5). In the La Faurie area it is confined to the Cretaceous where it may occur in large numbers, often associated with *Tintinnopsella*.

Genus STOMIOSPHAERA Wanner 1940

Stomiosphaera minutissima (Colom) 1935

Discussion. The spherical body 50 μ in diameter, referred to by Colom as a fibrosphere but shown by Durand-Delga (1957) to be of different although unknown systematic position, occurs fairly frequently at all horizons. It shows two distinct layers—an outer layer of calcite 10 μ to 12 μ thick, composed of radiating fibres, and an inner, structureless opaque layer (5 μ). The centre is filled by fine-grained calcite similar to the enclosing sediment (Pl. 51, fig. 4).

STRATIGRAPHICAL DISTRIBUTION

The forms described occur in successive assemblages of local stratigraphical significance. Their distribution is shown in text-fig. 1, from which it can be seen that the Kimmeridgian is characterized by numerous crinoid fragments and *Globochaeta alpina* and by the absence of tintinnids. A typical limestone is shown in Pl. 51, fig. 2. The lowest Tithonian contains a mixture of *Saccocoma*, *Globochaeta alpina*, and calpionellids, and the Upper Lower Tithonian and the Upper Tithonian contain large numbers of *Calpionella alpina* and *C. elliptica* but are without crinoid fragments (Pl. 51, fig. 1). The Berriasian is distinguished by the incoming of large numbers of *Cadosina fusca* and *Tintinnopsella carpathica* (Pl. 51, fig. 3). This distribution compares closely with that described by Charollais and Rigassi-Studer from Châtel-Saint-Denis, in the Pre-Alps of Switzerland (1961, pp. 267, 272), where abundant *Calpionella alpina* and *C. elliptica* with rare *T. carpathica* characterize the Portlandian (= Upper Tithonian) and where this latter species only becomes frequent in the Berriasian. Similarly crinoid fragments do not occur above the Kimmeridgian (the upper part of this stage at this locality probably being equivalent to part of the Lower Tithonian). Comparable distributions occur over a wide area of the Tethyan province including North Africa (Colom *et al.* 1954), Spain and Mallorca (Colom 1948, 1955), Italy (Zia 1955), and elsewhere.

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ORIGIN, LIMITS, AND SYSTEMATIC POSITION OF *SCAPHITES*

by JOST WIEDMANN

ABSTRACT. Up to the present interpretations concerning the origin and systematic position of the Cretaceous heteromorph *Scaphites* have been extremely divergent. On one hand, scaphitids have been regarded as a monophyletic group of either lycoceratid (e.g. Spath 1933, 1934; Wright 1953, 1957) or ammonitid origin (Luppov and Drushtchic 1958; Drushtchic 1962), on the other hand, as a more or less polyphyletic accumulation (Nowak 1911; Reeside 1927a; Schindewolf 1961). Wright and Wright (1951) established a superfamily Scaphitaceae, directly connected with the lycoceratid stock, while in the recent Russian literature they are placed in the Ammonitina. Reeside distributed the scaphitids among four different ammonitid lineages. All these possibilities of scaphitid classification are discussed here. A monophyletic but hamitid origin of the true scaphitids is asserted; 'Otoscapitinae' Wright are regarded as heterogeneous (*Otoscapites* is a true *Scaphites*, but *Worthoceras* should be placed in Ptychoceratinae), and Labeceratidae Spath are referred to the anisoceratids. The suture line of the restricted *Scaphites* was found to be quadrilobate throughout, as in all other heteromorphs. This makes the superfamily rank unnecessary, in the author's opinion, and places the remaining family Scaphitidae in the Ancylocerataceae, as recently defined by Wiedmann (1962b).

IN the last half-century many opinions have been given about the systematic position and origin of the scaphitids. The divergent interpretations naturally depend on the different evaluations placed on features such as general morphology, sculpture, suture elements or suture development. They also depend on the stage of evolution, and we will obtain differing results through the study of primitive Upper Albian or highly specialized Maastrichtian material. It is a curious fact, but nearly all these opinions, Spath (1934) and Wright (1953) excepted, were founded on late uppermost Cretaceous species. This publication is based on early scaphitids of Upper Albian and Cenomanian age and traces a new outline of history and extent of these peculiar Cretaceous heteromorphs.

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I am also indebted to Dr. P. Rodda (Austin) for making Adkins's and Moreman's types of the Texan *Worthoceras* available to me, and to Professor Dr. W. P. Popenoe (Los Angeles) who kindly sent me some Californian *Otoscapites* from his collection for comparison. Further thanks are due to Mr. W. Wetzel (Tübingen) who made the photographs in a superior manner as always, and to Mr. Springer, the draughtsman of the Institute of Tübingen. Cordial thanks are also due to R. Pichler (Tübingen) who revised the English text, and especially to Mr. C. W. Wright (London) for critical reading of the typescript.

Abbreviations. The terminology of the suture-line used here is that of Wedekind and Schindewolf. It is not only the most simple, but also the most natural, now generally accepted in the Western

hemisphere. In the scaphitids we find the most simplified suture-line, with only four true lobes: internal lobe (*I*), umbilical lobe (*U*), lateral lobe (*L*) and external one (*E*). In addition to these true lobe elements the term pseudo-lobe (*p*) will be introduced here for a group of saddle incisions, situated in *Scaphites* between the elements *L* and *U*, and increasing to normal lobe size. The saddles will be defined according to Schindewolf by the surrounding lobes, i.e. *L/E* for the so-called first lateral saddle, *L/U*, &c. The continuously proposed Russian terminology (Ruzhencev 1960) should definitely be rejected, because the lobe symbols of Wedekind are used in a completely different sense, which leads to general confusion. Moreover the Russian terminology is too complicated for application to Cretaceous ammonites (Wiedmann 1963).

The measurements are expressed with the following symbols:

- D* Greatest diameter of spiral portion and final hook,
- B* Maximum thickness of spiral portion and final hook,
- d* diameter of the spiral portion,
- h* maximum whorl height of the spiral portion,
- b* maximum whorl thickness of the spiral portion,
- u* umbilical diameter of the spiral portion.

The types described here are deposited in the following institutions: Institut für Geologie und Paläontologie, Tübingen (GPIT); Muséum d'Histoire Naturelle à Genève (MHNG); Musée Géologique de Lausanne (MGL); Bureau of Economic Geology, University of Texas, Austin (BEGA); Muséum National d'Histoire Naturelle à Paris (MHNP), and the British Museum of Natural History, London (BMNH).

PREVIOUS WORK AND CURRENT PROBLEMS

Subsequent to Parkinson who created the genus *Scaphites* in 1811, all Cretaceous heteromorphs with scaphitoid living chamber were included here. D'Orbigny (1842, p. 514) was the first to recognize that the Lower Cretaceous *yvanii* group should be separated, which was named *Macroscaphites* by Meek (1876). Furthermore Meek proposed a separate family Scaphitidae to include only the genus *Scaphites*. He did not, however, explain his concept of its relationship. One year before, Neumayr (1875) had published his reflections on the systematics of Cretaceous ammonites. He interpreted *Scaphites* as a true monophyletic group, and related them, because of the form of their inner whorls, suture-line, and aptychus, with the perisphinctid genus *Olcostephanus*. He was the first who stated that the scaphitids are distinguishable from all other heteromorphs through the presence of so-called 'auxiliary' (= umbilical) lobes. From this point on the family Scaphitidae was moved through nearly the complete ammonite system.

It was Zittel (1884) who placed *Scaphites* in the Stephanoceratidae, and *Macroscaphites*, according to its suture-line, correctly in the Lytoceratidae. The opinion that *Scaphites* might also represent a lytoceratid descendant was rigorously rejected by Grossouvre (1894) on the grounds that the strong ornamentation of the scaphitid shells is more significant than their bifid lateral lobes. Thus scaphitids were included in the Pulchelliidae or the Acanthoceratidae, and interpreted as direct derivatives of *Stoliczkaia dispar*.

Logan (1899) came to an unusual opinion; he placed *Scaphites* in the Stephanoceratidae as usual, but regarded the highly incised suture-line of *Scaphites* as a progressive and not degenerate feature. *Scaphites* was referred to the lytoceratids for the first time by Hyatt (1900), but there we also find the observation (op. cit., p. 572) that

the young stages of *Scaphites* 'possess the general aspect of *Pachydiscus*, and there are species transitional between them'. At the same time he proposed a number of new scaphitid genera, but without any diagnosing descriptions.

J. P. Smith (1901) seems to be the author of the polyphyletic theory. He thought of at least two different origins of scaphitids, one in the hoplitids, the other in lytoceratids. He was followed by W. D. Smith (1905) who studied the ontogenetic suture development of different scaphitid species. In *Sc. nodosus* and its allies the lateral lobe was found to be trifold at first, becoming bifid in the adult stage. The group of *Sc. perrini-inermis-condoni*, however, was said to have a bifid lateral lobe throughout, a wider umbilicus, and reduced ribbing. Thus the former were included in stephanoceratids, the latter in lytoceratids. Contrary to Logan he emphasized the reduction of the fourth main lobe (*U*) during the ontogeny, and therefore interpreted the scaphitid suture as degenerate. Pervinquière (1907) came to a similar result, believing that also in the scaphitid type species, *Sc. equalis*, the original shape of the lateral lobe is trifold, becoming bifid with age. Therefore and with regard to morphologic differences in the early ontogeny, the lytoceratid ancestry of true scaphitids as well as the attachment to *Stoliczkaia* was rejected. He returned to Neumayr's opinion, i.e. that of an olcostephanid (or holcodisid) origin for the true *Scaphites*. Decisive for these interpretations was not only the originally tripartite *L*, but also the sculpture and general aspect of the primitive scaphitid whorls. He persisted in favouring a lytoceratid ancestry only for a restricted group of Upper Cretaceous forms like *Sc. cunliffei*, considering as significant a bifid *L* which keeps symmetry throughout, despite its different sculpture and general appearance.

Yabe's (1910) scaphitid classification using the internal saddle (*I/U*) should be mentioned. The species with entire saddles *I* and *U*, which form Yabe's new genus '*Yezoitites*', agree only in their small size. In reality they belong to three different scaphitid developments. It was Nowak (1911) who rectified this conception with the statement that the character of the internal suture should not be regarded exclusively, but only in combination with all other systematic features; shell form, sculpture, and, naturally, also external suture. He regarded the ontogenetic development in its complexity, as the main feature in ascertaining a natural relationship. Through this he proposed a treble origin of *Scaphites*: the Cenomanian *equalis* group was derived from *Olcostephanus*, the Campanian *tridens* group from *Acanthoceras*, and the Maastrichtian *constrictus* group was said to have a hoplitid origin. This conception is reflected in the new generic names which Nowak proposed: '*Holcoscaphites*' (= *Scaphites* s. str.), *Acanthoscaphites* and *Hoploscaphites*. According to Nowak a scaphitid living chamber was produced repeatedly by parallel development.

It should be mentioned that J. P. Smith placed a subfamily Scaphitinae in Cosmocera-tidae in the 2nd edition of Eastman's Textbook.

In 1915 Frech tried to introduce a new grouping of scaphitids. This was based on the mode of ribbing and tuberculation, but it was of more stratigraphic than systematic significance, and therefore rejected by Nowak (1915).

As a curious fact we note the opinion of Rollier (1922), where the Upper Cretaceous *Scaphites* was related to Upper Jurassic oppeliids, the so-called *Proscaphites*. In his first paper dealing with scaphitid systematic, Spath (1922) retained Nowak's interpretation and related through sculptural evidence some of the Upper Senonian *Hoplo-* and *Acanthoscaphites* to a hoplitid (*Hoplitoplacenteras*), some others to a desmoceratid source

(*Menuites*). This was probably the reason for Reeside (1927*b*) to propose a further generic name, *Desmoscaphites*, for a restricted group of Upper Senonian forms (*Sc. bassleri* and allies) which have the morphological appearance of *Desmoceras*. Furthermore Reeside gave the first correctly drawn development of the scaphitid suture from the Campanian *Sc. hippocrepis*. He recognized the quadrilobate first suture, consisting only of the elements *I*, *U*, *L*, and *E*. The adult suture-line was interpreted as having two or three 'auxiliaries' (= umbilical lobes). The lateral lobe was found to be bifid throughout.

In the same year Reeside published a summarizing paper (1927*a*) containing a review of all previous works and a catalogue of the known scaphitid species with their new generic attributes. He eliminated some of Nowak's genera, identifying *Hoploscaphites* with the American *Discoscaphites* Meek, and '*Holcoscaphites*', '*Anascaphites*' Hyatt, '*Jahmites*' Hyatt, and '*Yezoites*' Yabe with the true *Scaphites*. In phylogenetic aspects he followed Nowak unreservedly and proposed the following arrangement for the four remaining genera:

(1) *Scaphites* was placed into a subfamily of its own, which was referred to the Stepheoceratidae,

(2) *Desmoscaphites* in the desmoceratid Silesitinae,

(3) *Discoscaphites* in the Hoplitidae, and

(4) *Acanthoscaphites* in the Acanthoceratidae.

This was the maximum ever attained in splitting the scaphitid heteromorphs.

In 1928 Adkins called attention to the Upper Albian scaphitoid group of '*Macroscaphites*' *platydorsus* Scott, for which he proposed the new genus *Worthoceras* of 'uncertain position'. It was said to differ from both *Scaphites* and *Macroscaphites* through its reduced suture-line in spite of its hooked body-chamber. Its sutural affinities with *Mastigohamites* and even with *Adkinsia* were considered and it was provisionally placed with the latter as an annex to the lytoceratid heteromorphs. *Scaphites* was still included in Stepheoceratidae.

In 1933 and finally in his monograph '*Ammonoidea of the Gault*' (1934, 1937) Spath brought new classifying aspects into the confusion of the scaphitid history. He drew attention to *Sc. circularis* (J. de C. Sowerby) of the British Upper Albian, an evidently lytoceratid member, which he considered to be the origin of all later *Scaphites*. Unfortunately this species remained poorly illustrated, as also the somewhat more advanced *Sc. subcircularis* Spath. The poor specimen illustrated by Spath of *Sc. circularis* makes it evident, that this species is a true heteromorph. It preserves a quadrilobate suture-line, bifid lateral lobe, fine lytoceratid striation of the shell, and a crioceratitid uncoiling of its septate portion. Through the very insufficient figures of suture and inner whorls of *Sc. subcircularis* (Spath, op. cit., text-fig. 175*e*, pl. 57, figs. 10-12) we are unable to decide whether this species belongs to the same quadrilobate suture type or to that of the true Upper Albian *Scaphites*, like *Sc. hugardianus* or *Sc. simplex*. In these species the uncoiling of the chamber is distinct as also a highly differentiated umbilical suture and a sometimes 'trifid' lateral lobe. The only visible difference from *Sc. subcircularis* is the higher involution of the inner whorls.

Spath's attempt to connect a monophyletic scaphitid stock (*Worthoceras* included) with a true lytoceratid ancestor was not accepted by all succeeding authors.

Roman (1938) continued though to distribute *Scaphites* among three different ammonite families: Olcostephanidae (*Scaphites* and *Holcoscaphtes*), Palaeohoplitidae (*Hoploscaphtes*), and Acanthoceratidae (*Acanthoscaphtes*). In full accord with Spath, Breistroffer (1947) proposed the separation of *Sc. circularis* and *subcircularis* into the new subgenus *Eoscaphtes*, which he regarded like Spath as the most primitive scaphitid member. In his magnificent paper Cobban (1952) treated the evolutionary lines of *Scaphites*, originating from the Colorado group (Turonian to Campanian) of the United States. He very clearly demonstrated (op. cit., text-fig. 3), that it is impossible to isolate the Upper Cretaceous forms with trifold *L* from their bifid forerunners. He made it evident that the connexion between these apparently different lobe types can be proven by all intermediaries. The different lineages of scaphitid development in the Colorado group were found to converge on a single initial-point, the Turonian *delicatulus* group, which is otherwise of evident morphologic relationship with the Cenomanian type *Scaphites*, *Sc. equalis*. This was the first detailed demonstration of the change in sutural characters which was entailed by the monophyletic interpretation of the scaphitid development as proposed by Spath. Cobban furthermore showed that the asymmetric development of *L* was accompanied by a progressive reduction of the uncoiled body chamber, which at the end overlapped the initial coil. At the same time the sculpture was found to decrease in its degree of differentiation (main and secondary ribs, tuberculation) and become denser and more uniform (op. cit., text-fig. 2).

In the same year C. W. Wright (1952) presented 'A Classification of the Cretaceous Ammonites' in relation to the forthcoming *Treatise on Invertebrate Palaeontology*. We find here a monophyletic superfamily Scaphitaceae (proposed one year earlier (1951) by Wright and Wright), derived from the lytoceratid main stock (op. cit., text-fig. 1). In a short note on Scaphitidae C. W. Wright (1953) explained his position in more detail. He agreed completely with Spath regarding *Eoscaphtes* as the 'probably earliest scaphitid' and the family Scaphitidae as a natural unity, with one exception; he believed that there is a parallel scaphitid stock with lappeted mouth-border and more evolute spiral portion, connecting *Worthoceras* with the Turonian *bladenensis* (= *Sc. auritus* auct.) group. For the latter he proposed the new generic name *Otoscaphtes* and grouped the two genera in a subfamily 'Otoscaphtinae' which were thought to originate, like the true *Scaphites*, in *Eoscaphtes*. In Wright (op. cit., p. 474) already we find the critical remark that 'were it not for the evidence that they are in series it might be thought that they were merely a group of separate lappeted offshoots of various Scaphitinae'. This question will be treated below in detail.

In 1952 the ammonite part of the 'Traité de Paléontologie' was published by the French ammonitologist Madame Basse. This first in the recent series of text-books needs no further discussion for our purpose, because the scaphitid classification was evidently taken from Wright (1952). Scaphitaceae were regarded as a monophyletic section of the Lytoceratina.

Second in the sequence of standard works about cephalopods, was the ammonite volume of the *Treatise of Invertebrate Palaeontology*. The excellent description of Cretaceous ammonites is due to C. W. Wright (1956) who standardized Spath's views of the scaphitid problem. The superfamily Scaphitaceae was included in Lytoceratina, containing Scaphitidae and (following Spath 1925, 1939) Labeceratidae, an exclusively Upper Albian group of hamitoid and scaphitoid uncoiled heteromorphs with trifold *L*.

Labeceratids are confined to the Southern hemisphere. The family Scaphitidae is said to be 'probably derived from some member of the Lytocerataceae'.

Two years later Luppov and Drushtchic (1958) published the Russian treatise on mesozoic ammonites, where Scaphitaceae are also regarded as a monophyletic unit, including both Scaphitidae and Labeceratidae. But here the superfamily is placed among the true Ammonitina, following the acanthoceratid family Vascoceratidae. Indeed we occasionally find in the Turonian *Vascoceras* (but also in some Senonian tissotiids) a tendency to scaphitoid uncoiling of the living-chamber. The trifold lateral in *Sc. equalis* and the labeceratids is responsible for the arrangement in the Ammonitina, as also the strong ornamentation of many scaphitid and labeceratid species.

In his doctorate thesis (Wiedmann 1960, published 1962a) the author was able to demonstrate that there is no good reason to assume an originally trifold lateral lobe in *Sc. equalis*. In the early ontogeny of this species the lateral shows a distinct bifid shape up to a diameter of 1.5 mm. Thereafter the lobe outline becomes more and more trifold through asymmetrical growth, but soon after it again acquires its original form. It is evident that Pervinqui re recognized only the ultimate change. As in the case of the Senonian trifold scaphitids, the lytoceratid origin can be ascertained also for the Cenomanian type forms as Spath and Wright maintained. Neither the polyphyletic interpretation of scaphitids nor its derivation from acanthoceratids seems necessary. Reeside's suture development was reproduced (op. cit., text-fig. 1) and compared with that of other lytoceratids and phylloceratids. While the quadrilobate first suture-line was found to be in complete agreement with that of other heteromorphs (*Baculites*), the extreme degree of its sutural regeneration was noted. According to Reeside the acquisition of three additional umbilical lobes was supposed in the adult suture of *Scaphites*, while in all other heteromorphs the suture-line remains quadrilobate throughout (in the Lytocerataceae the first suture contains five elements, but a single additional lobe can occasionally be acquired). Thus the scaphitid suture development approaches to that of some phylloceratids. This convergence was interpreted as the result of the unusual increase of involution in *Scaphites*.

The last important contribution to the systematics of *Scaphites* was made by Schindewolf in the first part of his 'Studien zur Stammesgeschichte der Ammoniten' (1961). Here he describes the ontogenetic suture development of Phylloceratina, Lytoceratina, and the heteromorphs. Like Reeside he studied, in '*Acanthoscaphites roemeri*, a highly developed Campanian member of the scaphitid stock, in which he also recognized (op. cit., text-fig. 58) up to three additional umbilical lobes in the adult suture. Different from the previous citations, however, is the existence of five elements in the first reproduced suture (as in all Lytocerataceae, Ammonitina, and Phylloceratina). The first suture reproduced by Schindewolf does not coincide with the true 'Prim rsutur'.

Schindewolf regards this highly differentiated suture type as characteristic of all true *Scaphites* which he claims cannot be connected with the reduced quadrilobate sutures of *Eoscaphtes* or *Worthoceras*. He proposes to separate these, including Labeceratidae, from *Scaphites*, but the systematic position of the latter seems difficult to interpret. On the one hand, he does not hesitate to relate *Scaphites* and the other heteromorphs to the Lytoceratidae (p. 109, top): on the other, he states that the 'greater number of suture elements, shape and sculpture place *Scaphites* near those forms which are placed in the suborder Ammonitina' (translated from p. 109, bottom). The solution

to this interesting problem is announced for the summarizing part of his forthcoming 'Studien'.

Drushtchic (1962) gave a short review of the systematic position of the different superfamilies generally included in *Lytoceratina*. While *Turrilitaceae* and *Tetragonitaceae* are retained as true *lytoceratids*, he again proposes to remove *Scaphitaceae* (and also *Ancylocerataceae*) from the *Lytoceratina* to the true *Ammonitina*, because they were 'evidently separated from all *lytoceratids* by general shape, septal surface and trifid lateral lobe' (translated).

The present author discussed on another occasion (1962*b*) the systematics of the complete suborder *Lytoceratina*. Here *Labeceratidae* were separated from the *Scaphitaceae*, and included as a subfamily in the revised *Anisoceratidae*. The *otoscapitids* were elevated to family rank, and remained with the *Scaphitidae* in the superfamily *Scaphitaceae*.

To better illustrate the poorly known *Jauberticeras? majorcense*, I joined to the Balearic type material a supposed paratype (op. cit., pl. 10, fig. 5) from the Perte du Rhône (Ain, France). It agreed in general shape and dimensions completely with the Balearic types, with the exception of its greater size. In the meantime I became aware that I had been deceived by a striking shell homoeomorphy. The French form, in which the suture line was, as the only distinguishing feature, not perceptible, represents in reality the spiral portion of the poorly known Albian *Eoscaphtes subcircularis*. This error was the occasion for the present paper.

From this review the actual problem becomes evident. The extreme splitting of the scaphitids in up to four different ammonitid superfamilies needs no further discussion. It was rejected provisionally by Spath (1937) and Wright (1952) but mainly by Cobban, who gave a striking demonstration of the derivation of the trifid Upper Cretaceous lobe form from a bifid origin. Schindewolf's new 'polyphyletic' interpretation raises a different and more difficult problem: the incompatibility of the reduced quadrilobate suture of *Eoscaphtes* with the highly differentiated true scaphitid suture-line.

On the other hand, two monophyletic interpretations of the *Scaphitaceae* seem in principle to be possible, derivation via *Eoscaphtes* from the conservative main stock of *Lytoceratina*, or from some ammonitid ancestor, which is suggested by the trifid lobe shape, sculpture, and whorl involution.

The actually remaining questions are:

- (1) Is *Eoscaphtes* indeed a link between *Lytoceras* and *Scaphites*?
- (2) Is the regressive quadrilobate suture type of *Eoscaphtes* compatible with the progressive scaphitid suture line, containing four umbilical lobes?
- (3) Is a trifid lateral lobe (or 'second lateral') admissible for a member of *Lytoceratina*?
- (4) Is it possible to connect the closely coiled initial portion of *Scaphites* with the evolute *Lytoceras*?
- (5) What is the presumed ancestor of *Scaphites*?

We believe all these questions can be answered through the study of the early Upper Albian scaphitids, especially the poorly known *Eoscaphtes circularis* and *subcircularis*. In addition to these, the first true scaphitids will be treated, and thereafter the scaphitid relationship can be discussed.

SYSTEMATIC DESCRIPTIONS

Family SCAPHITIDAE Meek 1876

Genus *Eoscaphtes* Breistroffer 1947

Type species. Annul.? circularis J. de C. Sowerby 1836.

Following C. W. Wright (1957) and Wiedmann (1962a) *Eoscaphtes* will here be regarded as an independent genus including *Eoscaphtes circularis* (J. de C. Sowerby), *E. subcircularis* (Spath), *E.? tenuicostatus* (Pervinquière).

The latter can only be included with doubt, since the internal suture is still unknown. But in all other features it agrees with the preceding species that the proposed attachment to *Eoscaphtes* seems to be correct.

Breistroffer's (1947, p. 77) very brief diagnosis of *Eoscaphtes*: 'Sous-genre très primitif de *Scaphites*, caractérisé par ses cloisons lytocératiformes, ses tours internes plus ou moins évoluées et sa crosse macroscaphtoïde sans bouche individualisée', should be completed and modified in the following manner: Rounded whorls rapidly increasing in size. Whorls at first crioceratitoid, uncoiling, or in contact, but always with umbilical perforation. Final macroscaphtitoid hook. Dorsal impression lacking on inner whorls, sometimes throughout. Fine and dense, sometimes bifurcating lytoceratid striation of the shell. No tubercles. Suture consists of the lobes *I*, *U*, *L*, and *E* only and remains quadrilobate throughout. *L* distinctly bifid, also *U*, but with the tendency to be largely divided by the incoming umbilical seam. Septal surface hamitoid. Constricted mouth-border seems to be present.

The genus seems to be restricted to the Upper Albian of England, Southern France, Madagascar, and the Cenomanian of Algeria.

Eoscaphtes circularis (J. de C. Sowerby)

Plate 53, figs. 1-3; text-figs 1a-c

1836 *Annul.? circularis* J. de C. Sowerby in Fitton, p. 337, pl. 11, fig. 20.

1837 *Annul. circularis* Sowerby; Brown, pl. 20, fig. 10.

1933 *Scaphites circularis* (J. de C. Sowerby); Spath, p. 427, text-figs. 4d-j.

1937 *Scaphites circularis* (J. de C. Sowerby); Spath, p. 499, text-figs. 174a-i, pl. 57, figs. 1-9.

1947 *Sc. (Eoscaphtes) circularis* (J. de C. Sowerby); Breistroffer, p. 77.

1953 *Eoscaphtes circularis* (J. de C. Sowerby); C. W. Wright, p. 473.

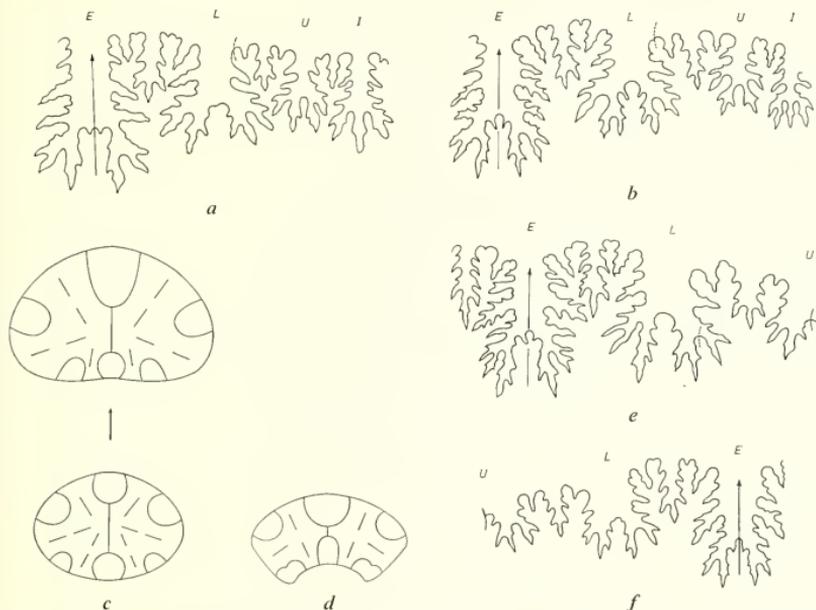
1957 *Eoscaphtes circularis* (J. de C. Sowerby); C. W. Wright, p. L228, text-figs. 255, 6a-c.

1962 *Eoscaphtes circularis* (J. de C. Sowerby); Wiedmann, p. 212 (1962a).

Type. The neotype proposed by Spath (1937, pl. 57, fig. 1), from the Upper Albian (*varicosum* subzone) of Folkestone, preserved in the BMNH collection; here reproduced, Plate 53, fig. 3.

Description. Broadly rounded whorls without distinct dorsal impression at any stage, rapidly increasing in size. First whorls crioceratitoid uncoiled or in contact, but with umbilical perforation. Later whorls uncoiling anew; living-chamber is said to be scaphitid. Fine radiate ribbing of lateral sides and venter, consisting of single and bifurcating ribs, which are somewhat raised at the point of bifurcation on the middle side. Dorsum smooth. Suture with four elements of normal size; highly incised. *L* and *U* distinctly bifid, *I* trifid. Saddles symmetrically bipartite and normal-sized.

Remarks. Some of Spath's (1937) figurations of this interesting species are drawings. Therefore it was necessary to re-examine the type material deposited in the BMNH collection, where the drawings were found to be correct. However, I was unable to localize the specimen described by Spath (1937, text-fig. 174i) as 'transitional to *S. subcircularis*', the only one with a final hook. Neither in the collections of London nor



TEXT-FIG. 1. *Eoscapites*, suture and whorl sections. *a-c*: *E. circularis* (J. de C. Sowerby). *a*, Complete suture of the ammonitid coiled hypotype MGL 12341/1; Upper Albian, Perte du Rhône. *h* = 3.5 mm. *b*, Suture of the crioceratitid uncoiled specimen, GPIT Ce 1221/1; Upper Albian, Folkestone. *h* = 5 mm. *c*, Development of whorl section, and hamitid septal surface; the same, $\times 4$. *d-f*, *E. subcircularis* (Spath). *d*, whorl section and subscaphitid septal surface, MGL 12342; Upper Albian, Perte du Rhône, $\times 2$. *e*, External suture-line, MGL 12340; same locality. *h* = 5 mm. *f*, External suture of the Madagascan hypotype (cf. Collignon 1963, fig. 1144); Upper Albian, Mt. Raynaud. *h* = 4 mm.

in the abundant French material which I studied, did I find any full-grown specimen attributable to *E. circularis*. Therefore the presence of a scaphitid living-chamber in this species remains doubtful for the moment. Whereas all specimens with ammonitoid or crioceratitoid coiling which I saw were septate throughout, in the case of the neotype the straightening of the outer whorl coincides with the beginning of the chamber. This makes it probable but not certain that the present species develops indeed a scaphitid final hook.

The first whorl is also generally not preserved, a result of its extreme fragility. There is no doubt though that it includes an open umbilical perforation. The whorl section is rounded at first, increasing rapidly in size (Pl. 53, fig. 1*b*), and becoming more depressed

in the adult stage. For this reason 'var. *depressa*' Spath becomes unnecessary, because it represents only the gerontic stage.

The coiling of the septate portion may be crioceratitoid (Pl. 53, fig. 2) or ammonitoid (Pl. 53, fig. 1). Here the whorls barely touch the preceding ones, and generally no dorsal impression can be observed. In the neotype for example, the dorsum of the initial part of the chamber remains completely flat. In this respect and with regard to the problem of scaphitid origin, the crioceratitoid portion here described (GPIT Ce 1121/1) seems significant. Plate 53, fig. 2*b* and text-fig. 1*c* makes it evident, that the dorsal impression gradually appears in late ontogeny, that *Eoscaphtes* though must be derived from completely uncoiled heteromorphs without dorsal impression, and that it leads to more involute ones. *Sc. subcircularis*, which I regard as the direct descendant of the present species, rapidly acquires an involute initial coil, but the dorsal impression is much more pronounced on the outer whorls. If *E. circularis* indeed represents the source of the true *Scaphites*, then the ammonitoid coiling of the septate portion is a secondary feature, and the final uncoiling a tertiary one. Then the origin of this peculiar group lies neither in normally coiled ammonitids or lytoceratids, but in uncoiled hamitids.

The type of suture and the septal surface are further arguments for this view. The latter offers a clear hamitid configuration (Pl. 53, fig. 2*b*; text-fig. 1*c*), and also the quadrilobate suture-line has a striking affinity to that of some Upper Albian hamitids, like *Plesiohamites* (= '*Lytohamites*' Casey) and *Stomohamites* Breistroffer, as figured in Spath (1941) or Wiedmann (1962*a*, text-figs. 42, 43). Especially the Upper Albian *Plesiohamites similis* (Casey) (= *Hamites multicostatus* Spath, non Brown) greatly resembles *Eoscaphtes* in mode of uncoiling, suture, and sculpture; it is difficult to distinguish them from fragmentary *E. circularis*. The constricted and collared mouth-border, a very characteristic scaphitid feature, and now recognized in *Eoscaphtes* (Pl. 54, fig. 4*b*), is furthermore a common feature of the adult *Stomohamites*.

Turning back from these speculations to *E. circularis*, we further note the fine and dense radiate striation which crosses the venter, and is interrupted on the dorsum. It consists of alternating simple and bifurcating ribs, the latter somewhat pronounced at the point of branching (Pl. 53, fig. 2*a*). This is applicable especially to the living-chamber

EXPLANATION OF PLATE 53

- Figs. 1-3. *Eoscaphtes circularis* (J. de C. Sowerby). 1, Ammonitid coiled hypotype, MGL 12341/1 (leg. Lorient); Upper Albian (?*varicosum* subzone), Perte du Rhône (Ain, France). *a*, Lateral, *b*, sagittal, *c*, frontal, *d*, ventral view. 2, Crioceratitid uncoiled hypotype, GPIT Ce 1221/1; Upper Albian (*varicosum* subzone), Folkestone (Kent, Great Britain). *a*, Lateral, *b*, dorsal view, showing the incoming dorsal impression, *c*, ventral view. 3, Neotype (ex Spath 1937, pl. 57, fig. 1), with straight portion of body-chamber, BMNH coll. (coll. Casey); Upper Albian (*varicosum* subzone), same locality. *a*, Lateral, *b*, frontal view; $\times 1$.
- Figs. 4-6. *E. subcircularis* (Spath). 4, Frontal view of septate hypotype, MHNG Wi 'Sc'/5 (leg. Pictet); Upper Albian (Hysteroцерatan), Perte du Rhône (Ain, France). 5, Septate hypotype, MGL 12340 (leg. Lorient); Upper Albian (Hysteroцерatan), same locality. *a*, Lateral, *b*, frontal view. 6, Septate hypotype, MHNG Wi 'Sc'/1 (leg. Pictet); Upper Albian (Hysteroцерatan), Folkestone (Kent, Great Britain). *a*, Frontal, *b*, lateral view; $\times 3$.
- Fig. 7. *E. ?tenuicostatus* (Pervinquière). Holotype (ex Pervinquière 1910, pl. 2, fig. 18); Lower Cenomanian of Berrouaghia (Algeria). *a*, Ventral, *b*, lateral, *c*, frontal view.
- All $\times 2$ unless otherwise indicated.



1a



1b



1c



1d



3a



2a



2b



2c



3b



4



5a



5b



7a



7b



7c



6a



6b

of the neotype. I believe that Spath's 'var. *rugosa*', which was based on this peculiarity, does not need separation.

The suture-line (text-figs. 1a, b) was found to be highly incised and consisting only of the elements *E*, *L*, *U*, and *I*. These, as well as the saddles, are of normal size, gradually decreasing from *E* to *U*. Only the trifold internal lobe exceeds *U* in depth. *U* and *L* are distinctly bifid, the latter occupies nearly the centre of the lateral sides. The saddles also are symmetrically bipartite, and subdivided by strong median incisions. Finally it should be mentioned that an absolute identity of suture-lines in the ammonitoid (text-fig. 1a) and the crioceratitoid specimens (text-fig. 1b) was observed. This proves that specific separation of these two types is unnecessary. The mode of coiling evidently possesses an extreme degree of plasticity, as it is common in phylogenetically primitive material—and again in *Hamites*.

The dimensions (in millimetres) of the specimens figured here are:

	<i>d</i>	<i>h</i>	<i>b</i>	<i>u</i>
GPIT Ce 1221/1	~18	5.5 (0.31)	8.0 (0.45)	~9.0 (0.50)
MGL 12341/1	19	7.0 (0.37)	10.0 (0.53)	8.0 (0.42)
(penultimate whorl)		3.0 —	3.5 —	—

Both specimens foreshadow the next species, *E. subcircularis* through the loss of coiling and incoming of the dorsal impression.

Distribution. *E. circularis* is known from the base of the British Upper Albian, mainly the *varicosum* subzone (bed x) from Folkestone (Kent) and Glynde (Sussex). The species can also be recorded here from the condensed Upper Albian beds of the Perte du Rhône (Ain, France).

Eoscaphtes subcircularis (Spath)

Plate 53, figs. 4–6; Plate 54, figs. 2–4, 8, 9; Plate 55, figs. 1–3; text-figs. 1d–f, 2

1937 *Scaphites subcircularis* Spath, p. 501, text-fig. 175e, pl. 57, figs. 10–12.

1937 *Scaphites simplex* Jukes-Browne; Spath pars, text-fig. 177c only.

1947 *Sc. (Eoscaphtes) subcircularis* Spath; Breistroffer, p. 77.

1962 *Jauberticeras ?majorcense* Wiedmann pars, pl. 10, fig. 5 only (1962b).

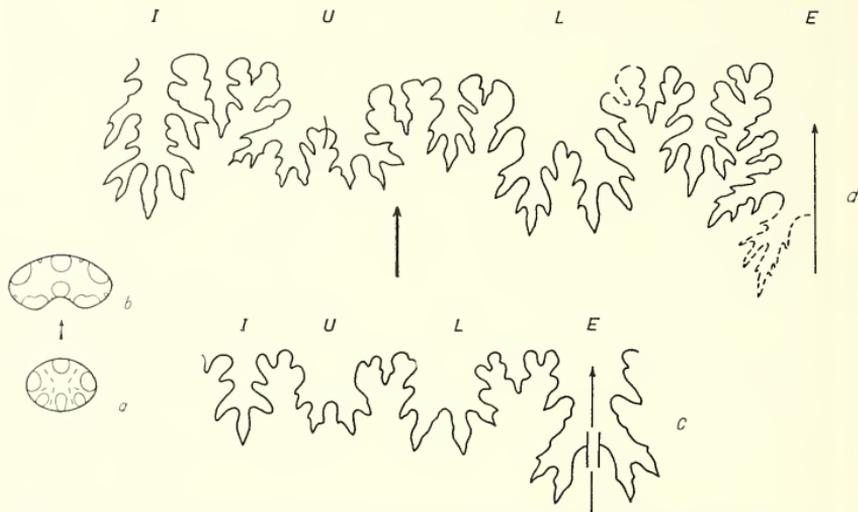
1963 *Scaphites cf. subcircularis* Spath; Collignon, p. 57, pl. 262, figs. 1143, 1144.

Holotype. BMNH specimen no. 38206, figured by Spath (1937, pl. 57, fig. 10) from the Upper Albian (*varicosum* subzone) of Folkestone; here reproduced Plate 54, fig. 8.

Description. First whorl slender, with almost circular section and umbilical perforation. Then rapidly increasing in size and involution, developing a distinct dorsal impression. Hooked body-chamber present. Sculpture like that of *E. circularis*, but stronger. Suture still quadrilobate and highly incised; with the beginning increase of saddles, saddle incisions, and umbilical lobe, which becomes divided by the incoming umbilical seam. Septal surface hamitid at first, later scaphitid.

Remarks. As in *E. circularis* all three specimens figured by Spath are defective, generally consisting only of the spiral portions, hence the original description and figuration of this species are inadequate (Pl. 54, fig. 8). For this reason I am glad to be able to validate this doubtful, but extremely interesting species through rich and well-preserved material from different French localities.

The main character of *E. subcircularis* is evidently its more involute septate whorls, and in consequence the existence of a distinct dorsal impression. But this impression does not persist throughout as Spath mentioned; I found an inner whorl of a somewhat surprising shape. In the centre of Plate 55, fig. 1*b* (arrow) there is a narrow, elevated ridge which marks the rapidly decreasing first whorl. This is so fragile, that I could not clean it from the adherent matrix, where the pronounced striation of the extremely inflated outer whorl is noticeable. To a diameter of 4.5 mm. corresponds a whorl



TEXT-FIG. 2. Suture development and septal surfaces of *E. subcircularis* (Spath), MHNG Wi 'Sc'3; Upper Albian, Crioud (?). *a*, Whorl section and hamitid septal surface; $h = 1.7$ mm. *b*, Whorl section and subsaphitid septal surface; $h = 3.5$ mm. *c*, Suture at $h = 1.7$ mm, *d* at $h = 6$ mm.

height and thickness of 1.5–2.0 mm. From all these features an open umbilical perforation can be expected. At the indicated whorl height the section is rounded throughout with distinctly convex and not impressed dorsal area; the septal surface shows the simplified hamitid configuration, and only the four, nearly equidistant, main lobes exist (text-fig. 2*a*, *c*). With the next whorl, which is visible in the background of Plate 55, fig. 1*b*, the whorl height and thickness become extremely amplified (300–400 per cent.). Now the dorsal impression gradually becomes visible, and the whorl section receives its typical depressed to coronate outline (Pl. 55, figs. 1*a*, *c*). The maximum whorl thickness is situated in the centre of the flanks, where a kind of lateral keel (like in *Jauberticeras*) is generally present.

At the same time the suture changes considerably (text-figs. 2*b*, *d*). It retains many aspects of the preceding species, for instance in the degree of incision, the distinctly bifid *L*, the trifold *I*, and the importance of the median saddle incisions. But the elements *U* and *L/U* now become more and more differentiated, evidently in relation to the in-

creasing involution. While *L* is now placed outside of the lateral keel, the umbilical lobe becomes divided through the umbilical seam and therefore more and more amplified. The saddle *L/U* also becomes lengthened and its median incision more pronounced. The suture-line continually loses its hamitid character, while the septal surface can already be designated as sub-scaphitid (text-fig. 2*b*).

The septate portion has an average diameter of 15 mm. Thereafter the body-chamber uncoils with a typical scaphitid hook, which is straight at first and then recurved (Pl. 54, figs. 2, 4). The mouth border, which does not overlap the spiral portion, seems to be constricted (Pl. 54, fig. 4*b*). The whorl section of the living-chamber is depressed with rounded sides and slightly impressed dorsum. The maximum thickness lies in the apical part of the chamber and near the final hook the whorl thickness decreases.

The sculpture is of the same type as in *E. circularis*, but the ribbing is more pronounced on the body-chamber, where it passes the dorsum with a distinct incurvation. The specimen from Folkestone here figured (Pl. 53, fig. 6) completely preserves the sculpture of the preceding species, while another specimen from Mt. Saxonet demonstrates an injured body-chamber and the mode and difficulty of its restoration (Pl. 54, fig. 9).

Intraspecific variation in the present species is also considerable, as in *E. circularis*. This can easily be shown through the dimensions (in millimetres) of the specimens studied:

	<i>D</i>	<i>B</i>	<i>d</i>	<i>h</i>	<i>b</i>	<i>u</i>
MGL 12342	33	15	16	7.2 (0.45)	12.6 (0.79)	4.5 (0.28)
MHNG Wi 'Sc'/1	—	—	10	4.5 (0.45)	6.8 (0.68)	3.0 (0.30)
MHNG Wi 'Sc'/2	24.5	11.5	14	6.0 (0.43)	9.0 (0.64)	4.7 (0.34)
MHNG Wi 'Sc'/3	—	—	17	7.0 (0.41)	13.5 (0.80)	4.5 (0.27)
			4.5	1.5 (0.33)	2.0 (0.44)	~2.0 (0.44)
MHNG Wi 'Sc'/4	—	—	14.5	6.3 (0.43)	9.4 (0.65)	4.0 (0.28)
MHNG Wi 'Sc'/5	—	—	16	6.0 (0.37)	10.5 (0.66)	5.4 (0.34)
MGL 12340	—	—	16.5	6.8 (0.41)	11.8 (0.72)	~6.0 (0.36)
Collignon's fig. 1143			12	5.0 (0.42)	9.0 (0.75)	3.5 (0.29)
Collignon's fig. 1144			11	4.5 (0.41)	7.1 (0.64)	3.2 (0.29)

Especially the whorl thickness of the spiral portion seems highly variable (0.64–0.80), not counting the dimensions of the slender first whorl. The same can be stated about the umbilical diameter (0.27–0.36). In order to receive an impression of this variability quite a number of specimens are figured here. Without any doubt the two specimens from Madagascar (Pl. 55, figs. 2, 3), labelled *E. cf. subcircularis* by Collignon (1963), also fall into the variability of the present species.

E. subcircularis connects directly *E. circularis* with the first true *Scaphites*, *Sc. simplex*. It agrees with *E. circularis* in the open initial coil with umbilical perforation, sculpture, and shape as well as suture of the first whorls. On the other hand, the distinctions are well pronounced in the incoming dorsal impression and the amplified suture elements *U* and *L/U*, caused by the more closely coiled initial portion. All these features foreshadow *Sc. simplex* with a completely closed initial spire, distinctly bipartite *U*, asymmetric *L*, and elongated saddle *L/U*. The open-whorled specimen from Entrèves-en-Bauges referred to *Sc. simplex* by Spath (1937, text-fig. 177*c*), evidently belongs to the present species. This demonstrates that these two species, as well as the genera *Eoscaphtes* and *Scaphites*, are closely connected. If only the initial coil is present, *E. subcircularis* resembles the tetragonitid genus *Jauberticeras*, which is also laterally keeled.

Both also have a very similar sculpture. Only the suture-line gives us the decision that there is no real relationship.

The material which I located in the collections of Pictet and Campiche, was generally labelled '*Sc. meriani*' or '*Sc. hugardianus*'. However, these species are easily distinguishable from *E. subcircularis* through their pronounced ventrolateral tuberculation.

Distribution. Spath indicates that *E. subcircularis*, which was described from beds x and xi of Folkestone, Blue Bell Hill, Burham (Kent), and Glynde (Sussex), is of Upper Albian, *varicosum* to *auritus* subzone age. The French specimens here figured are from the condensed Upper Albian of the Perte du Rhône (Ain), Mt. Saxonet and Criou (?) (Haute-Savoie). (There are some specimens in the Pictet collection which are labelled 'Criou and Grand Bornand'. Dr. Lanterno kindly informed me, that these are two different localities in Haute-Savoie. Considering this fact, this material will be cited under the locality name 'Criou (?)'.) The '*simplex*' specimen which was incorrectly identified by Spath, has nearly the same provenance (Entrèves-en-Bauges). Approximately the same Hysteroцерatan age can be stated for the Madagascan material, originating from the famous Mt. Raynaud near Diégo-Suarez.

Eoscaphtes ? *tenuicostatus* (Pervinquierè)

Plate 53, fig. 7

1910 *Scaphites tenuicostatus* Pervinquierè, p. 28, text-fig. 12, pl. 2, figs. 17-19.

1962 *Eoscaphtes tenuicostatus* (Pervinquierè); Wiedmann, p. 212 (1962a).

Holotype. The originally designated specimen (Pervinquierè 1910, pl. 2, figs. 17, 18) from the Cenomanian of Berrouaghia (Algeria); here reproduced Plate 53, fig. 7.

EXPLANATION OF PLATE 54

Figs. 1, 7. *Scaphites* (*Scaphites*) *simplex* Jukes-Browne. 1, One of the two syntypes of *Sc. 'hugardianus'* in coll. d'Orbigny (MHNP) 5805-1; Upper Albian (Hysteroцерatan), La Fiz (Haute Savoie, France). Lateral view. 7, Complete hypotype, GPIT Ce 1221/5; Vraconian, Cambridge Greensand. *a*, Lateral, *b*, frontal view.

Figs. 2-4, 8, 9. *Eoscaphtes subcircularis* (Spath). 2, Hypotype with complete body-chamber, MGL 12342 (coll. Campiche); Upper Albian (Hysteroцерatan), Perte du Rhône (Ain, France). *a*, Ventral, *b*, frontal, *c*, lateral view, *d*, frontal view of spiral portion. 3, Sagittal view of spiral portion, MHNG Wi 'Sc'/4 (leg. Pictet), in which the extreme increase of whorl thickness becomes visible. Same age and locality. $\times 3$. 4, Hypotype with preserved body-chamber, MHNG Wi 'Sc'/2, (leg. Favre); Upper Albian (Hysteroцерatan), Mt. Saxonet (Haute Savoie, France). *a*, Ventral, *b*, lateral view. 8, The crushed holotype (Spath 1937, pl. 57, fig. 10); Upper Albian (*varicosum* subzone), Folkestone (Kent, Great Britain). Lateral view. 9, Injured body-chamber, MHNG Wi 'Sc'/6 (leg. Favre); Upper Albian (Hysteroцерatan), Mt. Saxonet (Haute-Savoie, France). *a*, Lateral and *b*, ventral view of shaft, *c*, of hook.

Fig. 5. *Sc. (Sc.) hugardianus* d'Orbigny. The first figured specimen, which agrees with the original description (Hébert and Munier-Chalmas 1875, pl. 5, fig. 7); proposed lectotype (Spath 1937); Upper Albian (*substuderii* zone), Salazac (Gard, France). *a*, Lateral, *b*, ventral view.

Fig. 6. *Sc. (Sc.) meriani* Pictet and Campiche. Lectotype (cf. Pictet and Campiche 1861, pl. 44, fig. 1), MHNG P & C 'S-CR'/44, 1, (leg. Pictet); Vraconian, Sainte Croix (Vaud, Switzerland). *a*, Ventral, *b*, lateral view.

All figures natural size unless otherwise stated.



1



2a



2b



2c



3



4a



4b



2d



7a



5



6a



6b



7b



8



9a



9b



9c

In the mode of uncoiling and in the involution of the initial coil *E. ? tenuicostatus* is very similar to the preceding species. It differs especially through its smaller size. From the holotype the following measurements (in millimetres) were taken:

<i>D</i>	<i>B</i>	<i>d</i>	<i>h</i>	<i>b</i>	<i>u</i>
12	4.5	7.3	2.5 (0.34)	3.6 (0.49)	2.5 (0.34)

E. ? tenuicostatus differs from *E. subcircularis* in that the increase of whorl thickness is not so rapid and the sculpture is finer and more sinuate on the spiral portion, while it consists of straight single ribs on the hooked chamber. The sides are more rounded on the involute whorls and more flattened on the final hook. The suture-line (Pervinquierè 1910, text-fig. 12) is much less incised than that of the preceding species but probably belongs to the same type. Since its internal portion is unknown, the attachment to *Eoscaphtes* remains somewhat doubtful.

From *E. ? tenuicostatus* it seems possible to derive a group of open-whorled Cenomanian species (*Sc. peroni*, *africanus* and *evolutus* Pervinquierè), which are probably the direct fore-runners of the Turonian *auritus* group (= *Otoscaphtes* Wright). Up to the moment the species is known only from the Lower Cenomanian of Berrouaghia (Algeria).

Genus SCAPHITES Parkinson 1811

Type species. Scaphites equalis J. Sowerby 1813. The specimen figured originally by Parkinson (1811, pl. 10, fig. 10) was later described as *Sc. equalis* (J. Sowerby 1813) and subsequently designated as type species by Meek (1876).

The difficulty in summarizing the characteristics of the genus *Scaphites* become evident through the diagnosis given by C. W. Wright (1957, p. L228): 'Compressed to very inflated, more or less involute, early whorls invariably in contact, shaft short or moderately long, hook not curved over camerate whorls; aperture constricted and commonly collared, in some shells with long dorsal lappet; ribs normally branching or intercalated on coiled part, commonly single or joining at ventrolateral tubercles on shaft; umbilical and normally ventrolateral tubercles present on shaft or hook. Suture soon ceases to be regularly lytoceratid.'

It becomes evident that in *Scaphites* we have a high variation of different modes of coiling, sculpture, and even suture, lappeted or unlappeted mouth-borders joined inseparably. Even the acanthoceratoid, desmoceratoid, or sphaeroceratoid homoeomorphs of the Uppermost Senonian (*Acanthoscaphtes*, *Desmoscaphtes*, *Clioscaphtes*), preserved by C. W. Wright with a number of other Upper Senonian genera, are linked with the true *Scaphites* by intermediaries in a way which sometimes make generic separation doubtful. In particular the Wright's subfamily Otoscaphtinae, which I raised to family status (Wiedmann 1962b), now needs critical revision.

It might be noted that the splitting in scaphitids is nevertheless of reasonable extent. *Scaphites* is regarded as a long-living genus by Wright, persisting from the Upper Albian to the Campanian, and splitting off at this time into several divergent types. But in the Albian and Cenomanian scaphitid material here studied, a high degree of plasticity was also found. The main part of the diverging types here recognized (*meriani* stock, *similaris* stock) is inseparably connected with the *equalis* main stock, and needs no further separation. Subgeneric distinction seems necessary, however, for *Sc. thomasi* Pervinquierè

(= *S. (Metascaphites)* Wiedmann) and the laterally keeled *S. stephanocerooides* Yabe (= *S. (Hyposcaphites)* subgen. nov.). Contrary to Wright *Otoscaphtes* will also be regarded here as a subgenus of *Scaphites*, in which *Pteroscaphtes* Wright has already been (Wiedmann 1962a) included.

Scaphites favoured the Northern hemisphere including India and Northern Africa, but is recorded also from Madagascar and Australia.

For our problem, the development of the early scaphitids, only the Upper Albian and Cenomanian representatives of the genus and the cited subgenera are briefly treated here.

Subgenus SCAPHITES (SCAPHITES) Parkinson 1811

In pursuing the early scaphitid development I recognized three different lineages; the *equalis* main stock, the *meriani* stock, and the *similaris* stock.

THE EQUALIS MAIN STOCK

The species belonging to the main stock described here are, *Sc. (Sc.) simplex* Jukes-Browne, *Sc. (Sc.) obliquus* J. Sowerby, and *Sc. (Sc.) equalis* J. Sowerby. *Sc. (Sc.) simplex* connects these type forms with both the *meriani* and the *similaris* group. I regard as characteristic for the present stock the gradually increasing importance of untubercled primary ribs, the rounded to oval whorl section, and the absence of lateral bulges. This group appears with *Sc. simplex* in the higher Albian and can be traced into the Upper Campanian.

Sc. (Scaphites) simplex Jukes-Browne

Plate 54, figs. 1, 7; Plate 55, figs. 4, 5; text-figs. 3e,

- 1848 *Scaphites Hugardianus* d'Orbigny; Pictet, p. 370, pl. 12, fig. 2.
 1861 *Scaphites Meriani* Pictet and Campiche pars, pl. 44, fig. 7 only.
 1875 *Scaphites Meriani* var. *simplex* Jukes-Browne, p. 287, pl. 14, fig. 3.
 ?1907 *Scaphites aequalis* Sowerby; Pervinquière, p. 118 pars, text-fig. 37, pl. 4, figs. 22, 23 only.
 1937 *Scaphites simplex* Jukes-Browne; Spath, p. 504, text-figs. 176c-f, 177a, b, d, e (non c, sed *E. subcircularis*), pl. 57, figs. 13-22, ?23.
 ?1962 *Scaphites (Sc.) simplex* Jukes-Browne; Wiedmann, p. 213, text-fig. 52, pl. 10, fig. 8.

Holotype. The fragmentary living chamber from the Cambridge Greensand, originally figured by Jukes-Browne (1875, pl. 14, fig. 3) and reproduced by Spath (1937, text-figs. 177a, b).

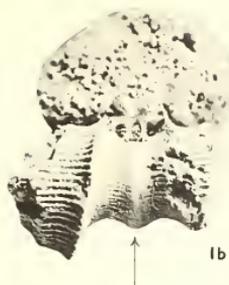
EXPLANATION OF PLATE 55

- Figs. 1-3. *Eoscaphtes subcircularis* (Spath). 1, Spiral portion with first whorl preserved, MHNG Wi 'Sc'/3 (leg. Pictet); Upper Albian, Crioud? (Haute Savoie, France). *a*, Frontal, *c*, lateral view of outer whorl, $\times 2$. *b*, first whorl with hamitid septal surface; the adhering matrix shows the strong ribbing of the outer whorl, which is visible in the background, $\times 6$. 2, Madagascar hypotype (Collignon 1963, pl. 262, fig. 1143); Upper Albian (Zone à *Hysterocheras binum*), Mt. Raynaud near Diégo-Suarez (Madagascar). *a*, Frontal, *b*, lateral view, spiral portion. 3, Madagascar hypotype (Collignon 1963, pl. 262, fig. 1144); same age and locality. *a*, Lateral, *b*, ventral view.
- Figs. 4, 5. *Scaphites (Scaphites) simplex* Jukes-Browne. 4, Spiral portion, GPIT Ce 1221/4; Vraconian, Sainte Croix (Vaud, Switzerland). The sculpture of the inner whorl foreshadows that of the Cenomanian species. *a*, Frontal, *b*, ventral, *c*, lateral view. 5, Spiral portion of hypotype with nearly rectangular whorl section, GPIT Ce 1221/3; same locality. *a*, Frontal, *b*, lateral, *c*, ventral view.

Figures $\times 3$ unless otherwise stated.



1a



1b



1c



2a



2b



3a



4a



4b



4c



3b



5a



5b



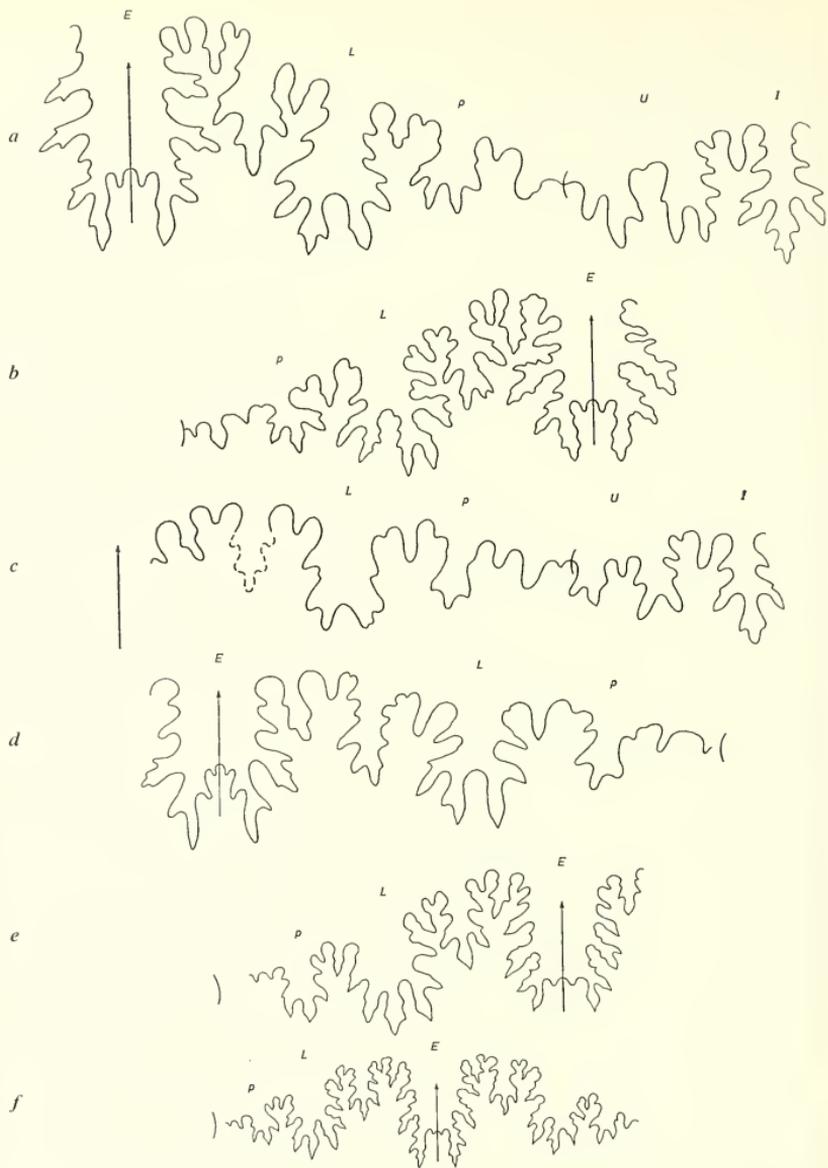
5c

Value and extent of the species. Despite the deficient holotype, the species can be regarded a good one in the light of the additional description and figures given by Spath. The species, as interpreted by Spath, includes three different types, which differ only in the detail of sculpture. Besides the typical costate form there are specimens with an almost smooth cast ('var. *sublaevis*' Spath) and costate ones with umbilical tubercles on the shaft ('var. *nodata*' Spath). The latter links the *equalis* main stock with *Sc. lugardianus* of the *meriani* group. I agree with Spath and believe that *Sc. simplex* covers all these different sculpture types. Whether *Sc. hilli* Adkins and Winton belongs also to the present species, as I formerly believed (Wiedmann 1962a, p. 213), or not, will be discussed below. Here it is referred to the *similaris* stock, where a group of small-sized scaphitids and a further problem of early scaphitid development will be treated. The main distinguishing feature between these two stocks is their different size. Each species of the main stock can be matched with an extremely similar species of the smaller *similaris* stock. Isolated innermost whorls, like the Tunisian (Pervinquière 1907) or Spanish (Wiedmann 1962a) nuclei cited above, may be referred to the one as well as to the other.

Description. Globose spiral portion with semilunate whorl section, closely coiled umbilicus already at an early age. Final hook generally curved throughout, without long straight shaft; constricted mouth-border nearly touching initial spire. Sculpture of spiral part consists of fine and dense, generally bifurcated ribs, which are somewhat convex on the sides and cross the venter in a moderately concave sinus. The point of bifurcation seems to be tuberculate on the innermost whorl, sometimes also on the shaft. On the body-chamber the ribs become more radiate and pronounced and single ones are often intercalated. At the umbilical seam the suture-line is distinctly retracted, thus *L* becomes asymmetric; the median incision of the enlarged element *L/U* increases in size, and is therefore generally confused with the 'second lateral' of normally coiled ammonites. The bipartite *U* remains inside the umbilical seam, and cannot be recognized in the external suture of any true *Scaphites*.

Remarks. For the present, *Sc. simplex* is of importance as an intermediate link between *Eoscapites* and typical species of *Scaphites*. It combines the characters of both, and specimens were even confounded by Spath (1937, text-fig. 177c) with *E. subcircularis*. While preserving the sculpture-type and whorl-shape of the preceding, the ribs become more distinctly separated into primary and secondary ones, and the septate whorls are more closely coiled as in the Cenomanian species. The suture-line changes more noticeably, but also gradually. The umbilical lobe, originally divided through the umbilical seam in *E. subcircularis*, passes from its original position to the internal suture-line, where it remains bipartite in all subsequent scaphitids. At the same time *L/U* becomes more and more amplified by its adopted position on the umbilical seam; its median incision also increases distinctly in size. Because of its phylogenetic development, its distinctly trifid shape, and its position in the external suture-line, it is completely impossible to interpret this element as an equivalent of the so-called 'second lateral' or *U₂* of ammonites. Also the suture developments here represented (text-figs. 7-9, 15) make it evident, that this element which we propose to name pseudo-lobe (*p*) always remains outside the umbilical seam, where as a rule the true umbilical lobes originate.

Moreover the theory of an origin of the scaphitids in Ammonitina can easily be rejected



TEXT-FIG. 3. Suture of *Scaphites* (*Scaphites*). *a*, *Sc. (Sc.) equalis* J. Sowerby, complete suture of typical specimen, GPIT Ce 1221/12; Cenomanian, Chardstock. *h* = 6 mm. *b*, the same, external suture of inflated form, GPIT Ce 1221/13; Upper Cenomanian, Rouen. *h* = 9 mm. *c*, *Sc. (Sc.) obliquus* J. Sowerby, nearly complete suture of hypotype GPIT Ce 1221/9; Cenomanian, Rouen. *h* = 4.5 mm. *d*, *Sc. (Sc.) yonekurai* Yabe, hypotype GPIT Ce 1221/10; Upper Cenomanian, Rouen. *h* = 8 mm. *e*, *Sc. (Sc.) simplex* Jukes-Browne, GPIT Ce 1221/3; Vraconian, Ste Croix. *h* = 5 mm. *f*, the same, GPIT Ce 1221/4; same locality. *h* = 4 mm.

by the different suture-lines here figured (text-figs. 3*e, f*). In *Sc. simplex* the lateral lobe is distinctly bifid at first, but becomes more and more asymmetric through the retraction of the umbilical suture. I stated nearly the same development in *Sc. equalis*, where *L* recovers its originally bifid shape in the adult stage (Wiedmann 1962*a*, p. 214).

To give a clearer impression of the singular initial coil of the present species, I figure here (Pl. 55, figs. 4, 5), besides a typical Cambridge Greensand specimen, two well-preserved camerate portions from my collection. They make the identity of Pictet and Campiche's fig. 7 (especially the suture-line, fig. 7*d*) with the present species obvious. The same may be stated for the first complete suture-line of '*Sc. equalis*' in Pervinquierè (1907, text-fig. 37) and reproduced by Nowak (1911, text-fig. 5), which has been regarded as typical for *Sc. equalis* up to the present. In reality it belongs to a completely closed initial coil, with semilunate section (Pervinquierè 1907, pl. 4, figs. 22, 23), which belongs to *Sc. simplex* or *Sc. hilli*.

The measurements (in millimetres) of the specimens here figured are:

	<i>D</i>	<i>B</i>	<i>d</i>	<i>h</i>	<i>b</i>	<i>u</i>
GPIT Ce 1221/3	—	—	11.5	7 (0.61)	10 (0.87)	—
GPIT Ce 1221/4	—	—	10	5.7 (0.57)	8.1 (0.81)	—
GPIT Ce 1221/5	26	16	15	8 (0.53)	13 (0.86)	—
GPIT Ce 1221/6	30	18	17	10 (0.59)	16 (0.94)	—
MHNP no. 5805 (<i>Sc. 'hugardianus'</i> ex coll. d'Orbigny)	26.5	17	16	9.4 (0.59)	15 (0.94)	—

In comparison with the preceding species, there is little variation in height and thickness of the septate whorls, and also in absolute size. *Sc. simplex* foreshadows *Sc. hugardianus* of the *meriani* stock not only with its 'var. *nodata*', but also with the tuberculation of the innermost whorls (Wiedmann 1962*a*, and here Pl. 55, fig. 4). One of the two poorly preserved syntypes of *Sc. hugardianus* d'Orbigny is reproduced here (Pl. 53, fig. 1), to demonstrate that it evidently belongs to the nodate variety of the present species. As can be seen in the table of measurements, it also agrees completely in its dimensions with the *simplex* specimens described here.

Distribution. In England *Sc. simplex* seems to be restricted to the lower part of the Upper Albian (*varicosum* to *aequatorialis* subzone age in Spath) from Folkestone, Maidstone (Kent), Glynde (Sussex), and the Cambridge Greensand. The species is also frequent in Southern France and Switzerland. It can be cited with certainty from the undivided Upper Albian from Entrèves-en-Bauges, Criou (?) and the Montagne La Fiz (Haute-Savoie), and the Vraconian of Ste Croix (Vaud). The citations from the Spanish Albian IV (Wiedmann 1962*a*) and the Tunisian Vraconian (Pervinquierè 1907) remain doubtful. Nevertheless *Sc. simplex* is a long-living species which persists throughout the whole Upper Albian.

Sc. (Scaphites) obliquus J. Sowerby

Plate 56, figs. 5, 6; text-fig. 3*c*

- 1813 *Scaphites obliquus* J. Sowerby, p. 54, pl. 18, figs. 4-7.
 1822 *Scaphites striatus* Mantell, p. 119, pl. 22, figs. 3, 4, 9, 11, 13-16.
 1822 *Scaphites obliquus* Sowerby; Brongniart, p. 83, pl. 6, fig. 13.
 ?1831 *Scaphites aequalis* Sowerby; Deshayes, p. 231, pl. 6, figs. 7, 8.
 1832 *Scaphites obliquus* Sowerby; Passy, p. 333, pl. 14, figs. 5-7.
 1842 *Scaphites aequalis* Sowerby; d'Orbigny pars, pl. 129, figs. 3-7 only.

- 1847/48 *Scaphites aequalis* Sowerby; Quenstedt, p. 274, pl. 20, fig. 14.
 1850 *Scaphites obliquus* Sowerby; Dixon, p. 359, pl. 29, fig. 11.
 1861 *Scaphites obliquus* Sowerby; Pictet and Campiche, p. 14.
 non 1865 *Scaphites obliquus* Sowerby; Stoliczka, p. 168, pl. 81, figs. 1-3 (sed *Sc. (Sc.) yonekurai* Yabe).
 non 1867 *Scaphites obliquus* Sowerby; Guéranger, p. 6, pl. 5, fig. 8 (sed *Sc. (Sc.) yonekurai* Yabe).
 1872 *Scaphites aequalis* Sowerby; Schlüter, p. 72, pl. 23, figs. 1-4.
 1872 *Scaphites aequalis* Sowerby; Fritsch pars, p. 41, pl. 13, fig. 5 only.
 1876 *Scaphites aequalis* Sowerby; Simonović, Bačević, and Sorokin, pl. 6, fig. 6.
 1951 *Scaphites obliquus* J. Sowerby; Wright and Wright, p. 13.
 1959 *Scaphites aequalis* Sowerby; Cieśliński, p. 33, pl. 3, fig. 4.
 ?1961 *Scaphites obliquus* Sowerby; Sučić-Protić, p. 124, pl. 6, figs. 2, 3.

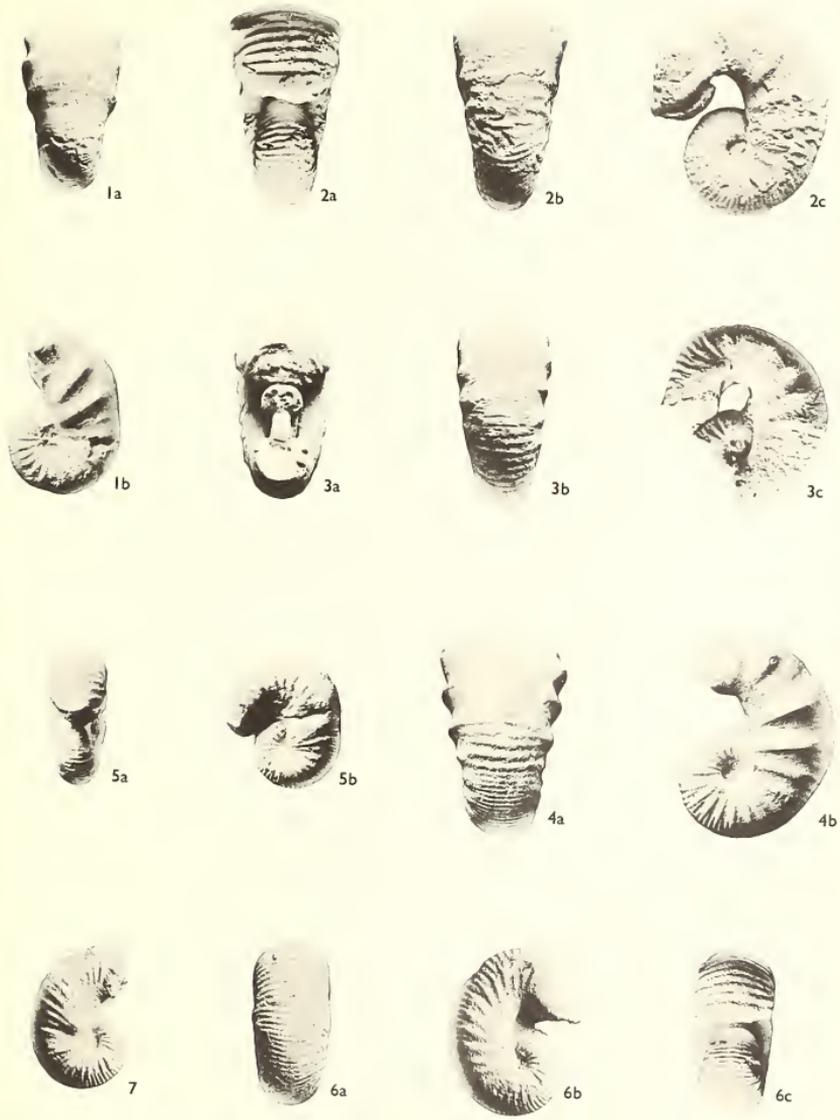
Holotype. The specimen figured by J. Sowerby (1813, pl. 18, figs. 4-7) from the Cenomanian Hamsey Marl pit near Lewes (Sussex), here reproduced (Pl. 56, fig. 5), BMNH 4387a.

Sc. (Sc.) obliquus closely links *Sc. simplex* with the later *Sc. equalis*. It is often confused or wrongly identified with the latter because of the identical inner whorls and the fact that both species are generally found together. In reality it is not difficult to separate them, by means of the different coarseness of primary ribs on the living-chamber. Moreover *Sc. obliquus* is somewhat smaller in size and generally less inflated. But indeed there is little phylogenetical change between these two species, which nearly completely agree in suture (text-fig. 3a-c) and sculpture of the inner whorls.

On the other hand, there is also little progress from *Sc. simplex* to the present species. The sculpture type is the same in both, but the ribs are coarser in *Sc. obliquus*, and the point of bifurcation nearer the venter. The primary ribs are less numerous and more pronounced, both on the spiral portion and on the straight shaft. At the same time the initial coil is more evolute and compressed in section, but in this respect some variation can be observed. Variable is also the number of secondary ribs originating in each primary one. The same variation can be recognized in the figurations which Mantell gave of his *Sc. 'striatus'*. This species was regarded as identical with *Sc. obliquus* by subsequent authors, including Wright and Wright (1951, p. 13). In a recent paper, however, C. W. Wright (1963, p. 602) changed his opinion and retained *Sc. 'striatus'* by choosing

EXPLANATION OF PLATE 56

- Figs. 1-4. *Scaphites (Scaphites) equalis* J. Sowerby. 1, Holotype, Sowerby Coll., BMNH no. 43986, figured by J. Sowerby (1813, pl. 18, figs. 1-3). Exact locality unknown: Cenomanian (?), almost certainly from the Dorset or Devon coast (Great Britain). *a*, Ventral, *b*, lateral view. 2, Representative hypotype with preserved mouth-border, GPIT Ce 1221/11. Cenomanian, Chardstock (Great Britain). *a*, Frontal, *b*, ventral, *c*, lateral view. 3, Compressed hypotype with finer costulation, GPIT Ce 1221/12; septate coil partly removed, to recognize the evolute, 'otoscapitid' inner whorls. Same locality. *a*, Frontal, *b*, ventral, *c*, lateral view. 4, Inflated specimen with stronger sculpture, GPIT Ce 1221/13. Upper Cenomanian, Rouen (France). *a*, Ventral, *b*, lateral view.
- Figs. 5, 6. *Sc. (Sc.) obliquus* J. Sowerby. 5, Holotype, Sowerby Coll., BMNH no. 43987a, figured by J. Sowerby (1813, pl. 18, figs. 4-7). Varians Zone, Cenomanian, Hamsey Marl Pit near Lewes, Sussex. *a*, Frontal, *b*, lateral view. 6, Complete hypotype, GPIT Ce 1221/8. Upper Cenomanian, Rouen (France). *a*, Ventral, *b*, lateral, *c*, frontal view.
- Fig. 7. *Sc. (Sc.) yonekurai* Yabe. Fragmentary hypotype, agreeing with *Sc. 'dailyi'* Wright; GPIT Ce 1221/10 (leg. Wiedmann). Upper Cenomanian, Rouen (France). Lateral view.
- All figures natural size.
 The photographs 1 and 5 were taken from casts made available through the kindness of Dr. M. K. Howarth.



as lectotype the figs. 9 and 11 of Mantell (1822, pl. 22). But unfortunately the proposed lectotype agrees completely with the diagnosis of *Sc. obliquus*, as given by J. Sowerby. There, two or three secondary ribs are indicated as typical for this species. If also forms with up to six secondaries belong to *Sc. obliquus* (Wright 1963, p. 602), I see no reason to renew *Sc. 'striatus'*. The proposed lectotype seems of interest in one aspect only; through its somewhat less pronounced primary ribs it is obviously intermediate to *Sc. simplex*.

It should be added that the number of secondaries is very constant (2 or 3) on the spiral portion; the indicated variability concerns the shaft, where the higher number (2-6) can only be observed. This can be predicted, however, by the intermediate position of *Sc. obliquus* between *Sc. simplex* and *Sc. equalis*.

The specimen from the Cenomanian of Rouen here figured (Pl. 56, fig. 6) can be regarded as typical. Its measurements (in millimetres) are:

<i>D</i>	<i>B</i>	<i>d</i>	<i>h</i>	<i>b</i>	<i>u</i>
26	12.5	16	9 (0.56)	11 (0.69)	1.5 (0.09)

Including *Sc. 'striatus'* Mantell, the present species can be diagnosed as follows: Middle-sized scaphitid with moderately evolute spiral coil. The whorl section changes from broadly depressed to rounded on the innermost whorls, and to slightly laterally compressed on the shaft. Whorl thickness of spiral portion is variable. The shaft is straight at first, then slightly recurved, but without touching initial coil. Sculpture consists of strong main and subordinate secondary ribs. The point of bi- or tri-furcation is generally raised, but not tubercled, and situated outside of central flank. About twenty primaries on the last septate whorl; ribs generally bi- or trifurcating, curved slightly backward on lateral sides and venter. Common on the shaft are ten prorsiradial main ribs, which are more or less pronounced, and give rise to generally three or four secondaries. On final hook sculpture of initial coil returns. The suture-line here figured (text-fig. 3c) is characterized by a distinctly bifid *L*, a well-developed *U*, the pronounced incision *p*, and an asymmetrically tripartite saddle *L/E*.

To *Sc. yonekurai* Yabe a number of similar forms will be referred, which differ from *Sc. obliquus* especially through their smaller size.

The age of *Sc. obliquus* from the British type localities was indicated by Wright and Wright as Lower Cenomanian, 'but perhaps also occurring earlier'. In France the species can be recorded also from the Upper Cenomanian, where the specimen from Rouen was collected. The German and Polish material again is of Lower Cenomanian age, while the Bohemian specimens may also be of Upper Cenomanian provenance. In Algeria and Tunisia the citation of the species (Pervinquier 1907, 1910) remains doubtful; the Serbian specimens figured by Sučić-Protić are in reality indeterminable, and the Indian forms will better be treated under *Sc. yonekurai* Yabe. Thus *Sc. obliquus* is a long-living species appearing probably in the uppermost Albian and overlapping here with *Sc. simplex*. It is frequent in the European Cenomanian, while all younger citations (for example Alth 1850) cannot be proven at the moment.

Sc. (Scaphites) equalis J. Sowerby

Plate 56, figs. 1-4; text-figs. 3a, b

1811 *Scaphites* Parkinson, pl. 10, fig. 10.

1813 *Scaphites equalis* J. Sowerby, p. 53, pl. 18, figs. 1-3.

- 1822 *Scaphites costatus* Mantell, p. 120, pl. 22, figs. 8, 12.
 non 1831 *Scaphites aequalis* Sowerby; Deshayes, p. 231, pl. 6, figs. 7, 8 (sed *Sc. obliquus*).
 1832 *Scaphites aequalis* Sowerby; Passy, p. 333, pl. 14, figs. 8, 9.
 1842 *Scaphites aequalis* Sowerby; d'Orbigny pars, p. 518, pl. 129, figs. 1, 2 only.
 1846 *Scaphites aequalis* Sowerby; Geinitz, p. 301, pl. 12, fig. 1.
 non 1847/8 *Scaphites aequalis* Sowerby; Quenstedt, p. 274, pl. 20, fig. 14 (sed *Sc. obliquus*).
 non 1850 *Scaphites aequalis* Sowerby; Alth in Haidinger, p. 206, pl. 10, fig. 31.
 1850 *Scaphites aequalis* Sowerby; Dixon, p. 359, pl. 27, figs. 37, 38.
 non 1865 *Scaphites aequalis* Sowerby; Stoliczka, p. 167, pl. 81, figs. 4-6 (sed *Sc. similaris*).
 non 1872 *Scaphites aequalis* Sowerby; Schlüter, p. 72, pl. 23, figs. 1-4 (sed *Sc. obliquus*).
 1872 *Scaphites aequalis* Sowerby; Fritsch pars, p. 41, pl. 13, fig. 6 only.
 non 1876 *Scaphites aequalis* Sowerby; Simonović, Bačević, and Sorokin, pl. 6, fig. 6 (sed *Sc. obliquus*).
 non 1888 *Scaphites aequalis* Sowerby; Herbich, p. 288, pl. 15, figs. 6, 7.
 ?1907 *Scaphites aequalis* Sowerby; Pervinquieré pars, pl. 4, figs. 24-26.
 ?1907 *Scaphites aequalis* Sowerby; Boule, Lemoine and Thevenin, p. 51, pl. 13, fig. 6.
 1911 *Hoploscaphites aequalis* Sowerby; Nowak, p. 566, text-fig. 5 only, pl. 10, fig. 11.
 1927 *Scaphites aequalis* Sowerby; Reeside, p. 27, pl. 9, fig. 1, pl. 10, figs. 13-15 (1927a).
 1928 *Scaphites aequalis* Sowerby; Adkins, pl. 24, figs. 4, 5.
 non 1929 *Scaphites aequalis-obliquus* Sowerby; Collignon, p. 49, pl. 5, figs. 1-6 (sed *Sc. obliquus*).
 1951 *Scaphites equalis* J. Sowerby; Wright and Wright, p. 13.
 1959 *Scaphites aequalis* Sowerby; Moskvin pars, pl. 7, fig. 1 only.
 non 1959 *Scaphites aequalis* Sowerby; Cieśliński, p. 33, pl. 3, fig. 4 (sed *Sc. obliquus*).
 1962 *Scaphites* (*Sc.*) sp. juv. aff. *equalis* J. Sowerby; Wiedmann, p. 214, text-fig. 53, pl. 10, fig. 11.

Holotype. The incomplete specimen figured by Sowerby 1813, pl. 18, figs. 1-3 and here reproduced, Plate 56, fig. 1. BMNH 43986. Exact locality unknown,? Cenomanian from Dorset or Devon coast.

In spite of the poorly preserved type and its evidently wrong drawing by Sowerby, this species can be recognized without any difficulty. If we recall that the evolutionary trend between *Sc. simplex* and *Sc. obliquus* consists of the tendency to get more evolute inner whorls and coarser sculpture especially on the shaft, the main features of *Sc. equalis* can be recorded theoretically.

Diagnosis. Middle-sized scaphitid, but generally larger than the preceding species. Spiral part relatively large with moderately open umbilicus. Final hook very inflated with its distinctly constricted mouth-border nearly touching initial coil. Sculpture of septate coil similar to the preceding form; primaries generally bifurcating on the middle of lateral sides; on the venter one intermediate rib generally intercalated. Number and course of ribs as in *Sc. obliquus*. Sculpture changes considerably on living chamber. Four to five distantly placed primary ribs persist only on the shaft, especially inflated on the outer margin. In the venter, the sculpture is completely different, consisting of two to six fine and dense secondary ribs rising from each primary one. Here also one or two intermediates are generally intercalated. The dorsum, however, remains completely smooth. Also in the well-defined *Sc. equalis* we find some variation in the coarseness of the sculpture and the shell inflation. In the more inflated forms the sculpture is generally coarser (Pl. 56, fig. 4), while the compressed specimens (Pl. 56, fig. 3) are more weakly ribbed. The intermediate specimen from Chardstock (Pl. 56, fig. 2) can be regarded as representative for this species.

In the case of the suture-line, there is little difference from that of *Sc. obliquus*. The umbilical suture of *Sc. equalis* is somewhat more retracted (text-figs. 1a, b), consequently

the saddle L/E seems to be very high and L somewhat more asymmetric (but never trifold). The incision p is also well developed and becomes occasionally (text-fig. 1a) bifid. Furthermore the element L/E is more asymmetrically bipartite than tripartite, and the suture as a whole is somewhat more incised.

The measurements (in millimetres) of the three specimens treated here are:

	D	B	d	h	b	u
GPIT Ce 1221/11	32	17.5	19	11 (0.58)	10 (0.53)	2.5 (0.13)
GPIT Ce 1221/12	29	14	17	9 (0.53)	9 (0.53)	4 (0.24)
GPIT Ce 1221/13	31	19	19	10 (0.53)	12 (0.63)	3.5 (0.18)

Further remarks. The specimen GPIT Ce 1221/12 (Pl. 56, fig. 3), evidently referable to the present species, is reproduced, to give an impression of the degree of uncoiling of the inner whorls. This fact is not unknown, since Nowak (1911, pl. 10, fig. 11) demonstrated the evolute, lytoceratid shape of the innermost whorls of *Sc. equalis*. But it needs recapitulation, because these inner whorls agree completely with those of true *Otoscaphtes* (Pl. 58, fig. 2), which were separated from the *equalis* stock and all true *Scaphites* by C. W. Wright.

The theory of an ammonitid origin of *Scaphites* was developed in part on the suture-line drawing given by Pervinquierè (1907, text-fig. 37) from a specimen collected in the Vraconian of Tunisia. This form shows a distinctly trifold L , which is said to become bifid with age, contrary to the expected derivation from *Lytoceras*. This was adopted without query, and therefore became the reason for many authors to connect *Scaphites* with the ammonitid stock (Pervinquierè 1907, Reeside 1927a, Nowak 1911, Drushtchic 1962). Unfortunately it was never proven on original *equalis* material, whether the development from the trifold to the bifid lobe form can be confirmed, or whether the attribution of Pervinquierè's specimen to *Sc. equalis* was correct. I think we have reason to doubt both.

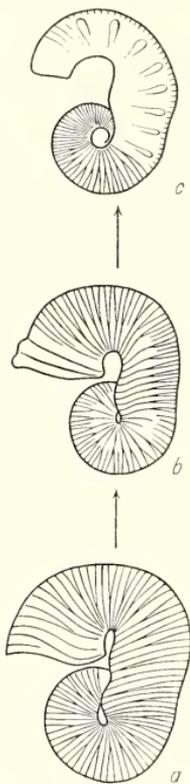
Above we noted the evolute lytoceratoid initial coil of *Sc. equalis*. The suture specimen in Pervinquierè (1907, pl. 4, figs. 22, 23) is, contrary to our knowledge of *Sc. equalis*, a nearly unsculptured and involute initial coil with a semi-lunate whorl section. The comparison with the different initial portions figured here, as well as the Vraconian age, and the distinctly asymmetric L verify that Pervinquierè's specimen belongs in reality to *Sc. simplex* (or *Sc. hilli*).

Now there naturally remains the question of an originally trifold L in true *Scaphites*. On the one hand, we demonstrated the intimate connexion between *Sc. simplex* and the eoscaphtid specimens with distinctly bifid L ; on the other, we were able to demonstrate the early suture development of one of the earliest representatives of the *equalis* group from the Spanish Vraconian (Wiedmann 1962a, p. 214, text-fig. 53). L was here found to be distinctly bifid at first, becoming more and more asymmetric up to the diameter which was studied by Pervinquierè. Thereafter the original symmetry rapidly returns; evidently this change was only observed by Pervinquierè. These are the somewhat defective reasons for attributing *Scaphites* to the Ammonitina.

Distribution. *Sc. equalis* like *Sc. obliquus* is a widespread Cenomanian species. It probably passes into the lower Turonian (Jefferies 1963). It can with certainty be cited from England, France, Bohemia, and Poland. The first but not absolutely proven representatives of the species were found in the Vraconian of Spain, Algeria, and Tunisia. All remaining citations from India and Madagascar probably do not belong to *Sc. equalis*.

THE *SIMILARIS* STOCK

In this group I join a number of species which differ from members of the main stock merely through their smaller size. I believe that as in the *equalis* stock, three species are sufficient to cover the complete small-sized Upper Albian and Cenomanian material. These species are: *Sc. (Sc.) hilli* Adkins and Winton, *Sc. (Sc.) yonekurai* Yabe, and *Sc. (Sc.) similaris* Stoliczka.



TEXT-FIG. 4. The development of the atrophic *similaris* stock. All $\times 1.5$. a, *Sc. (Sc.) hilli* Adkins and Winton (= *Sc. bassei* Collignon), b, *Sc. (Sc.) yonekurai* Yabe (*Sc. dailyi* C. W. Wright), c, *Sc. (Sc.) similaris* Stoliczka.

These forms are separated from the main stock and briefly treated here, because they make us aware of an interesting problem in scaphitid development. As evident from text-fig. 4, these species parallel the above described members of the main stock completely in ornamentation and general appearance (cf. text-fig. 13). They differ only in their smaller size and the presence of more or less pronounced bulges at the initial shaft, which covers the umbilicus. We believe that the lateral bulges depend on the reduced size, because in all scaphitids at hand, these peculiar bulges are restricted to small-sized specimens.

In his highly interesting paper about sexual dimorphism in ammonites, Makowski (1962, p. 31, text-pl. 4) also briefly treated *Scaphites*. For this purpose he had collected quite a number of *Hoploscaphites constrictus* from the same stratum and found that two forms of the same ornamentation, but separated by a distinct size gap, were present. This, and the abundance ratio 2:1 between the bigger (female) and smaller (male) specimens, were the basis for the establishment of sexual dimorphism in scaphitids, expressed here only through the different size.

Cobban (1952) drew attention to a similar phenomenon. Describing the scaphitids of the Western Interior United States, he was able to separate from the *Scaphites* main stock a lineage of dwarfed and mostly new species, which parallel the main development (Cobban, op. cit., text-fig. 1) and produce prominent lappets on the mouth-border (*Pteroscaphites* Wright). *Otoscaphites* evidently represents another micromorph development with lateral mouth lappets, which parallels the *Scaphites* main stock. The similarity of these lineages and Makowski's dimorphism is striking, especially if we agree with the Polish author, regarding the presence of mouth lappets as a common feature of the male sex in ammonites. But only the pteroscaphitids fulfil the suppositions for dimorphism:

to have the same stratigraphic and geographic distribution as the referable specimen of the normal lineage. The *similaris* forms diverge in both from the main stock: The large-sized stock seems to be restricted to the Northern boreal region of Europe, the *similaris*

group evidently favoured the Tethyan and Indo-Pacific areas. Moreover the latter generally have a longer stratigraphic range. Only in the Cenomanian of Northern France did I find both types together, where the separated areas may overlap. Thus the existence of the *similaris* group seems to have more ecologic and geographic reasons. *Sc. similaris* and its allies will be regarded as an atrophic parallel development to the main stock, which evidently favoured the boreal coldwater.

If this interpretation is correct, the generic separation of the present forms from the main stock is more reasonable than that of genus *Pteroscaphites* and family Otoscapitidae. Independent of these taxonomic problems is the question, whether the species of the *similaris* stock represent a true parallel development or single lateral offshoots of the equivalent species of the *equalis* group. For the moment this question cannot be decided.

Sc. (Scaphites) hilli Adkins and Winton

- 1907 *Scaphites obliquus* Sowerby; Pervinquière, pl. 4, fig. 27.
 ?1907 *Scaphites aequalis* Sowerby; Pervinquière, pl. 4, figs. 22, 23 only, text-fig. 37.
 1920 *Scaphites hilli* Adkins and Winton, p. 37, text-figs. 3, pl. 7, figs. 3-6.
 1920 *Scaphites hilli* Adkins and Winton; Adkins, p. 79, text-figs. 6-8, pl. 2, figs. 1-12.
 1928 *Scaphites hilli* Adkins and Winton; Adkins, p. 257, pl. 20, figs. 1-3, 7.
 1929 *Scaphites Bassei* Collignon, p. 51, pl. 5, figs. 8, 9.
 1931 *Scaphites Bassei* Collignon; Collignon, p. 46, pl. 5, fig. 6.
 1955 *Scaphites bassei* Collignon; Sornay, p. 10, text-fig. 3, pl. 10, figs. 7, 11.
 ?1962 *Scaphites (Sc.) simplex* Jukes-Browne; Wiedmann, p. 213, text-fig. 52, pl. 10, fig. 8 (1962a).

Holotype. The originally designated type specimen from the Pawpaw clay (Vraconian) of Fort Worth, Texas, in Adkins and Winton 1920, pl. 7, fig. 3.

The diagnosis given for *Sc. simplex* can be repeated here with the only difference, that *Sc. hilli* is smaller, develops a distinct living-chamber bulge which covers the umbilicus, and offers a somewhat more asymmetric *L*. The sculpture consists of the same fine ribs as in *Sc. simplex*, the spiral portion has the same closed umbilicus and initial tuberculation; it agrees in its more or less inflated whorl section, the strongly retracted umbilical suture and, consequently, the pronounced asymmetry of *L*. The congruence of *Sc. simplex* and *Sc. hilli* is so complete, that even the nodate variety (p. 413) can be recorded in *Sc. hilli* (Adkins 1928, pl. 20, fig. 3), and both species were combined on a previous occasion (Wiedmann 1962a). Indeed the initial coils of both species are indistinguishable, as the Tunisian and Spanish nuclei, cited in synonymy, make evident. If the body-chamber is present, then it is not difficult to separate them, because *Sc. hilli* does not attain a great diameter (*D*) of 15 mm. In *Sc. simplex*, however, we noted an average diameter of 30 mm.

There is no doubt that also *Sc. 'bassei'* Collignon, of the Mediterranean-Madagascan area, should be included here. Like the following species, also *Sc. hilli* survives its normal-sized equivalent: it is known from the uppermost Albian of Texas, Algeria, ? Tunisia and ? Spain, but the main distribution lies in the Cenomanian of Northern Africa and Madagascar.

Sc. (Scaphites) yonekurai Yabe

Plate 56, fig. 7; text-fig. 3d

- 1865 *Scaphites obliquus* Sowerby; Stoliczka, p. 168, pl. 81, figs. 1-3.
 1867 *Scaphites obliquus* Sowerby; Guéranger, p. 6, pl. 5, fig. 8.

- 1907 *Scaphites aequalis* Sowerby; Boule, Lemoine, and Thevenin, pl. 13, fig. 6.
 1910 *Scaphites* (?) *Yonekurai* Yabe, p. 165, pl. 15, figs. 4-7.
 1929 *Scaphites aequalis-obliquus* Sowerby; Collignon, p. 49, pl. 5, figs. 1-6.
 1963 *Scaphites dailyi* C. W. Wright, p. 602, pl. 81, fig. 6.

Lectotype. The complete specimen figured by Yabe (1910, pl. 15, figs. 4, 6) from the *Scaphites* beds of the Opirashibets region (Teshio, Hokkaido).

Sc. yonekurai as here interpreted covers a number of slightly different types which are, as we believe, inseparable. The diagnoses given by Yabe and C. W. Wright agree completely and can be summarized as follows: Like *Sc. obliquus* but smaller and with more globular, moderately involute initial whorls, and more or less pronounced bulge.

As in the case of *Sc. obliquus* we find all transitions between the preceding species and *Sc. similaris*: on one side we have the finely ribbed Utatur specimen Stoliczka's (1865, pl. 81, fig. 3), on the other the coarser ribbed specimen from Diégo-Suarez as figured by Collignon (1929, pl. 5, fig. 1). Also variable is the bulge size which is less pronounced in the Japanese type, moderately in Indian material, and more evident in the Australian type of *Sc. 'dailyi'* or the here figured French hypotype (Pl. 56, fig. 7). But all these forms are connected through their inflated and moderately involute initial coil, where about twenty primary ribs per whorl are present, as in *Sc. obliquus*. They are likewise bi- or trifurcating, and slightly curved backward on lateral sides and venter. On the shaft the primaries are more pronounced and the secondaries sometimes more numerous, as always in the case of *Sc. obliquus*. Generally the primaries are equally spaced and projected on the shaft (text-fig. 4b), but in the forms with inflated bulges (Stoliczka 1865, pl. 81, fig. 2; Wright 1963, pl. 81, fig. 6; here Pl. 56, fig. 7), they seem to be bundled at the umbilical margin. The suture with a distinctly bifid *L* (text-fig. 3d) also agrees completely with that of *Sc. obliquus*.

In the present form the difference in size is less pronounced than in the preceding form. The French specimen figured here for comparison with *Sc. obliquus* and *Sc. 'dailyi'* has the following dimensions (in millimetres):

	<i>D</i>	<i>B</i>	<i>d</i>	<i>h</i>	<i>b</i>	<i>u</i>
GPIT Ce 1221/10	22	11	14	7 (0.50)	9 (0.64)	2.5 (0.18)

A general distinguishing feature from *Sc. obliquus* is the much more opened umbilicus of *Sc. yonekurai*. Like *Sc. hilli*, the present species also favours the Southern hemisphere and outlasts the macromorph species. It is known from the Cenomanian of India, Madagascar, and the Bathurst Island (Northern Australia), from the Turonian/Coniacian of Hokkaido, and finally it was collected, together with *Sc. obliquus*, in the French type Cenomanian of the Sarthe. The Madagascan material links the present species with *Sc. similaris*.

Sc. (Scaphites) similaris Stoliczka

- 1865 *Scaphites aequalis* Sowerby; Stoliczka, p. 167, pl. 81, figs. 4-6.
 1868 *Scaphites similaris* Stoliczka, p. 36.

Lectotype. The specimen figured by Stoliczka (1865, pl. 81, fig. 5) from the Utatur group of Odium, Southern India.

This species is evidently a small-sized *Sc. equalis*, with which Stoliczka identified it at first. Besides the different size, the shell is somewhat less inflated as in the European

species. There is little difference, if not identity, with the somewhat younger *Sc. aequalis* mut. *turonensis* Roman and Mazeran (1913, pl. 4, figs. 10-14) of the Turonian from Uchaux (France) and Madagascar (?).

THE MERIANI STOCK

Through the possession of conical ventrolateral tubercles, a closed umbilicus, and an asymmetrically bifid *L*, the species here united: *Sc. (Sc.) hugardianus* d'Orbigny, *Sc. (Sc.) meriani* Pictet and Campiche, and *Sc. (Sc.) collignoni* sp. nov., are well distinguishable from the untuberculate groups treated above. But nevertheless they are so continuously connected with *Sc. simplex* that the generic separation from the main stock seems inadmissible. The three species mentioned above, are exclusively restricted to the Upper Albian.

Sc. (Scaphites) hugardianus d'Orbigny

Plate 54, fig. 5; Plate 57, figs. 1, 2, 6, 7; text-figs. 5*d, e*

- 1842 *Scaphites Hugardianus* d'Orbigny, p. 521, 525.
 non 1848 *Scaphites Hugardianus* d'Orbigny; Pictet, p. 370, pl. 12, figs. 2*a-d* (sed *Sc. simplex*).
 1850 *Scaphites Hugardianus* d'Orbigny; d'Orbigny, p. 125.
 1861 *Scaphites Meriani* Pictet and Campiche pars, p. 16, pl. 44, figs. 5, 6 only.
 1861 *Scaphites Hugardianus* d'Orbigny; v. Hauer, p. 649, pl. 2, figs. 11, 12.
 1875 *Scaphites Hugardianus* d'Orbigny; Hébert and Munier-Chalmas, p. 116, pl. 5, fig. 7.
 1875 *Scaphites Meriani* Pictet and Campiche; Jukes-Browne, p. 287, pl. 14, figs. 1, 2.
 1910 *Scaphites Hugardianus* d'Orbigny; Pervinquier, p. 24, text-fig. 8, pl. 2, figs. 1, 2.
 1911 *Scaphites Hugardianus* d'Orbigny; Nowak, p. 570, text-fig. 7.
 ?1929 *Scaphites Hugardianus* d'Orbigny; Collignon, p. 53, pl. 5, fig. 12.
 1937 *Scaphites Hugardianus* d'Orbigny; Spath, p. 502, text-figs. 175*a, b*, 176*a, b, g-i*; pl. 57, fig. 24.

The original description of *Sc. hugardianus* given by d'Orbigny (1842, p. 525) is inadequate: '... voisin du *Sc. aequalis*, en diffère par le manque des côtes, ces ornements étant remplacés par une pointe aigüe. Elle se trouve dans le gault supérieur des Fis en Savoie.' Nevertheless this sentence allows us to recognize that the two syntypes which are preserved in d'Orbigny's collection do not correspond to the diagnosis.

Because d'Orbigny never figured a type specimen, it is not surprising that Pictet (1848), who figured the species for the first time, was unable to interpret it correctly. We agree completely with Spath in regarding these forms with three umbilical tubercles on the shaft as an extreme variety ('var. *nodata*') of *Sc. simplex*.

However, not only Spath but all subsequent authors followed the description given by Hébert and Munier-Chalmas (1875, p. 116), because these authors mentioned that they had examined d'Orbigny's type specimens. Here the species is interpreted as follows: 'Test orné de côtes fines, égales et équidistantes, partant deux par deux sur la spire et sur le commencement du tour projeté, de côtes en peu plus fortes venant de l'ombilic. La partie supérieure du tour projeté présente cinq ou six tubercules aigües et comprimés situés sur les flancs, plus près du dos que de la région ventrale; de chacun d'eux partent seulement deux ou trois côtes; les autres passent, simples ou bifurquées, entre ces tubercules, qui disparaissent quelquefois sur certains individus.'

The specimen figured by Hébert and Munier-Chalmas and here reproduced (Pl. 54,

fig. 5), unfortunately does not belong to d'Orbigny's types, but to the material from Salazac (Gard) described by these authors. Contrary to the rules of nomenclature it was proposed as lectotype by Spath. Naturally this proposal cannot be accepted, since the specimen did not come from the preserved type material nor from the type locality. Through the kindness of Dr. Sornay I received some of the original syntypes, but only two of the three specimens mentioned by Hébert and Munier-Chalmas are preserved. Unfortunately they are neither conspecific nor identical with *Sc. hugardianus* auct. Both are labelled 'La Fiz', but one of them is in greensand matrix and probably belongs to *E. subcircularis*; the other here reproduced (Pl. 57, fig. 1) is of phosphatic material and can evidently be identified with the nodate variety of *Sc. simplex*. In order to avoid any further confusion, we leave this problem open, hoping that the missing specimen will be found in the Sorbonne collections, not accessible at the moment. Here Hébert and Munier-Chalmas' types are deposited.

With these reservations some specimens are figured here from the Cambridge Greensand and Southern France which are referred to *Sc. hugardianus*. They exactly agree in their dimensions with the 'typical' specimen from Salazac, while d'Orbigny's tuberculate syntype also agrees in this respect with *Sc. simplex* (cf. p. 415).

	<i>D</i>	<i>B</i>	<i>d</i>	<i>h</i>	<i>b</i>	<i>u</i>
GPIT Ce 1221/7	21	13	12.5	7 (0.56)	11 (0.88)	—
MHNG Wi 'Sc'/7	18	10	9.5	4.5 (0.47)	7 (0.74)	1.5 (0.16)
MHNG Wi 'Sc'/8	21	12	11	7 (0.64)	9.5 (0.86)	—
MHNG Wi 'Sc'/9	21	12.5	12	6.5 (0.54)	11 (0.92)	—

The material in my possession permits the following supplement to the diagnosis: *Sc. hugardianus* is a middle to small-sized species. The umbilicus of the phragmocone is generally completely closed (Pl. 57, fig. 6), but sometimes somewhat open (Pl. 57, fig. 7). Lateral bulges on the initial shaft may be present (Pl. 57, fig. 1) or not (Pl. 57, fig. 6a). This makes evident, that the presence of lateral bulges—introduced in the scaphitid classification by Collignon (1929), Sornay (1955), and C. W. Wright (1963)—is without great systematic significance, but a common feature of many small-sized specimens. The hooked body-chamber of *Sc. hugardianus* is of peculiar shape: broad, inflated, with distinctly constricted and collared mouth-border (Pl. 57, figs. 1, 7) nearly touching the initial coil.

In the suture-line are found some interesting variations. *L* generally has a subsymmetric bifid shape (text-fig. 5d), but in the Cambridge Greensand form figured here, which cannot be separated from the present species, the lateral lobe is nearly trifid (text-fig. 5e). This emphasizes the intimate relationship to *Sc. simplex*, with which *Sc. hugardianus* is linked through the forms just mentioned. As indicated above and visible in text-fig. 5, this asymmetrical outline of *L* depends especially on the general course of the umbilical suture-line. Where it passes straight over the sides and the umbilical seam (text-figs. 5d, f), *L* remains bifid; where the umbilical portion is retracted, however (text-figs. 5a-c, e), *L* becomes distinctly asymmetric. This is the real and simple reason for the attribution of an 'ammonitid origin' to *Scaphites*.

In comparison with the following *Sc. meriani*, the suture-line is less incised, the saddle *L/E* enlarged and nearly symmetrically divided by a pronounced median incision.

The feature which joins all forms described here or cited as synonymous, are the five

small but pronounced tubercles of the living-chamber. They are equally spaced, somewhat nearer to the venter. The generally single primary ribs trifurcate at the tubercles, while two single or bifurcating untuberculate ones are intercalated. The umbilical portion of these ribs is more or less (Pl. 57, figs. 2 to 7) pronounced. The initial coil preserves the fine, dense ribbing of the preceding *Sc. simplex*.



TEXT-FIG. 5. Suture-lines of the *Scaphites meriani* stock. *a-c*, *Sc. (Sc.) meriani* Pictet and Campiche. *a*, Lectotype, MHNG P & C 'S-CR'/44, 1; Vraconian, Ste Croix. $h = 6$ mm. *b*, Madagascan hypotype (Collignon 1963, fig. 1141); Upper Albian, Mt. Raynaud. $h = 5$ mm. *c*, Hypotype GPIT Ce 1221/2; Upper Albian, Col de Teine. $h = 4$ mm. *d, e*, *Sc. (Sc.) hugardianus* d'Orbigny. *d*, Specimen with bifid *L*, MHNG Wi 'Sc'/7; Upper Albian, Crioud (?). $h = 4$ mm. *e*, Specimen with retracted umbilical suture and asymmetric *L*, GPIT Ce 1221/7; Cambridge Greensand. Intermediate to *Sc. simplex*. $h = 7$ mm. *f*, *Sc. (Sc.) collignoni* sp. nov. Holotype (coll. Collignon); Upper Albian, Mt. Raynaud. $h = 6$ mm.

Without any doubt *Sc. hugardianus* is directly linked with the latter. But at the base of sculpture, shell size, and inflation, separation is always possible, even in the nodate forms of *Sc. simplex*. All these forms preserve the globular coil and size of the untuberculate type, and the always weak and less numerous tubercles of the chamber are arranged in the neighbourhood of the inner margin.

The specimen figured on Plate 57, fig. 7, resembles in its open initial coil and the smoothness of its initial body-chamber, the younger *Sc. pseudoaequalis* Yabe, which has

distinct and tuberculate primary ribs on the septate portion. We are unable to decide at the moment whether the specimen from Criou (?) perhaps belongs to a distinct species. The differences from the direct descendant *Sc. meriani* will be treated below.

Distribution. *Sc. hugardianus* is widespread in the French Upper Albian. It is known from the Montagne La Fiz, Mt. Saxonet and Criou (?) (Haute-Savoie), and Salazac (Gard). It seems to be present in the Vraconian of Ste Croix (Vaud, Switzerland), the Bakony Forest (Hungary), and Berrouaghia (Algeria). In England the species seems to be restricted to the Upper Albian *substuderi* subzone of the Cambridge Greensand. The species will soon be described from the Upper Albian of Orosei (Sardinia). Collignon's specimen from the Madagascar Cenomanian is too poorly preserved for any identification with *Sc. hugardianus*.

Sc. (Scaphites) meriani Pictet and Campiche

Plate 54, fig. 6; plate 57, figs. 3, 4; text-figs. 5a-c

- 1861 *Scaphites Meriani* Pictet and Campiche pars, p. 16, pl. 44, figs. 1-4, 8 only.
 non 1875 *Scaphites Meriani* Pictet and Camp.; Jukes-Browne, p. 287, pl. 14, figs. 1, 2 (sed *Sc. hugardianus*).
 non 1888 *Scaphites Meriani* Pictet and Camp.; Herbich, p. 28, pl. 13, figs. 5-10.
 non 1929 *Scaphites* cf. *Meriani* Pictet and Camp.; Collignon, p. 54, pl. 5, fig. 15 (sed *Sc. sp. juv. indet.*).
 1963 *Scaphites Meriani* Pictet and Camp. pars; Collignon, p. 56, pl. 262, fig. 1141 only.

Lectotype. The adult specimen figured by Pictet and Campiche (1861, pl. 44, fig. 1) from the Vraconian of Ste Croix, and here reproduced (Pl. 54, fig. 6). Preserved in the Pictet collection, MHNG P & C 'S-Cr'/44, 1.

Description. Large species with completely involute, generally unsculptured initial coil. Different from the previously described scaphitids, first part of straight shaft always septate. Largely curved final hook. The specific feature is the sculpture of the body-chamber, consisting of looped main ribs amalgamating into nine or ten ventrolateral tubercles, and untuberculate intermediate ones. All ribs bi- or trifurcating at the height of the tubercles. On the spiral portion tubercles generally begin earlier than in the preceding species, but this is subject to variation. Very incised suture with asymmetric *L*, even in youth. Saddles moderately enlarged.

Remarks. *Sc. meriani* is not as common as generally believed. Its phylogenetic position is between *Sc. hugardianus*, with largely spaced tubercles on the chamber only, and *Sc. collignoni* sp. nov., with tuberculation on each second rib beginning at a very small diameter. The incoming of ribbing and tuberculation in the present species is evidently subject to variation. In the lectotype the septate coil remains nearly smooth with some very weak tubercles on the last half whorl (Pl. 54, fig. 6b). On the spiral portion here figured (Pl. 57, fig. 3), the ribs are more distinct as in the type (and the smooth initial coil figured by Pictet and Campiche as fig. 8), but no tuberculation can be observed up to a whorl height of 7.5 mm. In comparison with this, the nucleus figured by Collignon (1963, fig. 1141) and here regarded as synonymous (Pl. 57, fig. 4), is distinctly tuberculate at a whorl height of 2 mm. Despite this the sculpture has the same style (looped primary ribs, two intercalated untubercled ones, &c.) as the large lectotype. Also the

suture agrees so completely in all three forms (text-figs. 5a-c), that there is no possibility to separate them.

The second specimen which was referred to the present species by Collignon (1963, fig. 1142) differs in sculpture and suture-line so distinctly from *Sc. meriani*, that I propose to separate it as a new species.

Distribution. *Sc. meriani* occurs with certainty only in the Vraconian of Ste Croix (Vaud, Switzerland), and Col de Teine (Haute-Savoie). It is relatively abundant in the uppermost Albian of Orosei (Sardinia), and is also present in the Hysteroцерatan of Mt. Raynaud near Diégo-Suarez (Madagascar). The Cenomanian specimen figured by Collignon (1929) without suture drawing may belong, however, to *Sc. simplex* or *Sc. yonekurai*.

Sc. (Scaphites) collignoni sp. nov.

Plate 57, fig. 5; text-fig. 5f

Holotype. *Scaphites meriani* in Collignon 1963, pl. 262, fig. 1142, from the Upper Albian (Zone à *Hysteroцерas binum*) of Mt. Raynaud near Diégo-Suarez, Madagascar, and here reproduced Plate 57, fig. 5.

Description. Globular initial coil, belonging to the *meriani* stock. From a whorl height of 2 mm. every second primary rib provided with a small tubercle at the point of bi- or trifurcation; only one bifurcating and untubercled rib intercalated. Umbilicus completely closed and finally overlapped by a distinct lateral bulge. Body-chamber unknown. Suture moderately incised, and with distinctly bifid lateral lobe.

Remarks. *Sc. collignoni* sp. nov. can be regarded as the final member of the *meriani* stock. The lateral tuberculation in the present form starts at an early age and covers every second primary rib. Moreover the section of the initial coil is extremely globular (Pl. 57, fig. 5c), and the septal surface extremely incised by a great number of secondary elements. The number of tuberculate main ribs amounts to thirty per whorl (Pl. 57, fig. 5b). The suture-line (text-fig. 5f) is less incised than in *Sc. meriani*, even at a comparative diameter (text-fig. 5a). *L* has a distinctly bifid outline, and the element *L/E* is somewhat enlarged.

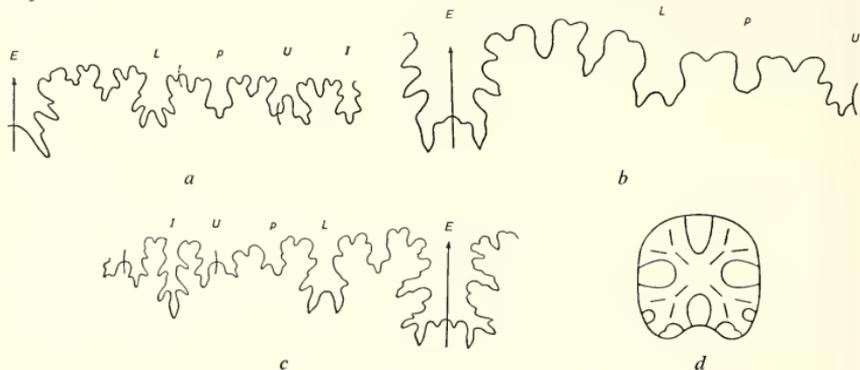
If we consider that in *Sc. meriani* only ten ribs per whorl are present which acquire ventrolateral tuberculation, and also that in this species sculpture and suture-line, even on the smallest known nucleus (Pl. 57, fig. 4, text-fig. 5b), completely agrees with that of the full-grown lectotype, then the separation of the present spiral portion becomes evident, despite the fact that the living-chamber is unknown. The inner whorl of the younger *Sc. pseudoaequalis*, as figured by Yabe (1910, pl. 15, fig. 2) approaches the present form, but there are no untuberculate ribs intercalated between the tuberculate ones. The species is known only from its holotype.

Subgenus SCAPHITES (METASCAPHITES) Wiedmann 1962

Type species. *Scaphites* (?) *thomasi* Pervinquier 1907.

Besides the three lineages treated above another early scaphitid stock developed in the Western Mediterranean area, which seems to be, however, of little phylogenetic interest. For the moment only two species can be included: *Sc. (Metascaphites) subthomasi*

Wiedmann and Sc. (*Metascaphites*) *thomasi* Pervinquière. Both are obviously different from the scaphitids hitherto described. They differ in their rectangular whorl-section (text-fig. 6*d*), and their strong and nearly straight main ribs which become tuberculated at the outer margin and cross the venter without bifurcation (Pl. 58, fig. 1). They differ also in the umbilical suture-line, where *U* remains on the umbilical seam. Thus they anticipate the general appearance of the Maastrichtian genus *Indoscaphites*. Therefore I proposed (1962*a*, p. 212) to separate these peculiar Upper Albian forms from the true *Scaphites*.



TEXT-FIG. 6. The different subgenera of *Scaphites*. *a*, Complete suture-line of *Sc.* (*Hyposcaphites*) *stephanocerooides* Yabe (ex Jimbo 1894, pl. 9, fig. 3*b*); Upper Turonian (?), Pombets, Hokkaido. *h* = 5 mm (?). *b*, External suture of *Sc.* (*Pteroscaphites*) *minutus* Moreman, holotype, BEGA 19814; Lower Turonian, Britton. *h* = 3.5 mm. *c*, Complete suture-line, and *d*, Septal surface of *Sc.* (*Metascaphites*) *subthomasi* Wiedmann (ex Wiedmann 1962*b*, text-figs. 57, 58); Upper Albian, Izurdiaga. *h* = 3.5 mm.

The origin of *Metascaphites* still remains doubtful, because there is nothing comparable in the Upper Albian. I believe that *Metascaphites* can be traced directly back to *Eoscaphites*, in spite of the much more simplified suture-line. As in the early *Eoscaphites* the umbilical lobe becomes subdivided through the umbilical seam, where it remains throughout. Moreover, the older *Metascaphites subthomasi* is much more evolute than the Vraconian type species with its completely closed spiral coil (Pl. 58, fig. 1). The lateral lobe is distinctly bifid, and thus we have little doubt that the present subgenus belongs to *Scaphites*, despite its acanthoceratoid sculpture.

If we compare the metascaphitid suture-line with that of *Otoscapites* (text-figs. 6*b*, 7) we find complete identity. Naturally it is difficult to make any decision about the systematic value of the definite position of *U*. The fixation of the latter on the umbilical seam can be regarded in scaphitids as a phylogenetically early feature; it is also present in the early ontogeny as well as probably depending on the degree of whorl evolution. If we use, therefore, the umbilical suture for systematic purposes, we risk combining not only early scaphitid representatives, but also micromorphs or evolute members of completely different scaphitid lineages. This becomes evident if we consider Yabe's genus '*Yezoites*' which was based nearly on the same feature: the presence of an undivided

saddle I/U naturally depends on the position of U on the umbilical seam. The three species joined in 'Yezoites' by Yabe in reality belong to three different scaphitid stocks.

These are the reasons why I do not directly connect with *Metascaphites* a group of scaphitids described from the Algerian Cenomanian by Pervinquière. These forms agree with the present in regard to suture-line and sub-rectangular whorl-section, but they differ in sculpture and whorl evolution. While in the present subgenus the tendency to close the umbilicus was observed, the spiral portion of the Cenomanian forms remain open whorled. Moreover, the untuberculate ribs are sigmoidal and bifurcating. These features are likewise representative for the Turonian *Otoscaphtes* to which the Cenomanian species are referred here. I believe that these forms also—like the similar *Metascaphites*—can be traced back to *Eoscaphtes*, and not to *Worthoceras*, as C. W. Wright believed. *Metascaphites* seems to be restricted to the Upper Albian of the Western Mediterranean region.

Subgenus SCAPHITES (OTOSCAPHTES) C. W. Wright 1953

Type species. Amm. (?) bladenensis Schlüter 1872.

Unfortunately *Amm. bladenensis* Schlüter (January 1872) is a very doubtful ammonitid species, known only through a small inner whorl with a diameter of 15 mm (Pl. 58, fig. 6). It differs through its single radial ridges considerably from the subsequently described but well-defined *Sc. auritus* Schlüter (March 1872). Here the ribs are distinctly sigmoidal, bi-, or triplicate; but Schlüter's syntypes (1872, pl. 23, figs. 5-9) vary considerably in the coarseness of their ribbing. Contrary to *Sc. bladenensis*, the later species can easily be referred to *Scaphites* in regard to its living-chamber and suture-line. The small size, the open-whorled spiral portion, and the presence of distinct lateral lappets at the mouth-border are further common features of the somewhat divergent syntypes.

Schlüter himself (1872, p. 77) intended to include *Amm. bladenensis* in the better-known *Sc. auritus*, but he was unable to localize *bladenensis*-like inner whorls in the full-grown *auritus* specimens. Thus *Amm. bladenensis* was abandoned by the majority of the subsequent authors. It was Diener at first (1925, p. 197), and C. W. Wright thereafter (1953), who preserved the anterior name according to the rules of nomenclature, and regarded *Sc. auritus* as synonymous with the poorly known *Sc. bladenensis*.

The material studied here permits the following decision. Schlüter's *auritus* syntypes belong to at least two different species. Only the third form (Schlüter's fig. 9) can be identified with *Amm. bladenensis*, which can be characterized through its pachydisoid lateral ridges in youth, and strong, sigmoidal ribs generally bifurcating at the centre of the sides in the adult stage. The specimen figured here (Pl. 58, fig. 2, text-fig. 7) belongs to this species, as also *Sc. 'auritus'* in Geinitz (1875, pl. 35, fig. 10). For the two remaining specimens in Schlüter the name *Sc. auritus* (lectotype the original of Schlüter 1872, pl. 23, figs. 5, 6) should, however, be preserved. The restricted *Sc. auritus* is then more closely and finely ribbed, the ribs trifurcate at small umbilical tubercles in the type, without tuberculation in the presumed paratype (Schlüter's figs. 7, 8). *Sc. 'auritus'* Fritsch (1872, p. 44, pl. 13, figs. 8, 9, 11, 14, 15) = *Sc. 'fritschi'* Grossouvre, agrees completely with this definition.

These identifications became curiously confirmed through Californian otoscaphtids,

for which I thank Professor Popenoe. The two specimens here reproduced (Pl. 58, figs. 3, 4) from the Cow Creek valley agree more with the original drawings of *Otoscaphtes bladenensis* than the European hypotypes mentioned above. These, and especially the specimen of Plate 58, fig. 2, offer more inflated and more involute inner whorls with less numerous lateral ridges. It may be regarded therefore as transitional to *Sc.* (*Otoscaphtes*) *cottae* (F. A. Roemer) with closed umbilicus. But the Californian hypotype (Pl. 58, fig. 4) agrees completely in whorl-section, degree of evolution and the elevated number of twenty lateral ridges per whorl with the juvenile holotype of *Otoscaphtes bladenensis*, while the adult specimen (Pl. 58, fig. 3) with the beginning of its chamber preserved, demonstrates the sculptural transition from lateral ridges to strong bifurcating ribs, as stated for the adult *Otoscaphtes bladenensis* (Schlüter 1872, pl. 23, fig. 9). Thus the latter can now be regarded as a valid and well-defined species.

For the question of the origin of otoscaphtitids it is necessary to recall the fact that the sculpture of *Otoscaphtes bladenensis* corresponds with that of the inner whorls of the contemporaneous *Sc. geinitzii* d'Orbigny, which is regarded as a direct descendant of *Sc. equalis*. Thus we again face the problem of sexual dimorphism in scaphitids. Indeed it was Fritsch (1872, p. 44) who for the first time stated that the dwarfed 'auritus' forms may only be the males of the normal-sized *Sc. geinitzii*. This relationship between small and normal-sized scaphitids of the same stratigraphic level does not harmonize with the modern systematics. Wright (1953) pointed out that *Sc. bladenensis*, on which the new genus *Otoscaphtes* was based, belongs to an independent scaphitid lineage of small forms with constricted mouth-border, and can be connected with the Albian *Worthoceras*. The latter was said to be derived from *Eoscaphtes*, and thus 'Otoscaphtinae' were separated as a different subfamily from the scaphitid main stock. This separation was mainly based on four suppositions which should be discussed here.

1. *Scaphites minutus* Moreman, described from the Turonian of Texas, can be directly related to *Sc. bladenensis* of the European Upper Turonian.
2. *Scaphites minutus* can also be related to the Upper Albian *Worthoceras platydorsum* (Scott), with which it is linked by a number of worthoceratids in the Texan Albian, Cenomanian, and Lower Turonian.
3. The lineage *Worthoceras-Otoscaphtes* parallels the scaphitid main stock, from which

EXPLANATION OF PLATE 57

- Figs. 1, 2, 6, 7. *Scaphites* (*Scaphites*) *hugardianus* d'Orbigny. 1, Lateral view of typical hypotype, MHNG Wi 'Sc'/8 (leg. Favre), with preserved mouth-border; Upper Albian (Vraconian?), Mt. Saxonet (Haute Savoie, France). 2, Hypotype GPIT CE 1221/7, with weak tuberculation, intermediate to *Sc. simplex*. Vraconian (*substuderi* zone), Cambridge Greensand. *a*, Ventral, *b*, lateral view. 6, Hypotype MHNG Wi 'Sc'/9 (leg. Pictet), with closed umbilicus; Upper Albian, Crioud? (Haute Savoie, France). *a*, Lateral, *b*, ventral view. 7, Hypotype MHNG Wi 'Sc'/7 (leg. Pictet), with open umbilicus, nearly smooth shaft and preserved mouth-border; same locality. Lateral view.
- Figs. 3, 4. *Sc.* (*Sc.*) *meriani* Pictet and Campiche. 3, Costate spiral portion, GPIT Ce 1221/2; Upper Albian, Col de Teine near Bonneville (Haute Savoie, France). *a*, Lateral, *b*, frontal view. 4, Tubercled spiral portion (cf. Collignon 1963, pl. 262, fig. 1141); Upper Albian (*Hysteroceeras binum* zone), Mt. Raynaud near Diégoc-Suarez (Madagascar). Lateral view; $\times 3$.
- Fig. 5. *Sc.* (*Sc.*) *collignoni* sp. nov. Holotype (cf. Collignon 1963, pl. 262, fig. 1142, sub *Sc. meriani*); same age and locality. *a*, Ventral, *b*, lateral, *c*, frontal view; $\times 3$.

All $\times 2$ unless otherwise stated.



1



3a



3b



2a



2b



4



5a



5b



5c



6a



6b



7

it is principally distinguishable through the presence of lateral mouth lappets, and an open whorled spiral portion. This makes a subfamily of its own necessary.

4. The origin of these 'Otoscapitinae' was presumed to be some scaphitid member, probably *Eoscapites*. Therefore the subfamily 'Otoscapitinae' was included in Scaphitidae.

We are extremely glad to have received, just before completing this manuscript, some interesting *Worthoceras* and '*Otoscapites*' of the Texan Cretaceous, through the kindness of Dr. P. U. Rodda. Only for this reason is it possible to comment on the above-mentioned suppositions.

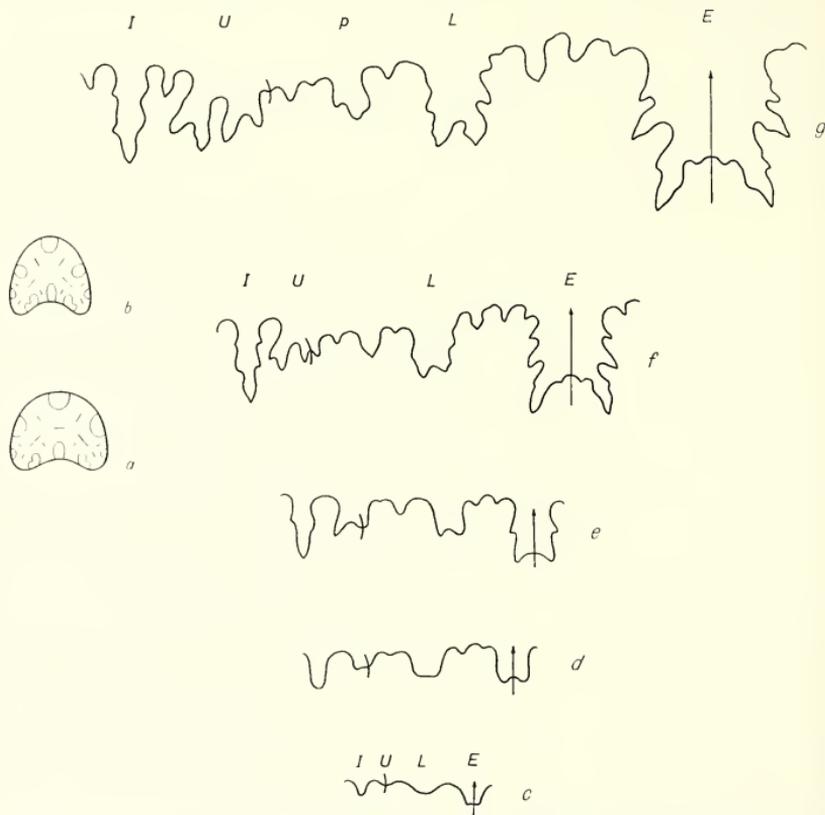
1. *Scaphites minutus* Moreman, here reproduced Pl. 58, fig. 5, text-fig. 6*b*, can neither be related to the European *Sc. bladenensis* nor included in Wright's genus *Otoscapites*. However, it is indistinguishable from the micromorph species *Sc. praecoquus* and *veterinovus* Cobban of the Western Interior Carlisle shale (Upper Turonian). Lateral lappets are also known from these forms, but Wright (1953, p. 474) indicates, that these are 'quite distinct from the type of lappets present' in *Otoscapites*. *Sc. minutus* makes it evident, however, that they are of the same type.
2. *Scaphites minutus* indeed agrees in its smaller size with the Turonian *Worthoceras gibbosum* Moreman, described from the same locality and here reproduced (Pl. 60, fig. 3, text-fig. 11*h*). But there is no further relationship between the two species, neither in sculpture, suture-line, nor in shape or septal surface of the spiral whorls.
3. We think that the arguments of lateral lappets, similar size and same occurrence are not important enough to retain the presumed relationship between *Worthoceras* and *Otoscapites*. This is indeed not surprising because:
4. *Worthoceras* absolutely differs in suture-line (text-fig. 11), sculpture and general appearance from all further scaphitids, and will be included here (p. 439) in Ptychoceratinae. *Otoscapites*, however, is a true *Scaphites* in all characteristic features. It is already represented in the Cenomanian and can thus be directly related to the fundamental genus *Eoscapites*.

In this way all problems concerning the subfamily 'Otoscapitinae' appear to be resolved. The results of a detailed study of *Worthoceras* may be anticipated here: As proven by its suture-line, lateral lobe, sculpture, and initial coil, *Worthoceras* is one of the common scaphitoid homoeomorphs, and should be completely separated from the family Scaphitidae. Therefore it is not treated here together with the early scaphitids, but with the convergent lineages (p. 439).

Otoscapites, however, cannot be separated from the *equalis* main stock. It agrees completely with true *Scaphites* in its suture-line (text-fig. 6*b*), septal surface (text-figs. 7*a*, *b*), and especially in its ontogenetic suture development (text-figs. 7, 8 to 15). The umbilical lobe becomes subdivided very early through the umbilical seam, where it remains throughout. *L* has a distinctly bipartite outline, and the median incision of *L/U* increases rapidly in size, and might be regarded as an independent element *p*. As pointed out above, its sculpture reflects that of the inner whorls of contemporaneous normal-sized species.

Thus we become confronted anew with the problem of parallel development in scaphitids. This question was largely treated above (p. 420), where the reason for the reduced

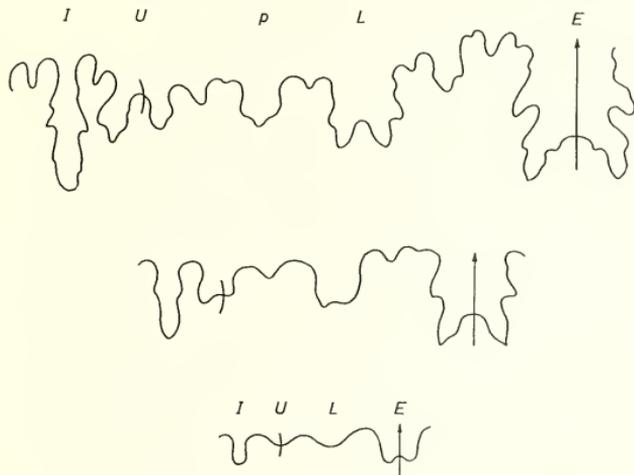
size of the *similaris* stock was found in geographic, probably ecologic factors. The European otoscapitids, however, are as well as the American pteroscaphitids of the same geographic and stratigraphic distribution as the normal-sized equivalents of the *equalis*



TEXT-FIG. 7. Suture development of *Sc. (Otoscapites) bladenensis* Schlüter, GPIT Ce 1221/14; Upper (?) Turonian, Postelberg. *a*, Septal surface at $h = 2.5$ mm, *b*, at $h = 5$ mm. *c-g*, Suture development, *g* at $h = 5$ mm.

stock. These reasons, the small size and the presence of mouth lappets in both lineages seem to be important arguments for the interpretation as sexual dimorphs. But besides these speculations we have more motives for the inclusion of the 'Otoscapitinae' in the genus *Scaphites*. In Wright *Otoscapites* represents a peculiar scaphitoid lineage, restricted to the Turonian and Coniacian. In reality, otoscapitids are traceable—like *Scaphites*—through the complete Upper Cretaceous. We note the presence of some micromorph species (*Sc. peroni* and *africanus* Pervinquière) in the Cenomanian of

Northern Africa (Pervinquière 1907, 1910; Sornay 1955), which are identical with otoscapitid inner whorls. Especially in *Sc. peroni* is the congruence so striking, that the Algerian species may merely represent a variety of *Sc. bladenensis*. The lateral ridges on the inner whorls are the same (Pervinquière 1910, pl. 2, fig. 10), as also the sculpture of the ultimate septate whorl (ibid., fig. 12). Even if we ignore the possibility of sexual dimorphism, all these species and probably also *Sc. evolutus* Pervinquière, can be traced back to *Eoscapites*, which is represented through the small-sized *E.? tenuicostatus* in the Cenomanian of Algeria. We believe that this derivation of *Otoscapites* is



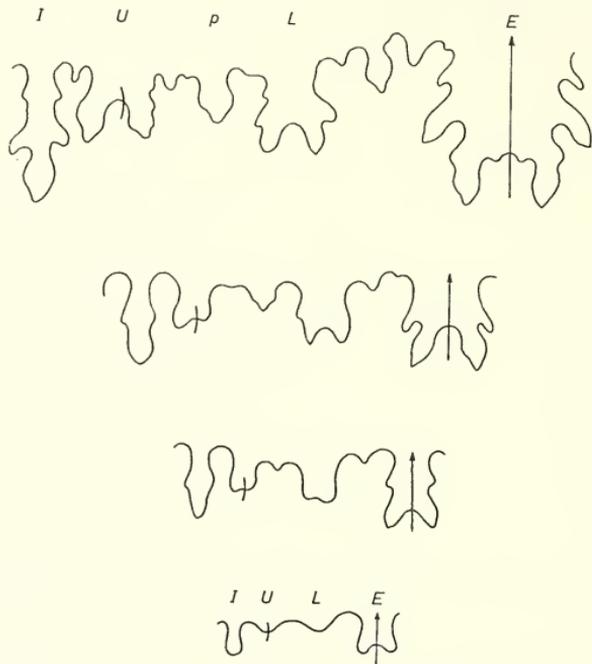
TEXT-FIG. 8. Suture development of *Sc. (Otoscapites) bladenensis* Schlüter, GPIT Ce 1221/16; Upper Turonian, Shasta County. Last suture at $h = 3$ mm.

by all means more natural, than that from some *Worthoceras* in the Texan Turonian. Moreover, *Otoscapites* can now be recorded from the European Campanian. *Sc. pachydiscoides* Wiedmann, previously doubtfully referred to *Pteroscapites* (Wiedmann 1962a, p. 217), can now be included in *Otoscapites* as here redefined. This species was found to be a true *Scaphites*, and therefore not included into the separate subfamily 'Otoscapitinae' in spite of its *bladenensis*-like sculpture. The recent position of *Otoscapites* is in complete accordance also with these previous observations.

Naturally we are unable at the moment to decide whether the otoscapitids are sexual micromorphs or not. It is likewise impossible to find out whether they represent merely a number of lateral offshoots from the main stock, or a completely different micromorph lineage. Regarding these facts and the clear relations to the true *Scaphites* in suture and sculpture, we propose to consider *Otoscapites* as merely a subgenus of the latter.

With *Scaphites puerculus* Jimbo (= *Sc. inermis* Anderson) we provisionally include in the present subgenus a peculiar form from the Japanese and Californian Upper

Turonian. It seems necessary to confine this species (*puerculus*) to the specimens figured by Jimbo (1894, pl. 5, fig. 4) and Anderson (1902, pl. 3, figs. 74-77). Yabe's presumed hypotypes (1910, pl. 15, figs. 20-22), however, belong to a different species, *Sc. (Otoscaphtes) yabei* sp. nov. (holotype: *Yezoites puerculus* in Yabe 1910, pl. 15, fig. 20), characterized by distinct concave ribs, ventrolateral tubercles, a high number of fine



TEXT-FIG. 9. Suture development of *Sc. (Otoscaphtes?) puerculus* Jimbo, GPIT Ce 1221/18; Upper Turonian, Shasta County. Last suture at $h = 2$ mm.

and dense secondary ribs on the venter, and a scaphitid living-chamber. In the true *Sc. puerculus* the ornamentation is very weak, nearly absent on the septate portion (Pl. 59, fig. 2). The sculpture of the living-chamber (Pl. 59, fig. 1) consists of weak primary ribs, which give rise to a high number of fine, sinuate secondary ones, at the centre of the lateral sides. The main characteristic of *Sc. puerculus* is the unusual living-chamber, which is only slightly uncoiled in the holotype. The adult form represented here for which I am also indebted to Professor Popenoe, can be regarded as an extreme variety with completely closed chamber of ammonitid coiling. Nevertheless, *Sc. puerculus* may belong to *Otoscaphtes sensu lato*, with which it agrees completely in suture-line and suture development (text-fig. 9).

Sc. perrini Anderson belongs to another group of small-sized scaphitids of the Pacific

area, which was referred to *Otoscaphtes* by Wright (1953, p. 476) and Matsumoto (1963). I will demonstrate that these forms, for which *Hyposcaphtes* nov. subgen. will be proposed, have nothing in common with *Otoscaphtes*, but are obviously related to *Pteroscaphites*.

The dimensions (in millimetres) of the otoscaphtid specimens reproduced here are:

	<i>Sc. (Otoscaphtes) bladensis</i>					
	<i>D</i>	<i>B</i>	<i>d</i>	<i>h</i>	<i>b</i>	<i>u</i>
GPIT Ce 1221/14	—	—	11.3	5 (0.44)	5 (0.44)	3.3 (0.29)
GPIT Ce 1221/16	—	—	7.5	3 (0.40)	3.2 (0.43)	3.2 (0.43)
	<i>Sc. (Otoscaphtes?) puerculus</i>					
GPIT Ce 1221/17	13.5	4.5	7.5	2.7 (0.36)	2.9 (0.39)	?
GPIT Ce 1221/18	—	—	7	2.8 (0.40)	2.8 (0.40)	2.5 (0.36)

Subgenus SCAPHITES (PTEROSCAPHTES) C. W. Wright 1953

Type species. Scaphites auriculatus Cobban.

The new genus *Pteroscaphites* was proposed by Wright for the group of micromorph species (*Sc. praecoquus*, *veterinovus*, *pisinnus*, *auriculatus* and *coloradoensis* Cobban) which parallel the true scaphitid stock in the Western Interior of the United States. The here reproduced holotype of Moreman's *Sc. minutus* (Pl. 58, fig. 5, text-fig. 6b) I regard as representative of this subgenus. It was regarded by Wright as a link between *Worthoceras* and *Otoscaphtes*, but it seems very near to the contemporaneous *Sc. veterinovus* and *Sc. auriculatus*, type species of *Pteroscaphites*.

The inner whorls are closely coiled, inflated to coronate, and generally provided with a weak lateral keel. This becomes lost with the beginning of the chamber. The latter coincides completely with the final hook which is distinctly separated from the coiled portion. Lateral and ventral lappets may be present on the mouth-border. The sculpture is similar to that of *Otoscaphtes*, consisting at first of lateral tubercles, and of an *equalis* like ribbing thereafter, which also approaches this lineage to the *equalis* main stock. The sculpture is generally reduced on the chamber (Pl. 58, fig. 5c). The suture (text-fig. 6b) is extremely similar to that of *Otoscaphtes*, likewise characterized by the fixation of *U* on the umbilical seam, and by a pronounced incision *p* in *L/U*. These elements and the lengthened saddle *L/U* make evident that there is no real relation to the worthoceratids, even to *W. gibbosum* (Pl. 60, fig. 3, text-fig. 11h). Shape and ornamentation of the spiral portion also differs considerably from that of *Worthoceras*, where the smoothness of the shells is an original feature, while it is a gerontic one in *Pteroscaphites*.

Despite the intimate relationship between *Ptero-* and *Otoscaphtes*, they are regarded here as different subgenera. In this way we receive a better idea of the surprising fact of parallel development in scaphitids, realized in completely the same manner in Europe and Northern America. This makes the interpretation as sexual dimorphism highly possible.

Sc. (Pteroscaphites) seems to be restricted to the Upper Turonian and Coniacian of Northern America. The specimen described recently by the present author as *Sc. (Pteroscaphites?) pachydiscoides* from the Spanish Campanian may be better referred to *Otoscaphtes*, as mentioned above.

Subgenus SCAPHITES (HYOSCAPHITES) subgen. nov.

Type species. Scaphites stephanoceroides Yabe 1909.

Description. Small-sized *Scaphites* with coronate whorl section. Lateral sides tubercled and keeled throughout. Homoeomorphous with *Astiericeras*. *U* subdivided, but fixed on umbilical seam. The genus includes *Sc. (H.) stephanoceroides* Yabe and *Sc. (H.) perrini* Anderson.

Remarks. *Sc. stephanoceroides* Yabe and *Sc. perrini* Anderson were included in 'Yezoites' by Yabe, but in reality they can directly be connected to the early pteroscaphitid *Sc. praecoquus* Cobban. In the latter species all characters of *Hyoscaphites* are foreshadowed: the spiral portion and the final hook are distinctly laterally keeled, while only on the straight shaft is the rounded whorl-section of all other scaphitids preserved. Therefore *Sc. praecoquus* remains in *Pteroscaphites* for the moment, but a definite decision is impossible. Both subgenera agree completely in their early ontogeny. The shape of the spiral portion, its involution and coronate whorl-section are the same in *Ptero-*, as in *Hyoscaphites*. But while in the latter this coronate section persists also on the body-chamber where the ribbing becomes more pronounced, in *Pteroscaphites* the chamber has a rounded whorl-section and decreasing sculpture. Thus *Hyoscaphites* becomes completely homoeomorphous with the Albian *Astiericeras* Parona and Bonarelli belonging to the douvilleiceratids.

The attribution of *Sc. perrini* to *Otoscaphtes* is artificial, based on the presence of lateral mouth lappets, which are also present, however, in *Pteroscaphites* and *Hyo-scaphites*. Because the proposed type species, *Sc. stephanoceroides* Yabe, never was described, a brief diagnosis will follow. *Hyoscaphites* seems to be restricted to the Upper Turonian and ? Coniacian of the Pacific border.

Sc. (Hyoscaphites) stephanoceroides Yabe

Plate 59, fig. 3; text-fig. 6a

1894 *Olcostephanus* sp., Jimbo, p. 33, pl. 9, fig. 3.

1909 *Scaphites stephanoceroides* Yabe, pp. 442, 443.

EXPLANATION OF PLATE 58

- Fig. 1. *Scaphites (Metascaphites) thomasi* Pervinquieré. Holotype (ex Pervinquieré 1907, pl. 4, fig. 31); Vraconian, Djebel Mrhila (Tunisia). *a*, Lateral, *b*, ventral view; $\times 2$.
- Figs. 2-4, 6. *Sc. (Otoscaphtes) bladenensis* (Schlüter). 2, Hypotype GPIT Ce 1221/14, intermediate to *Sc. (O.) cotta* (F. A. Roemer); Upper (?) Turonian, Postelberg near Priesen (Bohemia). *a*, Ventral, *b*, frontal, *c*, lateral view of phragmocone; $\times 3$, *d*, frontal, *e*, lateral view of pachydiscoid inner whorl; $\times 8$. 3, Typical hypotype, GPIT Ce 1221/15 (leg. Popenoe and Matsumoto), with straight body-chamber fragment, showing the sculptural change; Upper Turonian (Romaniceratan), Little Cow Creek valley (loc. 1512), Shasta County (California, U.S.A.). *a*, Lateral, *b*, ventral view; $\times 4$. 4, Characteristic inner whorl, in complete agreement with the holotype; GPIT Ce 1221/16 (leg. Popenoe and Matsumoto); same age and locality. *a*, Lateral, *b*, ventral, *c*, sagittal view; $\times 4$. 6, The small holotype (ex Schlüter 1872, pl. 10, figs. 5, 6); Upper (?) Turonian, Rote Mühle near Bladen/Leobschütz (Silesia). *a*, Frontal, *b*, lateral view; $\times 1$.
- Fig. 5. *Sc. (Pteroscaphites) minutus* Moreman. Holotype (cf. Moreman 1942, pl. 34, figs. 9, 10), BEGA coll. no. 19814; Lower Turonian (Eagle Ford group), 2-7 miles S. Britton, E. Midlothian highway, Ellis County (Texas, U.S.A.) *a*, Ventral, *b*, frontal, *c*, lateral view; $\times 3$; *d*, frontal, *e*, lateral view of phragmocone; $\times 5$.



1a



1b



2a



2b



2c



3a



3b



2d



2e



4a



5a



5b



5c



4b



4c



6a



6b



5d



5e

1910 *Yezoites perrini* Anderson; Yabe, p. 172, text-fig. 3, pl. 15, figs. 28, 29.

1963 *Otoscaphtes perrini* (Anderson) (?); Matsumoto, p. 46, pl. 68, fig. 3.

Holotype. The specimen figured originally as '*Olcostephanus sp.*' in Jimbo 1894, pl. 9, fig. 3, and reproduced by Yabe (1910, pl. 15, fig. 29) and here Plate 59, fig. 3, text-fig. 6a. Probably lower part of Upper Yezo group (= Upper Turonian) from Pombets valley, Ishikari province, Hokkaido.

Description. Small *Scaphites* with coronate whorl-section throughout. Distinct lateral keel persisting and tuberculate. These lateral tubercles give rise to two or three strong ribs which pass radially venter. Mouth-border with elongated lateral lappets, covering a great part of involute initial spire.

Remarks. *Sc. stephanoceroides* was proposed for '*Olcostephanus sp.*' in Jimbo by Yabe (1909) in a footnote generally overlooked. One year later the name was abandoned by Yabe (1910, p. 172) himself, who included the Japanese material, in spite of obvious differences, in '*Yezoites perrini* Anderson. The Hokkaido specimens were referred to the same species also in the subsequent literature, but in the reproduction of Jimbo's plates by Matsumoto (1963, p. 46) with a query. This was indeed reasonable, and we propose to separate the Japanese forms, and to renew Yabe's species name. While in *Sc. perrini* the whorl section is much more rounded and the venter remains nearly smooth, in the Japanese forms the whorl section is more compressed, the lateral angle sharpened, and the venter passed by strong bi- or triplicate ribs (Pl. 59, fig. 3a). I figure for comparison a body-chamber fragment of *Astiericeras astierianum* (Pl. 59, fig. 4), which demonstrates the nearly complete homoeomorphy between these two species. By means of the suture-lines the species are well distinguishable (text-fig. 6a, 13).

Once more the striking sutural congruence of all scaphitid micromorphs is noticeable (text-figs. 6-9). The similarity of the suture-line of *Oto*-, *Meta*-, *Ptero*-, and especially of *Hyposcaphtes* consists in the position of *U* on the umbilical seam, which evidently can be regarded as a common feature of the dwarfed scaphitid lineages. They are extremely near one to the other as well as to *Scaphites*, and are included therefore as subgenera into the comprehensive genus *Scaphites*. *Sc. stephanoceroides* is known only from the Upper Turonian of Hokkaido, but it may pass also into the Coniacian (Yabe 1910).

THE SCAPHITID HOMOEOMORPHS AND THE SCAPHITID ORIGIN

Before the principles of scaphitid development and the new systematics of this group can be treated, the different homoeomorphs and the problem of scaphitid origin need to be discussed briefly.

Macroscaphites. That there is no real relationship between *Scaphites* and *Macroscaphites* of Barremian/Aptian age, as was believed by the early authors, has been known for a long time. It is interesting that *Macroscaphites* (text-fig. 13) in respect of suture-line and initial coil is indistinguishable from the true lytoceratid genus *Costidiscus*. Therefore it remained connected with the latter within Lytocerataceae, despite its uncoiled living-chamber. That this co-ordination is indeed reasonable becomes clear, if we compare the suture-line with that of lytoceratids and heteromorphs respectively. While in all lytoceratid heteromorphs the second umbilical lobe (U_2) is reduced, it is generally retained

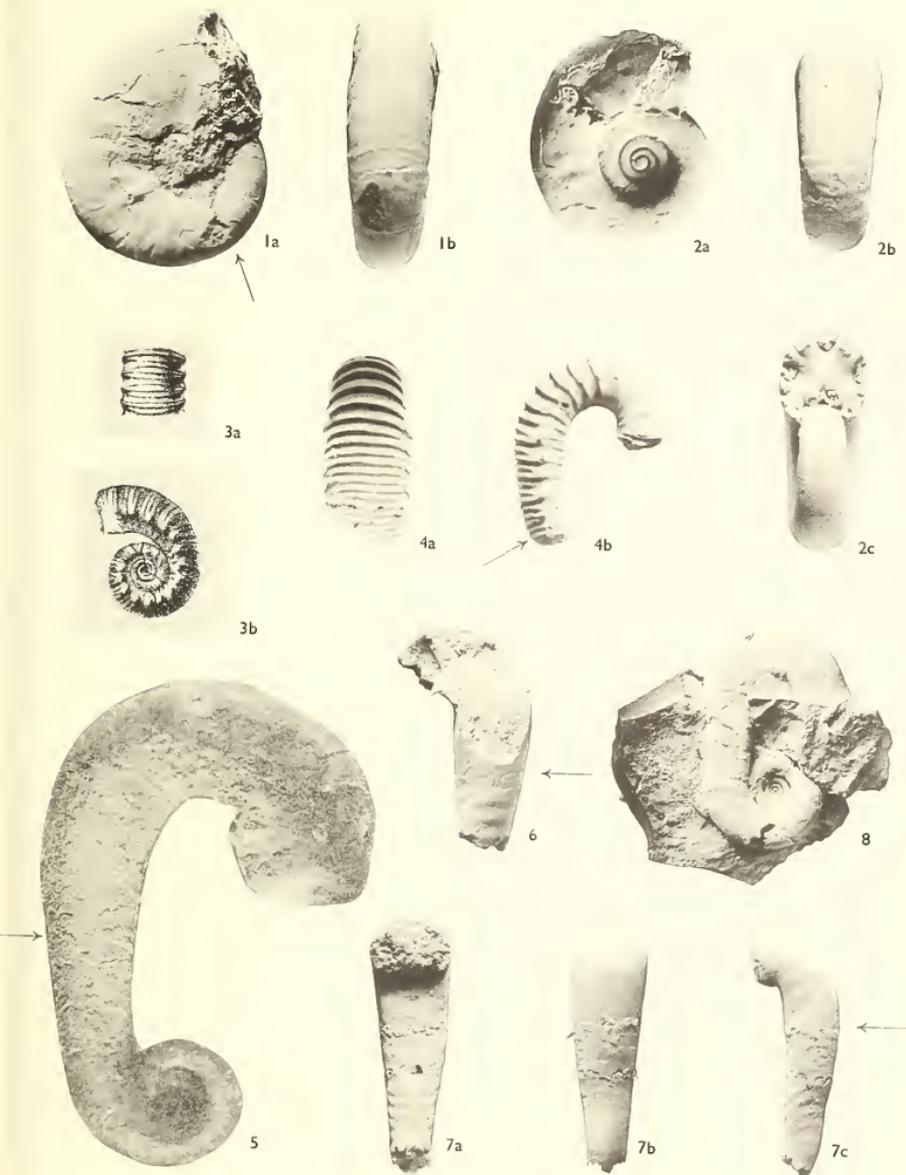
in the true *Lytoceras*. In *Costidiscus* and *Macroscephites* two umbilical lobes are preserved, and, moreover, the suture remains highly incised. In *Scaphites*, however, the suture is quadrilobate throughout and simplified as in all other heteromorphs. This is the strongest argument against the occasionally presumed relationship between the two genera separated by an evident time gap. In regard to the scaphitid micromorphs it seems noticeable, that Uhlig (1883, p. 206) was also able to recognize a greater and smaller variety in the scaphitoid homoecomorph *Macroscephites yvanni*. The smaller specimens with somewhat stouter final hook, were always found together with the greater-sized forms in the ratio 1:1. This fact was interpreted by Uhlig as sexual dimorphism.

Other lytoceratids. With exactly the same argumentation, the presence of more than one umbilical lobe, the general supposition of a scaphitid origin in any other true lytoceratid may be rejected (Spath 1934, Wright 1957), where not only in *Costidiscus* but also in *Gabbioceras* and *Jauberticeras* (text-fig. 13) convergent shell-types are developed. The resemblance between some of those species and the initial coil of *E. subcircularis* is striking. But in *Gabbioceras* two umbilical lobes are developed, in *Jauberticeras* even three, of which two are highly differentiated through their position on the umbilical seam, respectively the lateral keel. Thus we note in *jauberticeratids* a progressive tendency of suture development, and no suture reduction which is necessary for the derivation of *Scaphites*.

Astiericeras. '*Scaphites*' *astierianus* d'Orbigny of Middle Albian age has the greatest affinity to some early scaphitids, especially to *Sc. (H.) stephanocerooides*. This becomes evident through the living-chamber fragment from Quenstedt's collection, here reproduced (Pl. 59, fig. 4). This fragment is somewhat intermediate between the typical specimen with biplicate ribs (Parona and Bonarelli 1897, pl. 14, fig. 10), and the form with strong single ribs as represented by Quenstedt (1847/8, pl. 21, figs. 14a, b). Here the suture-line is also the decisive element. As visible in text-fig. 13, the complete suture-

EXPLANATION OF PLATE 59

- Figs. 1, 2. *Scaphites (Otoscephites?) puerculus* Jimbo. 1, Hypotype GPIT Ce 1221/17 (leg. Popenoe and Matsumoto), with normal coiled body-chamber; Upper Turonian (Romaniceratan), Little Cow Creek valley (loc. 1512), Shasta County (California, U.S.A.). a, Lateral, b, ventral view; $\times 3$. 2, Septate hypotype, GPIT Ce 1221/18 (leg. Popenoe and Matsumoto); same age and locality. a, Lateral, b, ventral, c, frontal view; $\times 5$.
- Fig. 3. *Sc. (Hyposcephites) stephanocerooides* Yabe. Holotype (ex Jimbo 1894, pl. 8, fig. 3, sub *Olcostephanus* sp.); (Coll. Geol. Inst. Univ. Tokyo); Upper Turonian?, Pombets valley (Ishikari province, Hokkaido). a, Ventral, b, lateral view. $\times 1$.
- Fig. 4. *Astiericeras astierianum* (d'Orbigny). Quenstedt's suture specimen, GPIT Ce 3/21/14d; Lower Middle Albian, Escragnoles (Var, France). a, Ventral, b, lateral view; $\times 1$.
- Fig. 5. *Worthoceras platydorsum* (Scott). Holotype (ex Scott 1924, pl. 5, fig. 4; Adkins 1928) (Mus. Tex. Christ Univ.); Upper Albian, Upper Duck Creek, N. Denison, Grayson County (Texas, U.S.A.). Lateral view, $\times 10$.
- Figs. 6, 7. *Worthoceras worthense* (Adkins). 6, The fragmentary holotype, partly septate (cf. Adkins 1920, pl. 2, fig. 26, sub *Hamulina*), Bega 20994; Upper Albian (Pawpaw form.), Forth Worth, Tarrant County (Texas, U.S.A.). Lateral view, $\times 5$. 7, Hypotype BEGA 20995, shaft without dorsal impression and partly septate; same locality. a, Dorsal, b, ventral, c, lateral view; $\times 4-5$.
- Fig. 8. *Worthoceras vermiculum* (Shumard). Hypotype with nearly unlappeted mouth-border, BEGA 35392; Lower Turonian (Eagle Ford group), Ellen Fork, Trinity River at St. Louis/Sta Fé Railroad bridge, Dallas County (Texas, U.S.A.). Lateral view, $\times 2$.



line of *Astiericeras astierianum* (GPIT Ce 3/21/14d) contains two distinct umbilical lobes, while *L* becomes subdivided into two different 'lobes', as it is characteristic for all douvilleiceratids. Thus no comparison with the hyposcapitid suture is possible. *Astiericeras* indeed represents no more than a striking homoeomorph with some specialized scaphitids. It is regarded as a direct descendant of the ammonitid genus *Douvilleiceras*.

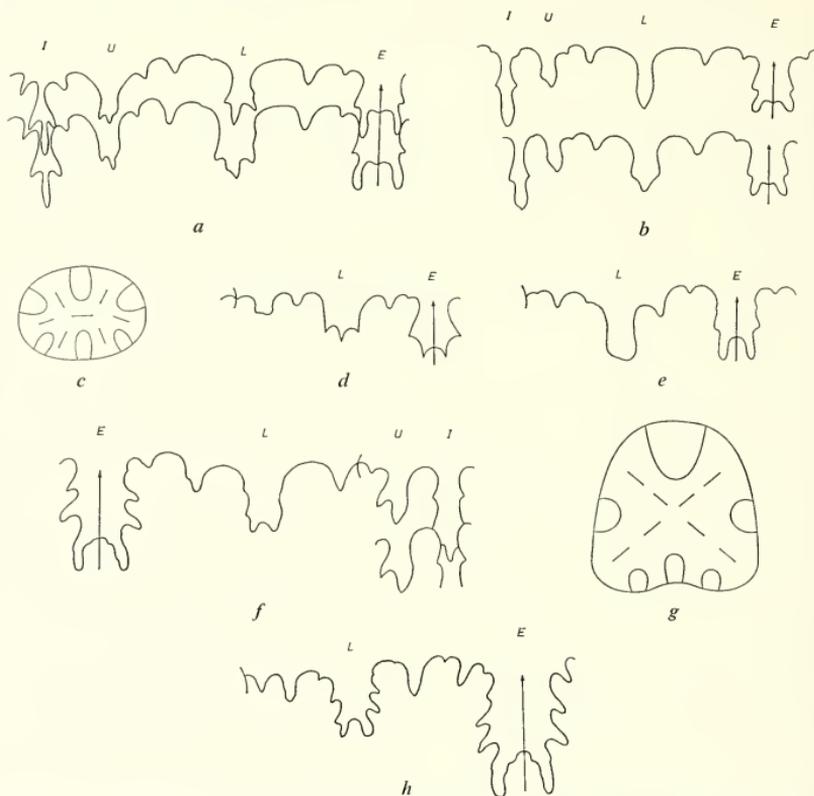
Worthoceras. Its systematic position and relationship to *Scaphites* is at the moment the most difficult problem, because *Worthoceras* was included in Scaphitidae and regarded as a direct ancestor of *Otoscaphtes* by Wright. It is evidently a New World form and has only occasionally been recognized in Europe, Northern Africa (?), and Madagascar. The different species which were separated in the Upper Albian, Cenomanian, and Turonian are merely distinguishable by their general appearance. They are of small size, nearly unsculptured, and with one exception provided with a completely open whorled initial coil. This is followed by a long straight shaft with flat, subparallel flanks and a distinctly impressed dorsum, which terminates in a final hook with occasionally lapped mouth-border.

The main distinguishing feature in *Worthoceras* is again the suture-line (text-figs. 10a, b, d-f, h), consisting of four narrow lobes, among them a distinctly trifold *L* and an undivided small *U*, despite the presence of a distinct dorsal impression. Also the septal surface (text-figs. 10c, g) preserves the simple, hamitid type. But there are more arguments against Wright's connexion of *Worthoceras* and *Eoscaphtes*.

The first representatives of the genus are *W. platydorsum* (Scott) (here Pl. 59, fig. 5) and *W. worthense* (Adkins), of which the holotype (Pl. 59, fig. 6, text-fig. 10a) and a further specimen are reproduced here (Pl. 59, fig. 7, text-figs. 10b, c). It may be mentioned that the last mentioned species was at first included by its author (Adkins 1920) in *Hamulina*. Later it was separated by the same author (Adkins 1928) in a new genus, *Worthoceras*, of 'uncertain position'. Both species are restricted to the Upper Albian of Texas, where *Eoscaphtes* is unknown up to the present. The distinct trifold outline of *L*, the undivided element *U*, the general character of the quadrilobate suture-line (text-fig. 10), and the originally flat and not impressed dorsum (Pl. 59, fig. 7a), make a heteromorph ancestor of *Worthoceras* evident. The ptychoceratids especially have nearly a world-wide distribution in the Albian, where they are represented by unsculptured dwarfed forms with trifold lateral lobes. Of further importance for this presumed attribution and the separation from *Eoscaphtes* is the fact that the phragmocone in early *Worthoceras* does not coincide with the spiral portion, as it does in *Eoscaphtes*. Generally almost all of the straight shaft is septate, as visible in the reproduced type material (Pl. 59, figs. 5-7). Moreover, no umbilical perforation is known from *Worthoceras*.

In Europe, the centre of the scaphitid development, only one worthoceratid species is known: *W. rochatianum* (d'Orbigny) of Cenomanian and Turonian age (Pl. 60, figs. 4-6). This species is barely distinguishable from the Albian *W. platydorsum* (Pl. 59, fig. 5). Even in regard to the sculpture, when it is preserved (Pl. 60, figs. 5b, 6a), it agrees with the forms of the Texan Albian. The suture-lines were found to be in accordance also; likewise in *W. rochatianum* (text-fig. 10d) they contain a distinctly trifold *L* and slightly enlarged saddles. The shaft is likewise septate (Pl. 60, fig. 4b). The only noticeable distinction is the dorsal impression (Pl. 60, fig. 4a), which is much more pronounced

than in the preceding species. It can perhaps be regarded as a reminiscence of the ptychoceratid ancestor, where the smaller shaft generally remains strongly impressed in the dorsum of the larger one.



TEXT-FIG. 10. *Worthoceras*. *a-c*, *W. worthense* (Adkins). *a*, The last suture-lines of the holotype, BEGA 20994; Upper Albian, Fort Worth. *h* = 3 mm. *b*, Last suture-lines, and *c*, Septal surface of hypotype, BEGA 20995; same locality. *h* = 2 mm. *d*, *W. rochatianum* (d'Orbigny), external suture of Madagascan hypotype (ex Collignon 1929, text-fig. 36); Cenomanian, Diégo-Suarez. $\times 8$. *e-g*, *W. vermiculum* (Shumard). *e*, Last suture of neotype (Moreman 1942), BEGA 19827; Lower Turonian, Britton. *h* = 3 mm. *f*, Last suture, and *g*, Septal surface of hypotypoid BEGA 35390; Lower Turonian, Dallas County. *h* = 3 mm. *h*, *W. gibbosum* Moreman, holotype, BEGA 19812; Lower Turonian, Britton; external suture at *h* = 4.5 mm.

Likewise the following species, the Lower Turonian *W. vermiculum* (Shumard) (here Pl. 59, fig. 8; Pl. 60, figs. 1, 2), is barely distinguishable from the forms described above. The spiral portion remains open whorled, the suture-line (text-figs. 10e, f) quadrilobate, the shell smooth and the final hook flat-sided and tender. In the septal

surface (text-fig. 10g) the simple configuration of the ptychoceratids is preserved. The differences concern the somewhat stouter final crozier, the shaft which is septate only in its lower part, the nearly bifid *L*, and especially the lateral mouth lappets perceptible only in this species.

The attribution of *W. gibbosum* Moreman of the Texan Lower Turonian to the present genus seems more difficult. The holotype, here reproduced (Plate 60, fig. 3, text-fig. 10h), has the general appearance of a true *Scaphites*, with a stout and inflated final hook which nearly touches the moderately involute spiral portion. The latter coincides with the septate whorls. Finally the suture, with its distinct bifid *L*, seems to belong to a true *Scaphites*. Therefore *W. gibbosum* was interpreted as a transitional form between *Worthoceras* and *Scaphites minutus* Moreman.

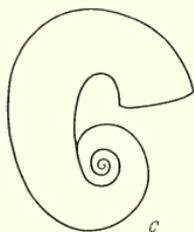
As indicated above, the latter species is a true *Scaphites* indeed, belonging to a group of dwarfed (and lappeted) forms which are separated from the *equalis* main stock as a distinct subgenus *Pteroscaphites*. After study of *W. gibbosum* we come to the following conclusion, that this species in all its characters belongs to *Worthoceras* and cannot be connected with *Sc. minutus* nor with any other known *Scaphites*. If we compare the suture-line (text-fig. 11h), the septal surface (Pl. 60, fig. 3a) and the ornamentation of the spiral coil (Pl. 60, fig. 3b) with that of its presumed descendant *Sc. minutus* (Pl. 58, figs. 5d, e; text-fig. 6b) or with the otoscapitid type species (Pl. 58, figs. 2-4; text-figs. 7, 8), then the fundamental differences become obvious. Unfortunately the internal suture-line is not exposed in the Texan forms, but it is possible to interpret it from the external portion and septal surface. As mentioned many times, all scaphitid micro-morphs are characterized through the position of the subdivided *U* on the umbilical seam and the importance of the median incision *p*. In *W. gibbosum* we find nothing comparable. Alone a small undivided *U* can be recognized, which remains in the internal suture, and the median incision of *L/U* does not increase in size. The initial coil of *Sc. minutus* is nearly closed and passes (as in all other *Ptero-* and *Otoscapites*) through an inflated pachydiscooid stage. The initial whorls of *W. gibbosum* remain well exposed and completely smooth as in all other *Worthoceras* species. Finally no lateral lappets can be observed on the mouth-border, which, on the other hand, are well developed in *Ptero-* and *Otoscapites*. It is therefore impossible to connect *Worthoceras* with any scaphitid member despite their striking homoeomorphy.

This is less surprising if we regard the phylogenetic position of *Worthoceras*. Its very slow evolutionary trend, which we intentionally demonstrated here in all details, makes it evident that the genus represents a phylogenetic end form. *Scaphites* is able to compete with the contemporaneous ammonites through genetic regeneration and the development of a high number of lateral offshoots, whereas *Worthoceras* is evidently unable to regenerate and thus does not pass the Turonian/Coniacian boundary. Regarding these reasons it might be better to place *Worthoceras* into Ptychoceratinae, as recently defined by me (Wiedmann 1962b).

The measurements (in millimetres) of some *Worthoceras* here represented are:

	<i>Worthoceras rochatianum</i>					
	<i>D</i>	<i>B</i>	<i>d</i>	<i>h</i>	<i>b</i>	<i>u</i>
MHNG Wi 'Sc'/10	20	4	6.8	2.8 (0.41)	2.5 (0.37)	2.6 (0.38)
MHNG Wi 'Sc'/11	—	—	7.0	3.0 (0.43)	2.5 (0.36)	3.0 (0.43)
MHNG Wi 'Sc'/12	—	—	7.0	3.0 (0.43)	2.7 (0.38)	2.8 (0.40)

	<i>Worthoceras vermiculum</i>					
	<i>D</i>	<i>B</i>	<i>d</i>	<i>h</i>	<i>b</i>	<i>u</i>
BEGA 19827	14	4.4	7.0	3.0 (0.43)	3.0 (0.43)	2.8 (0.40)
BEGA 35390	15	?4.0	6.5	2.8 (0.43)	2.7 (0.42)	2.7 (0.42)
BEGA 35392	17.5	5.1	9.5	3.8 (0.40)	?	3.2 (0.34)
	<i>Worthoceras gibbosum</i>					
BEGA 19812	17.5	7.8	10	4.5 (0.45)	5.2 (0.52)	3.0 (0.30)



TEXT-FIG. 11. The trend of worthoceratid development. $\times 2$. *a*, *W. platydorsum* (Scott), *b*, *W. vermiculum* (Shumard), *c*, *W. gibbosum* Moreman.



TEXT-FIG. 12. The presumed development of the labeceratids. $\times 0.25$. *a*, *Labeceratids*, *b*, *Ellipso-ceras*, *c*, *Myloceras*.

Finally we note the tendency to re-coil in *Worthoceras* (text-fig. 11), which seems to be a common trend in all Cretaceous heteromorphs (Cobban 1952, text-fig. 2; Casey 1960, text-fig. 5; Wiedmann 1962*b*, text-fig. 35; and here text-figs. 12 and 14).

Labeceratidae. The systematic position of the family Labeceratidae, included in Saphitaceae by Spath, Wright and others, was discussed on a previous occasion (Wiedmann 1962b, p. 98). This restricted group of Upper Albian forms, known only from the Southern hemisphere, was characterized by the following features:

1. Sculpture, especially in the primitive representatives, is hamitid; but it becomes rapidly anisoceratid through the development of umbilical and marginal tubercles.
2. Mode of uncoiling is hamitid/crioceratid at first, the middle-aged whorls are sometimes in contact, followed by a straight septate shaft and a scaphitoid final hook with lapped mouth-border. These are the unique similarities with *Scaphites*.
3. Suture-line consists of only four elements; *U* remains simple and undivided, and is trifid like *L*; the saddles are normal sized (text-fig. 13).

The lineage *Labeceras*-*Ellipsoceras*-*Myloceras* (text-fig. 12) represents, if correct, a further example for the general trend of many heteromorphs to re-acquire the original mode of coiling. This mode of uncoiling, the sculpture and especially the sutural characters are exactly the same as in some early *Anisoceras* like *Metahamites* or *Idiohamites*. *Hamitoides*, included in Labeceratidae by Spath and Wright, and perhaps the origin of the stock, is in all its characters a true *Anisoceras*. Therefore Labeceratidae were reduced to subfamily rank and included in Anisoceratidae by the author (1962b, p. 99). The reference of *Labeceras* to Hamitidae by Whitehouse (1926, p. 226) was found to be more correct than the attribution to the lytoceratid or scaphitid stock by Spath.

Zuluscaphites. This genus was established by van Hoepen (1955) on a single ammonitid spiral portion of Middle Albian (?) age. Its lateral lobe is trifid and no scaphitid living-chamber is known. It is impossible to regard a form with these negative characters as the source of the always later appearing *Scaphites*. I believe that *Zuluscaphites* merely represents a lyelliceratid inner whorl (Wiedmann 1962a, p. 209).

Other ammonitids with uncoiled body-chamber. True ammonitids with scaphitoid living-chamber are very common. They are represented in the Jurassic, with forms like the stephanoceratid genus *Kheraites* (text-fig. 13) or the oppeliid *Proscaphites*, as well as in the Cretaceous. Here especially in the acanthoceratids *Vascoceras*, *Fallotites* (text-fig. 13), *Pseudotissotia* and *Texasia*, the uncoiling of the body-chamber is a common feature. All these forms are evidently connected with the acanthoceratid stock, and cannot lead to *Scaphites* because of the presence of three or more umbilical lobes. The same difference can be stated for *Bimneyites* which has recently been referred to Haplocerataceae by Wright in Casey (1961, p. 118). Already the external suture-line (text-fig. 13) is completely different from the scaphitid one.

No real relationship to *Scaphites* can be recognized in the above-mentioned lytoceratids, heteromorphs, and ammonitids of scaphitoid appearance. In the eoscapitid species the presence of an umbilical perforation and the absence of a dorsal impression was demonstrated. Therefore it seems that we can find the true scaphitid ancestor among the uncoiled heteromorphs. This presumption is supported through the fact, that in all early scaphitids the suture-line consists only of four elements. Not only in *Eoscapitites* and early scaphitid ontogeny can the quadrilobate suture-line be stated, but it remains simplified throughout during the ontogeny of all scaphitids studied here. The presumed regeneration of three or four umbilical lobes in *Scaphites* cannot be accepted. *Scaphites*

is in its sutural characters a true heteromorph member. It should no longer be regarded as a degenerate offshoot of normal coiled ammonites; it is a hamitid heteromorph with the repeatedly noted trend to secondary re-coiling.

The similarity is striking if we compare the suture-line of *E. circularis* with that of contemporaneous hamitids, especially the Upper Albian *Plesiohamites* ('*Lytohamites*') *similis* (Casey). This form also agrees in sculpture and mode of uncoiling so completely, that the separation from *Eoscaphtes* seems to me to be more than arbitrary. If the biogenetic rule is of any phylogenetic significance, then the slender initial whorls of *Eoscaphtes* point to an also very slender hamitid species, of upper Middle Albian age, *Hamites tenuis*. This species is stratigraphically directly followed by the first *Eoscaphtes*, at the base of the English Upper Albian.

It might be added here, that the possibility of a hamitid source for *Scaphites* was briefly discussed but also abandoned by Spath (1942, p. 717), and therefore neglected thereafter.

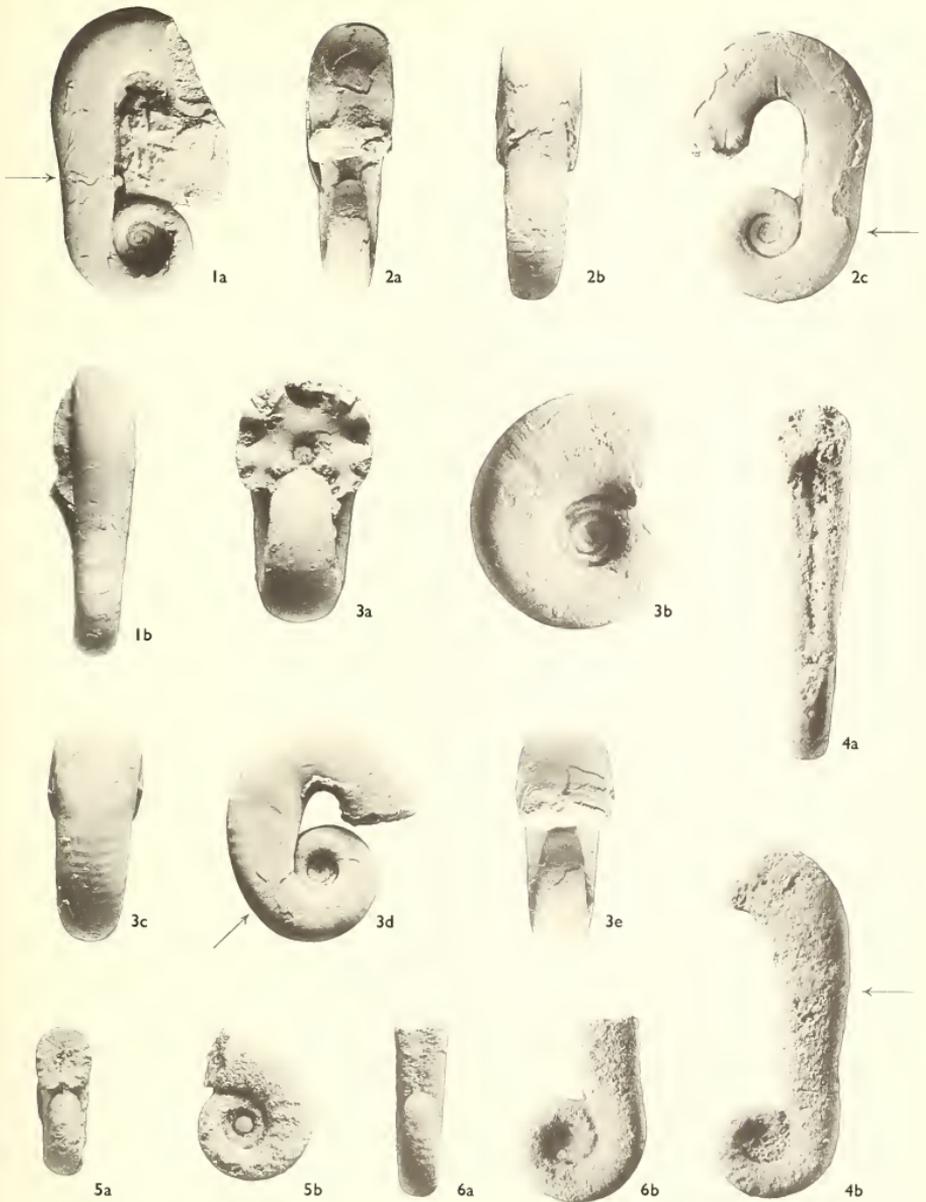
THE PRINCIPLES OF SCAPHITID DEVELOPMENT

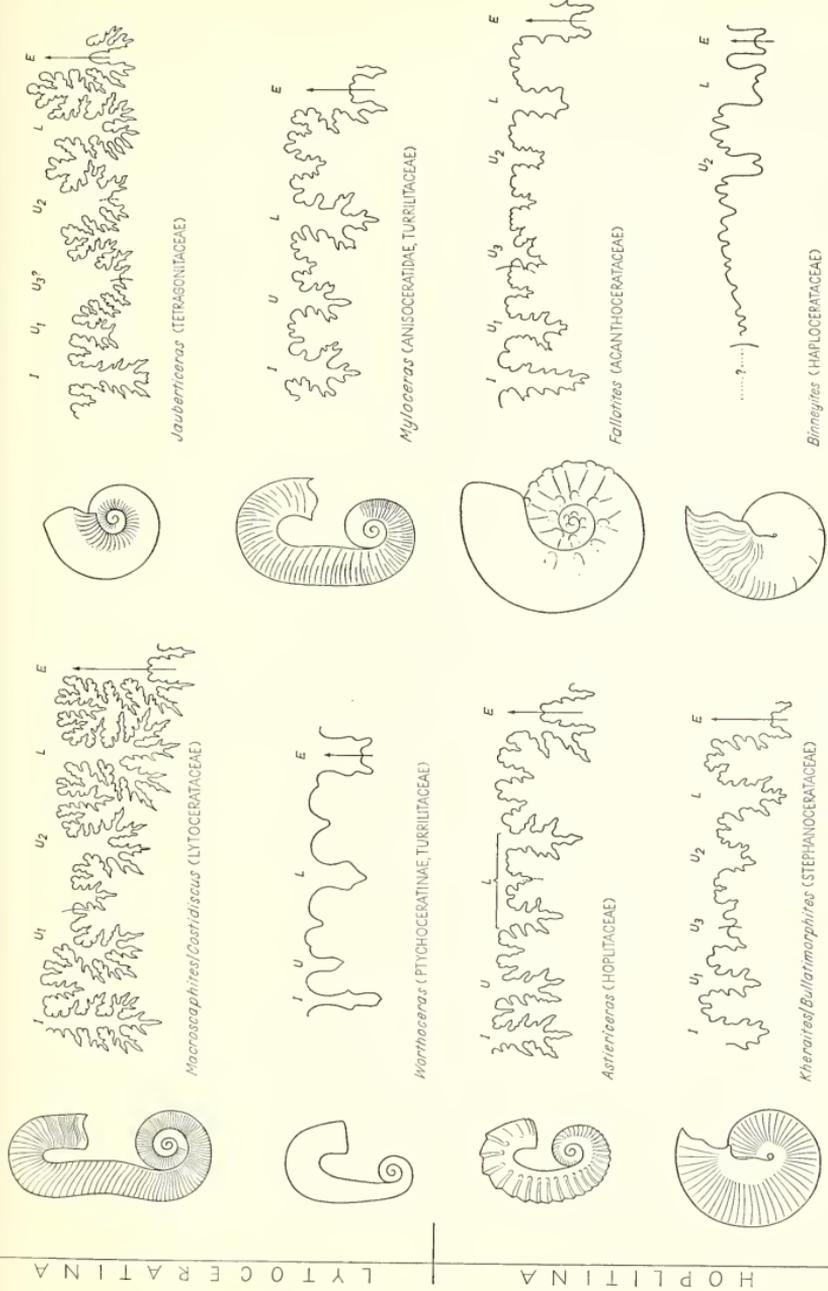
Having pursued the early scaphitid development step by step from the base of the Upper Albian, we have reached not only an idea of the principles of scaphitid development, but also the solution to some of the problems of interest here. It has been possible to demonstrate that there is no difficulty in connecting the ostensibly different suture types of *Eoscaphtes* and *Scaphites*. Schindewolf doubted that the quadrilobate suture-line which exists throughout in *Eoscaphtes* could be compatible with that of true scaphitid species from the uppermost Senonian. In the early ontogeny five lobes were stated to occur in these forms, and seven in the adult stage (Schindewolf 1961, text-fig. 58). As text-fig. 14 shows, the first eoscaphtid species from the basal Upper Albian and the latest Maastrichtian scaphitids are connected by continuous transitions in the sutures. We therefore have to conclude that also in the late *Scaphites* not more than four lobes (*I*, *U*, *L*, and *E*) are present. The presumably regenerated umbilical lobes are in reality the secondary saddle incisions of *L/U*, and therefore named pseudolobes (*p*). This becomes underlined, when we consider the ontogenetic suture development (text-figs. 7-9, 15). Here the questionable elements always remain outside of the umbilical seam,

EXPLANATION OF PLATE 60

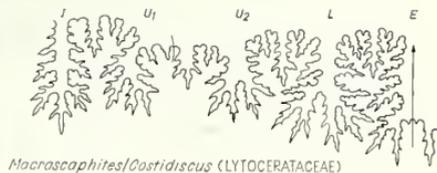
- Figs. 1, 2. *Worthoceras vermiculum* (Shumard). 1, Hypotype BEGA 35390; Lower Turonian (Eagle Ford group), Ellen Fork, Trinity River at St. Louis/Sta Fé-Railroad bridge, Dallas County (Texas, U.S.A.). The mouth-border seems unappetted; the first half of the shaft is septate. *a*, Lateral, *b*, ventral view. 2, The neotype with preserved mouth-border; proposed by Moreman (1942, pl. 34, figs. 12, 13), BEGA 19827; Lower Turonian (Eagle Ford group), 2.7 miles S. Britton, E. Midlothian highway, Ellis County (Texas, U.S.A.). *a*, Frontal, *b*, ventral, *c*, lateral view.
- Fig. 3. *Worthoceras gibbosum* Moreman. Holotype BEGA 19812 (cf. Moreman 1942, pl. 34, figs. 7, 8); same age and locality. *a*, Frontal, *b*, lateral view of smooth phragmocone; $\times 4$; *c*, ventral, *d*, lateral, *e*, frontal view; $\times 2$.
- Figs. 4-6. *Worthoceras rochatianum* (d'Orbigny). 4, Hypotype MHNG Wi 'Sc'/10, nearly complete, shaft is partly septate; Upper (?) Turonian, Uchaux (France). *a*, Frontal view with distinct dorsal impression, *b*, lateral view (leg. Rochat). 5, Hypotype with weak ribs, MHNG Wi 'Sc'/12 (leg. Rochat); same locality. *a*, Frontal, *b*, lateral view. 6, Hypotype MHNG Wi 'Sc'/11, with part of straight shaft; (leg. Rochat); same locality. *a*, Frontal, *b*, lateral view.

All $\times 3$ unless otherwise stated.

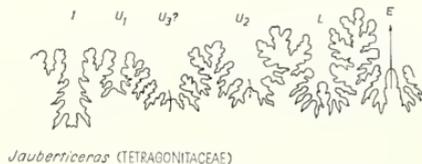




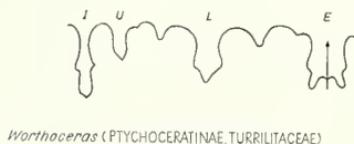
TEXT-FIG. 13. The scaphitoid homomorphs.



Macroscaphites/*Costidiscus* (LYTROCERATACEAE)



Jauberticeras (TETRAGONITACEAE)



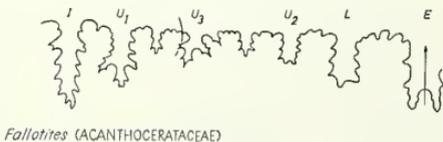
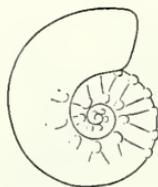
Worthoceras (PTYCHOCERATINAE, TURRILITACEAE)



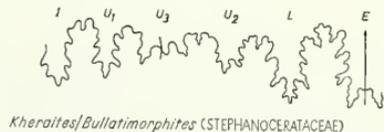
Myloceras (ANISOCERATIDAE, TURRILITACEAE)



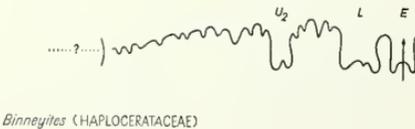
Astiericeras (HOPLITACEAE)



Fallotites (ACANTHOCERATACEAE)



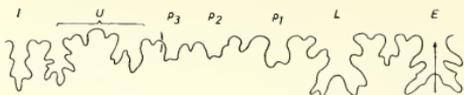
Kheraites/*Bullatimorphites* (STEPHANOCERATACEAE)



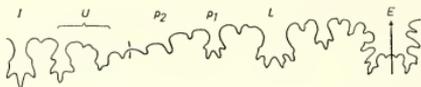
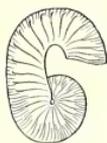
Binneyites (HAPLOCERATACEAE)

TEXT-FIG. 13. The scaphitoid homoeciomorphs.

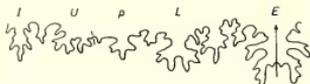
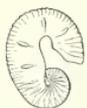
TURONIAN-MAASTRICHTIAN



Hoplasc. constrictus



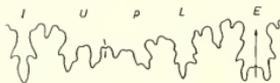
Sc nigricollensis



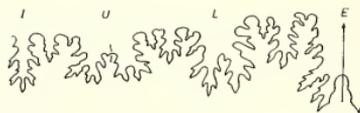
Sc equalis



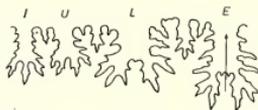
Sc obliquus



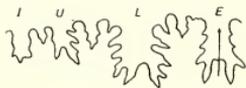
Sc simplex



Eosc. subcircularis



Eosc. circularis



Hamites tenuis

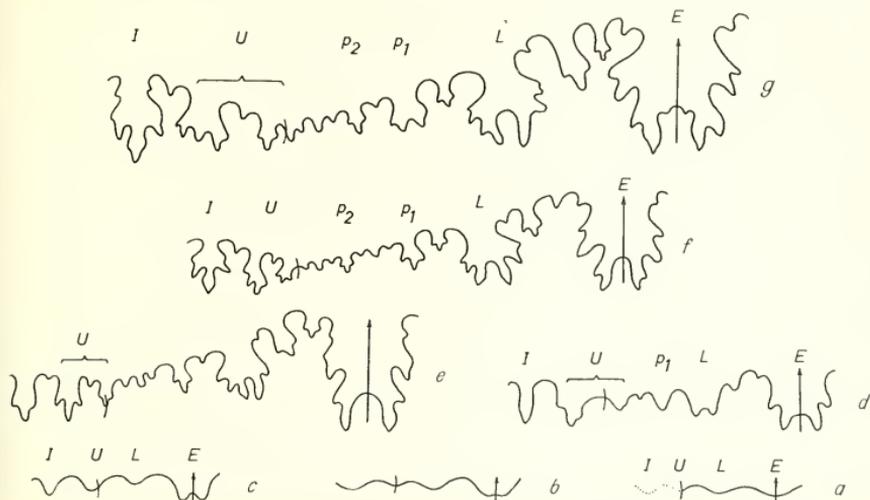
CENO MAN IAN

U P P E R A L B I A N

TEXT-FIG. 14. The scaphitid development.

where true umbilical lobes are generally produced. The suture development of the Campanian *Sc. hippocrepis* (Dekay) as given by Reeside (1927*b*), can now be shown precisely in the manner illustrated here (text-fig. 15).

Here the extreme lengthening of the external saddles, and the gradual increase of saddle incisions to lobe size, are the most obvious characters of the scaphitid suture development. Another important systematic feature is the element *U*, which becomes



TEXT-FIG. 15. The suture development of a late scaphitid species, *Sc. (Sc.) hippocrepis* (Dekay) (after Reeside 1927*b*, pl. 15); Campanian, Big Horn County.

divided by the umbilical seam at first (text-fig. 15*d*). Thereafter the two different branches become more and more separated, and pass to the internal suture-line (text-figs. 15*e*, *f*). *U* remained fixed on the umbilical seam only in the micromorphs, as in some primitive Albian forms. In the adult stage of the Upper Cretaceous forms (text-fig. 15*g*) a greater number of umbilical lobes are feigned. Naturally we come to wrong conclusions, if we pay exclusive attention to them. However, if we trace the suture development ontogenetically (text-fig. 15) and phylogenetically (text-fig. 14), we can easily recognize that the so-called umbilical lobes are merely the incisions ($p_1, p_2 \dots$) of the lengthened saddle *L/U*. Also the species with a 'trifid' lateral lobe should not be regarded exclusively. We have seen that there are indeed forms (*Sc. simplex* and the members of the *meriani* group) in the immediate neighbourhood of the type species, in which a 'trifid' *L* becomes developed. If we consider, however, the phylogenetic and ontogenetic evolution of this element, then we prefer to use the term 'asymmetric'. This asymmetry evidently depends on the retraction of the umbilical suture-line of some Upper Albian species, especially *Sc. simplex*. In the subsequent species, *Sc. obliquus* and *equalis*, the suture-line is less retracted, and the original bifidity rapidly becomes re-established. In *Sc. equalis* the lobe development of its ancestors becomes recapitulated. Bifid at first, the

lateral lobe becomes asymmetrical in early ontogeny and regains the primary bifid outline thereafter. Only this ultimate change was observed by Pervinquière (1907) and since then regarded as evidence for an ammonitid origin of all scaphitids. Likewise in some Senonian species a 'trifid' *L* was cited, but Cobban (1952) demonstrated that also in these forms an originally bifid lobe gradually becomes asymmetrical. On the contrary, the trifidity of the so-called 'second lateral' or ' U_2 ' is the original outline of the misinterpreted median incision of the saddle *L/U*.

Corresponding to the suture development, the septal surface is always hamitid in early *Eoscaphtites* (text-fig. 1c). It rapidly receives its typical scaphitid shape (text-figs. 1d, 2b, 6d, 7a, b), characterized by its comparatively small lobes, elongated saddles and only one distinctly bipartite umbilical lobe on or near the umbilical seam.

Also in the sculpture development a gradual change between *Eoscaphtites* and the *Scaphites* type species can be observed. In *E. circularis* the sculpture remains simple and uniform (comparable with that of the contemporaneous *Hamites*). The branching of ribs, at first only occasionally observable, is a common feature in the first true *Scaphites*. Now the differentiation in primary and secondary ribs becomes more and more pronounced. While the primaries increase in strength, the point of bifurcation approaches the outer margin, and may be tuberculate or not.

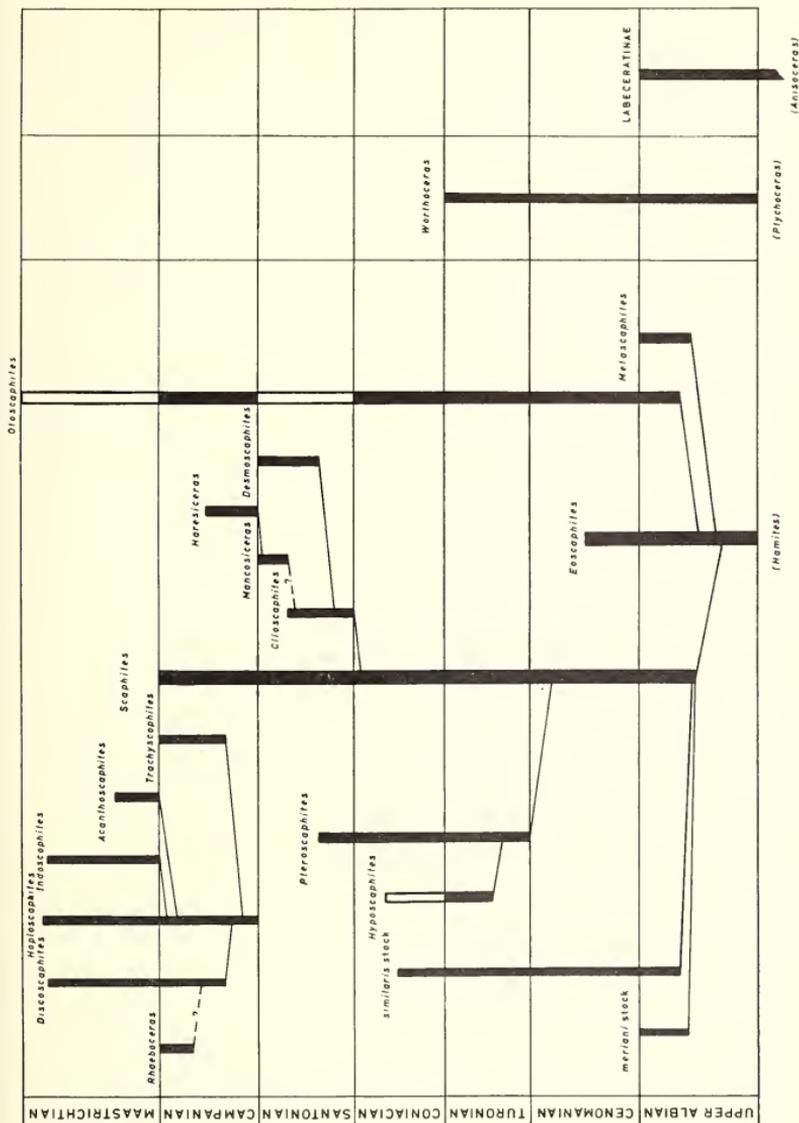
Likewise the degree of shell involution changes continually. In *Eoscaphtites* the first whorls are loosely coiled and no dorsal impression can be recognized. The first whorls are extremely slender and circular in section, but they rapidly increase in size (about 400 per cent. per whorl) and involution. This change can be followed step by step in the eoscaphtid species, and there is no doubt that *Eoscaphtites* had an uncoiled, hamitid ancestor. Already in the first true *Scaphites* (*Sc. simplex*) the maximum shell involution was reached. But an inversion of this tendency appears in the somewhat more open whorled Cenomanian species.

The final hook which is highly elongated in *Eoscaphtites* becomes more and more inflated and stouter in the true scaphitids. Finally, the mouth-border is merely separated from the initial coil. Here, one of the features of heteromorphous development becomes apparent, namely the tendency to abandon the loose coiling and to regain the normal ammonitid spire.

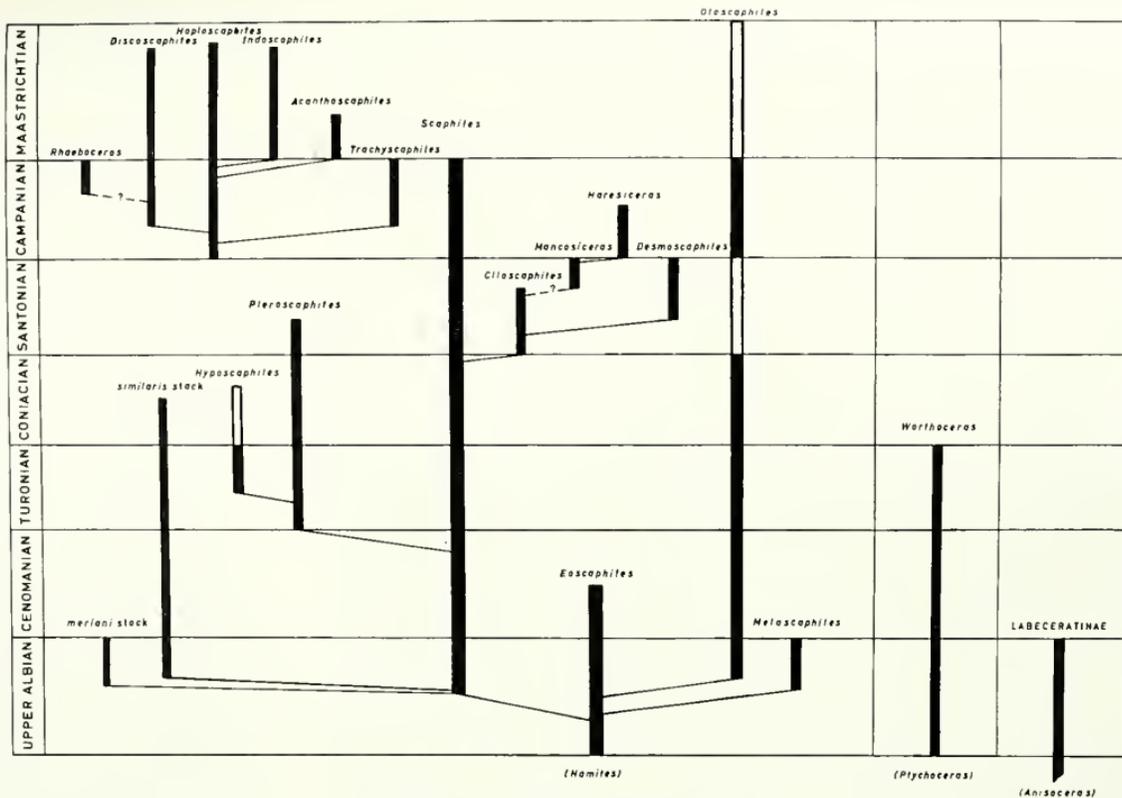
Through all these gradual transitions the generic separation between *Eoscaphtites* and *Scaphites* remains arbitrary. This separation, which we retain, may be based on the umbilical perforation of *Eoscaphtites*, its extreme increase of whorl size, the absence of a dorsal impression and the undifferentiated elements *U* and *L/U*.

In pursuing the development of early scaphitids, we recognized, contrary to the present knowledge, an extreme splitting off into different lineages, especially in the Upper Albian and Cenomanian (text-fig. 16). *Metascaphites* and *Otoscaphtites* can now be directly derived from an eoscaphtid origin, while the above separated *meriani* and *similaris* stocks originate from *Sc. simplex*, the first true *Scaphites*. All these forms merely need generic separation. *Sc. minutus* was erroneously regarded as a transitional form between *Worthoceras* and *Otoscaphtites* by Wright. While the former is now recognized as a homoeomorph development of ptychoceratid origin, *Otoscaphtites* is identified as a true scaphitid development, which parallels the *equalis* main stock, probably throughout the complete Upper Cretaceous.

Text-fig. 16 represents a convincing example for Schindewolf's typrostrophism. The



TEXT-FIG. 16. The scaphitid relationships.



TEXT-FIG. 16. The scaphitid relationships.

three stages of divergent evolutionary rate, which Schindewolf recognized in many different fossil groups and regarded as an essential evolutionary principle, are well represented here. In the primary stage of explosive development (typogenesis) nearly all diverging types are produced during a relatively short period (Upper Albian/Cenomanian). It is followed by a long and stable period (Turonian/Santonian), where the types barely change (typostasis). Finally, in the Campanian and Maastrichtian, a new stage of explosive development can be observed, which is generally destructive in nature and announces the imminent extinction of the scaphitid stock (typolysis).

The problem of parallel development in scaphitids has repeatedly been emphasized. The members of the *similaris* stock, the ptero- and otoscaphitids, are exclusively small-sized or dwarfed species, which almost exactly parallel the normal-sized members of the main stock. We have two solutions to this problem. The members of the *similaris* stock seem to represent atrophic equivalents of the normal-sized boreal scaphitids. They are restricted to the Southern areas and the Pacific border. The ptero- and otoscaphitid micromorphs, however, are generally found together with the normal-sized specimens. In the literature of the last century this fact was often interpreted as sexual dimorphism, and the micromorphs were not separated from the large-sized species. In the modern scaphitid systematics, as created by Wright, the micromorphs were treated as a distinct genus (*Pteroscaphites*) or subfamilies (Otoscapitinae). I am unable to follow Wright in regarding the mouth lappets, which are common in these forms, as the basis for the proposed separation. It has been known for a long time, that lappeted and unlappeted forms are inseparably joined in many ammonitid stocks. Makowski (1963) made the fact, that smaller size and presence of (lateral) mouth lappets in ammonites characterize the male sex, highly possible. Naturally it is impossible to solve this problem absolutely. But all these arguments seem reason enough to re-integrate the micromorph series into the *equalis* main stock.

Thus we come to the conclusion that the systematics of 'Scaphitaceae' may be rigorously simplified. Excluding *Worthoceras* and the Labeceratids as convergent developments, the remaining true scaphitids may be restricted to one single family. If we regard the reduced number of four-lobe elements as a characteristic of all heteromorphs, these also may be grouped into one single superfamily, Ancylocerataceae, in which Scaphitidae, in the neighbourhood of the ancestral hamitids, can now easily be included.

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ISORTHIS AND SALOPINA (BRACHIOPODA) IN THE LUDLOVIAN OF THE WELSH BORDERLAND

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ABSTRACT. Examination of the enteletacean brachiopod members of the faunal assemblages now used in British Ludlovian stratigraphy (Holland, Lawson, and Walmsley 1963) and comparison with a large collection of Silurian and Lower Devonian brachiopods from many parts of the world, reveals that the species commonly determined as *Dalmanella lunata* (J. de C. Sowerby) and *D. orbicularis* (J. de C. Sowerby), have not yet been found, (though sometimes recorded), from areas outside Britain. However, one of the new species of *Isorthis* here described has a wide distribution in Britain and occurs in North America (Maine and New Brunswick) and South America (Venezuela). *Salopina* Boucot is emended and *Salopina lunata* is described, figured and distinguished from *S. submedia* (McLearn), which was figured as *S. lunata* by Boucot 1960, from New Brunswick. *Isorthis* Kozłowski is emended and *Orthis orbicularis* J. de C. Sowerby together with two new species (*I. amplificata* and *I. clivosa*), and two new subspecies (*I. scuteformis scuteformis* and *I. scuteformis uskensis*), from the Welsh Borderland and a new, related species (*I. slitensis*) from Gotland, are assigned to *Isorthis* and described and figured.

IN order that the refinements of stratigraphy and correlation recently achieved in the Ludlovian of the Welsh Borderland (Holland, Lawson, and Walmsley 1963), may have greater value in wider correlations, it is necessary that the faunas on which the work has largely been based, should be studied in detail and descriptions made available.

Very little work has been published on British Upper Silurian brachiopods since Davidson's Monograph of the last century. The writer had begun a study of Ludlovian enteletacean brachiopods based largely on his own collections from the Welsh Borderland when the opportunity to spend a year in the U.S.A. made possible the essential comparative studies.

Enteletacean brachiopods of the following genera occur in the Ludlovian rocks of the Welsh Borderland: *Isorthis*, *Salopina*, *Resserella* (= *Parmorthis*), *Dalejina* (= *Rhipidomelloides*), and *Dicoelosia*. The purpose of the present paper is to describe and figure the several species commonly determined as *Dalmanella orbicularis* (J. de C. Sowerby) and *D. lunata* (J. de C. Sowerby), important members of the successive faunal assemblages now recognized in the type Ludlovian (Holland, Lawson, and Walmsley 1959, Lawson 1960, Holland, Lawson, and Walmsley 1963).

Further papers are in preparation (jointly with Dr. A. J. Boucot and Dr. C. W. Harper) on the genera *Isorthis*, *Salopina*, *Resserella*, and *Fascicostella*, based on the study of Dr. Boucot's collection from the U.S.A., Canada, South America, Europe, and New Zealand. Examination of the enteletacean brachiopods in this collection, together with material kindly loaned by various museums and private individuals, has shown that, despite several references to the contrary, the species *I. orbicularis* and *S. lunata* have not yet been found outside the British area. In Britain, however, several isorthisids, described here as new species and subspecies, have probably been confused as '*D. orbicularis*'. One of these new species (*I. clivosa*) has a wide distribution in Britain and occurs in North America (Maine and New Brunswick) and in South America (Venezuela).

The species *Orthis lunata* and *O. orbicularis* were first described by J. de C. Sowerby in Murchison's *The Silurian System*, 1839, p. 611 and figured on pl. 5, figs. 15 and 16 respectively. Sowerby commented on the difficulty of distinguishing these species 'unless it [the specimen] be very perfect, or show the impressions upon the cast of the characteristic ridges in the interior'. It was presumably this difficulty which caused Davidson (1869, p. 215) to put *O. orbicularis* in synonymy with *O. lunata* and his figs. 1-5 on pl. XXVIII show both species under the latter name, an unfortunate error which misled several later authors. Elles and Slater (1906), however, in their account of the rocks of the Ludlow district, recognized and listed both species, as did subsequent authors in the Welsh Borderland. Several of these faunal lists, moreover, also recorded '*Dalmanella* spp.' from the Ludlovian—an indication that there were dalmanellid shells present, not easily assignable to either *D. lunata* or *D. orbicularis*.

The genus *Dalmanella* was erected by Hall and Clarke (1892) and the complex nomenclatorial history of this group has been recounted recently (Williams and Wright 1963, pp. 1-3). Since 1892, the species *O. lunata* and *O. orbicularis* have usually been assigned to *Dalmanella*, but in 1960 Boucot (*in* Boucot *et al.*, p. 3) erected the genus *Salopina* with *O. lunata* Sowerby as type species. Unfortunately the shell described and figured by him, in his pl. 1, figs. 6-12, is not *O. lunata* J. de C. Sowerby, but *S. submedia* (McLearn) from the Jones Creek Formation (? Wenlockian-Ludlovian in age) of New Brunswick, Canada. This species has now been redescribed in a joint paper on the 'Silurian Brachiopods and Gastropods of Southern New Brunswick' (Boucot, Johnson, Harper, and Walmsley—in press).

Kozłowski 1929, p. 75, erected *Isorthis* as a subgenus of *Dalmanella*, and described *I. szajnochai*, the type species, in considerable detail. Schuchert and Cooper 1932, pp. 149-50, redescribed *Isorthis* and raised it to generic rank. They assigned to it a number of American and European species but did not include *D. orbicularis*. Boucot (*in* Boucot *et al.*, 1960, p. 5 and pl. I, figs. 13-20, pl. II, figs. 1-7) described and figured a small silicified isorthid from the Sutherland River Formation (late Silurian-early Devonian age) of Devon Island, Canadian Arctic Archipelago, as *I. orbicularis* (Sowerby) and recorded it (p. 6) as the first known occurrence of this species from North America. I have been able to study this material in Dr. Boucot's collection and to determine that it is a new species quite distinct from *I. orbicularis* (J. de C. Sowerby), (Walmsley, Boucot, and Harper—in preparation).

In the present paper the genus *Salopina* is emended and *S. lunata* (J. de C. Sowerby) is described and figured. *O. orbicularis* J. de C. Sowerby is assigned to *Isorthis* emended, together with two new species and two new subspecies from the Welsh Borderland and a closely related species from Gotland—all of which are here described and figured.

MORPHOLOGICAL TERMINOLOGY

The terminology used by Schuchert and Cooper (1932) and defined in their glossary, pp. 6-11 and pl. A, is largely adopted. However, further explanation is needed of a few terms found necessary in the following systematic descriptions:

(a) *Fulcral plate*. This term was used by Schuchert and Cooper for a small concave plate connecting the brachiophore to the shell wall (see their pl. A, fig. 14), and considerable taxonomic importance was attached to the presence or absence of such a plate. It is

clear from their definition (p. 8, pl. A, fig. 14), that this name was applied to a plate which formed the floor of the socket and beneath which there was a small cavity. The antero-lateral edge of such a plate (being also the edge of the socket), shows itself in the usual figures of the interior of the brachial valve as a short line connecting the brachiophore and the hinge line. In such views it is usually impossible to determine whether a cavity exists beneath the socket floor. A very similar, if not identical, aspect is produced by an alternative structure which is commonly present in enteletacean shells. Here, the socket is a depression in the upper surface of a solid block or pad of calcite, but in this case, there is no cavity beneath the socket floor. The antero-lateral edge of such a structure resembles that of a true fulcral plate.

Since all morphologic stages can be seen between a true fulcral plate and a solid socket pad, it would appear that the leading edge of the socket may be formed either by forward extensions of the calcite forming the socket floor so as to overhang and eventually produce a lower cavity and a fulcral plate, or, possibly by resorption of the antero-lateral face of a solid socket pad which could produce a lower cavity and hence a fulcral plate. A third possibility exists. The socket pad condition may be a result of a true fulcral plate becoming submerged in adventitious calcite which has filled in the lower cavity.

It is not known which, if any, of these possible processes operated in the species here described, but from a purely descriptive point of view it is necessary to distinguish between the two common aspects. It is proposed therefore to restrict the use of the term fulcral plate to those situations where there is a lower cavity beneath the floor of the socket and to use the term socket pad where the floor of the socket is raised above the general surface of the valve but does not have a lower cavity beneath it.

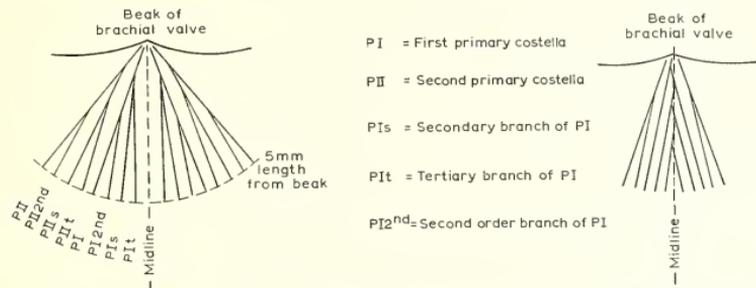
In their recent critical discussion of dalmanellid cardinalia, Williams and Wright (1963, pp. 4-11) also pointed out that transitional stages between fulcral plates and socket pads are to be expected. The useful term 'socket pad' is adopted from their paper.

(b) *Brachiophores*. This term is used to designate the plate-like structures which develop forward from the margins of the notothyrium, forming the inner (medial) margins of the sockets. No separate 'brachiophore processes' or 'brachiophore supports', terms used by Schuchert and Cooper, are distinguished.

(c) *Rib branching*. Although patterns of rib branching have been studied in the species here described, only minor differences occur and their taxonomic usefulness is outweighed by combinations of other morphological features. Nevertheless, the general pattern of branching in the medial region of the brachial valves of isorthis and salopinids has a character which immediately distinguishes these groups from *Resserella* [= *Parmorthis*], species of which have previously been confused with *I. orbicularis*. Davidson (1869, p. 218), for example, confused *O. orbicularis* (an isorthis) with *O. elegantula* (a resserellid) and found difficulty in convincing himself that *O. canaliculata* Lindstrom (again, an isorthis) was really different from *O. basalis* Dalman (a resserellid).

In *Isothis* and *Salopina* the branching of the costellae in the medial area of the brachial valve is symmetrical about the shell's plane of symmetry. Secondary and sometimes tertiary branches of the medial primary pair, appear on the medial side. In *Resserella*, however, an unusual asymmetrical arrangement occurs in which the successive branches appear alternately to 'left' and 'right' of the preceding costella. This occurs in all known species of *Resserella* and is responsible for the unusual appearance of the ribbing in the

sulcus, to which several authors have referred—notably Schuchert and Cooper 1932, p. 129, in discussion of *Parmorthis*. Text-fig. 1 shows diagrammatically the typical arrangement of medial costellae on the brachial valve of isorthids and salopinids. The abbreviations used in the following systematic descriptions are explained in this diagram. The 5 mm. length stage is chosen as arbitrary, but convenient for this group of brachiopods. This figure also shows diagrammatically by contrast, the asymmetrical arrangement of the branching of medial costellae on the brachial valve of a resserellid shell. There are of course other generic distinctions, but the asymmetrical pattern of rib branching has not hitherto been recorded and is an easily observed external distinction.



TEXT-FIG. 1. Contrast in patterns of costellae bifurcation in *Isorthis* and *Salopina* (on left) and *Resserella* (on right), in the medial region of the brachial valve. Also, key to notation of costellae referred to in the text.

Number of ribs. The abundance, strength, and angularity of costellae as well as their branching patterns can be important distinguishing characters and various authors have attempted to record these features. However, since the number of costellae reaching the anterior margin in a branching system depends to a large extent on the stage of growth of the shell, figures given for the number of costellae, or even the number per mm., along the anterior margin are not meaningful unless the size of shell is also quoted. Rarely in description of enteletacean brachiopods have figures concerning the frequency of costellae been related to size. Where the frequency of costellae is referred to in the following descriptions it is taken as the average number per mm. at the 5 mm. length growth stage.

SYSTEMATIC DESCRIPTIONS

Superfamily ENTELETACEA Waagen 1884

[Nom. transl. Altskhova 1960 (*ex* Entelitinæ Waagen 1884)]

Family SCHIZOPHORIIDAE Schuchert and LeVene, 1929

Subfamily SCHIZOPHORIINAE Schuchert and LeVene, 1929

Genus SALOPINA Boucot, 1960, emended

Type species. *Orthis lunata* J. de C. Sowerby in Murchison, 1839, p. 611, pl. 5, fig. 15.

Diagnosis. Relatively small schizophoriinids having a gently convex brachial valve, a more convex pedicle valve, hollow costellae, a poorly developed median ridge in the

pedicle valve and an adductor muscle field in which transverse ridges may be oblique and the margins meet the bases of the brachiophores in a sharp flexure.

Comparison. *Salopina* is distinguished from *Schizophoria* by having the pedicle valve always more convex than the brachial and by the absence of both a prominent median ridge in the pedicle valve and prominent antero-laterally directed transverse ridges in the adductor muscle field.

From *Isorthis*, *Salopina* is distinguished by its hollow costellae, and by the absence both of a distinct median ridge in the pedicle valve and of a strongly impressed adductor muscle field. The flexure by which the lateral margins of the adductor muscle field merge into the bases of the brachiophores in *Salopina* is distinct from the smooth continuity in the case of *Isorthis*.

The genus *Sphenophragmus* Imbrie 1959 also has hollow costellae and a general form very close to *Salopina* but is distinguished by its delicate cardinalia with a cardinal process raised on a notothyrial platform and the absence of a pronounced median ridge in the brachial valve. In the pedicle valve, the dental lamellae are not medially concave and there is no raised median area in the delthyrial cavity.

Description. Relatively small, subequally biconvex to almost plano-convex schizophoriinids with pedicle valve always having greater convexity. Brachial valve non-sulcate to gently sulcate. Outline variable from semicircular to subcircular or transversely elliptical. Hinge line straight, usually equal to about two-thirds of the greatest width, which is near mid-length. Lateral commissures straight to slightly flexed, anterior commissure crenulate and either rectimarginate or unisulcate. Pedicle valve interarea longer than interarea of brachial valve, usually gently curved, apsacline. Brachial valve interarea plane, anacline. Delthyrium and notothyrium open, latter usually partially filled by the myophore of the cardinal process. Pedicle valve beak usually distinct but not overhanging hinge line. Shell punctate, multicostellate with hollow costellae. Costellae increase by bifurcation and vary in degree of curvature as they radiate from the umbo. Costellae rounded to subangular. At 5 mm. length the number of costellae per mm. varies with species but is usually about three. The rate of appearance of secondary and tertiary branches varies with species.

Interior of pedicle valve. The muscle field is commonly weakly impressed, confined to the posterior half and the median third of the valve and in some species is even more restricted. No pronounced median ridge is present but there is a very faintly raised median area separating the elongate diductor tracks which are bounded laterally by low, forward extensions of the medially concave dental lamellae.

Teeth range in size with species and do not bear crural fossettes. Small lateral cavities external to the dental lamellae extend beneath the interarea. No pedicle callist present.

Interior of brachial valve. A commonly weakly impressed adductor muscle field, one-third or less the width of the valve, extends up to three-quarters of the valve length. A wide median ridge, at least a quarter as wide as the muscle field, separates the adductor impressions which are bounded laterally by not very pronounced, slightly raised margins sub-parallel to the median ridge. These margins become weaker as they curve to meet the median ridge in front of the muscle field. Posteriorly they are directed laterally to the brachiophores, but by a sharp flexure merge into the brachiophore bases (see Pl. 65, fig. 1). Faint transverse ridges directed normal to the median ridge or slightly antero-

laterally give a quadripartite aspect to the adductor field. The brachiophores vary in thickness and degree of divergence. Fulcral plates are present in most species, flooring triangular sockets beneath which are distinct, sometimes deep, lateral cavities.

The cardinal process has a short, thin shaft and a slightly bulbous simple non-lobed myophore bearing crenulations on its posterior face. Crenulations of the anterior margin of the shell are wide, low, flat or slightly rounded and bear a median groove. Interspaces are narrow and rounded. Crenulations commonly extend over one-fifth of the shell length.

Salopina lunata (J. de C. Sowerby)

Plate 64, figs. 15–27; Plate 65, figs. 1–12, 28, 29

- 1839 *Orthis lunata* J. de C. Sowerby in Murchison, p. 611, pl. 5, fig. 15 (non fig. 16) and pl. 3, fig. 12d.
 1869 *Orthis lunata* Davidson, pp. 215–16, pl. 28, figs. 1, 2, 4 (non figs. 3, 3a), ? fig. 5.
 non 1845 *Orthis lunata* Murchison, de Verneuil and Keyserling, Geol. de la Russie d'Europe, vol. 2, p. 189, pl. 13, figs. 6a–d.
 non 1913 *Dalmanella lunata* Williams, Proc. U.S. Nat. Mus., 45, p. 337, pl. 3, figs. 1–5 and 8.
 non 1922 *Orthis (Dalmanella) lunata* Barrois, Pruvost and Dubois, Mém. Soc. géol. du Nord, 6, p. 77, pl. 11, figs. 4–12; p. 155, pl. 17, figs. 16–18.
 non 1924 *Dalmanella lunata* McLearn, p. 55, pl. 4, figs. 5–6.
 non 1960 *Salopina lunata* Boucot et al., p. 3, pl. 1, figs. 6–12.

Diagnosis. Outline transversely elliptical to subquadrate, brachial valve sulcate with fine costellae which radiate with little curvature. Posterior costellae sub-parallel to hinge line in brachial valve. Brachiophores thin, long, pointed blades. Fulcral plates present.

Comparison. The New Brunswick shell figured by Boucot (1960, pl. 1, figs. 6–12) as *S. lunata* is now recognized as *S. submedia* (McLearn) which differs from *S. lunata* especially in the nature of the costellae. These are coarser and develop a distinct curvature which results in the most posterior costellae meeting the hinge line at a fairly high angle. *S. submedia*, which is redescribed in 'Brachiopods and Gastropods of Southern New Brunswick', Boucot, Johnson, Harper, and Walmsley (in press), also differs from *S. lunata* in its more circular outline and in the longer diductor impressions being bounded by less strongly curved dental lamellae.

Description. Unequally biconvex, pedicle valve having greater convexity and brachial valve sulcate. Outline transversely elliptical to subquadrate. Hinge line straight, equal to about three-fifths of greatest width which occurs slightly anterior to mid-length. Length equals about three-quarters of the width. Anterior commissure, crenulate and faintly unisulcate, lateral commissures straight.

Exterior of pedicle valve. Most convex in postero-medial region, curvature decreasing toward lateral margins and slightly towards anterior margin. Outline subelliptical with anterior margin parallel to hinge line and lateral margins rounded, convex outwards. Cardinal angles obtuse and slightly less rounded than the antero-lateral margins. Beak projects one-tenth of the total length posterior to hinge line. Interarea triangular, with sharp lateral margins. Delthyrial margins subtending about 60°.

Exterior of brachial valve. The shallow sulcus extends from umbonal region to anterior margin where it equals about a quarter of greatest width. Anteriorly diverging margins of sulcus poorly defined. Valve outline subelliptical with anterior margin parallel to

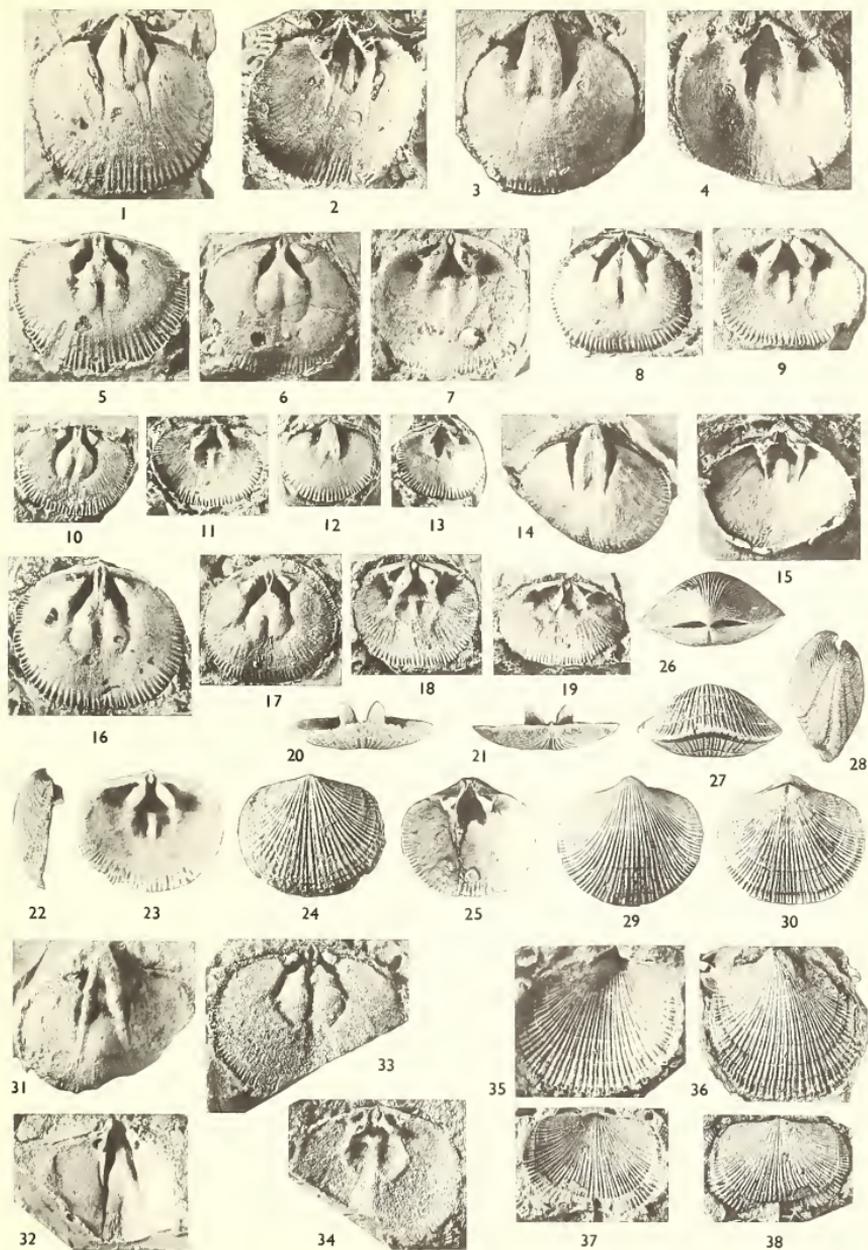
hinge line, lateral margins rounded, convex outwards. Cardinal angles obtuse, less rounded than anterolateral margins. Interarea plane, anacline, about half as long as area in pedicle valve.

Rib branching pattern in median area shows P I (see text-fig. 1) quickly giving off secondary and second order branches towards midline. Secondaries give off tertiaries also medially, these being the most medial ribs on the valve. These do not arise together and points of branching can be one-fifth of the total length of valve apart. At 5 mm. length from the beak all these ribs have appeared, P II has also at this stage (5 mm.) produced secondary, tertiary and second order ribs so that increase in costellae is rapid.

Interior of pedicle valve. The muscle field is confined to the posterior one-third of the valve and is also one-third as wide as greatest width. A very faintly raised median region is flat and up to a quarter as wide as the muscle field. In some specimens it narrows towards the anterior. This may represent the adductor muscle track but no distinct scars are impressed. Diductor tracks on either side are elongate, semi-elliptical with anteriorly convex anterior margins slightly raised above the valve floor. Laterally the diductor impressions are bounded by the dental lamellae which diverge outwards before converging again as walls of the delthyrial cavity. The teeth are small, triangular in plan

EXPLANATION OF PLATE 61

- Figs. 1-13. *Isorthis amplificata* sp. nov., Wenlock Limestone or basal Ludlovian siltstone, bank in field, 600 yards NW. of Porth-llong, Usk inlier, Britain (Nat. Grid Ref. 34829825). 1-2, Internal mould of pedicle valve ($\times 3$), GSM 102206 and latex impression ($\times 3$). Note deep crural fossettes. 3-4, Internal mould of pedicle valve ($\times 3$), GSM 102207, Paratype and latex impression ($\times 3$). Note vascular trunks. 5, Internal mould of brachial valve ($\times 3$), GSM 102208. 6-7, Internal mould of brachial valve ($\times 2$), GSM 102209, and latex impression ($\times 2$). Note impressions of slightly crenulated sockets, thick brachiophores and their close proximity near the cardinal process. (See also figs. 20-21.) 8-9, Internal mould of brachial valve ($\times 2$), GSM 102210, and latex impression ($\times 2$). Note large brachiophores. 10-11, Internal mould of brachial valve ($\times 2$), GSM 102211, and latex impression ($\times 2$). 12-13, Internal mould of pedicle valve ($\times 2$), GSM 102212, and latex impression ($\times 2$).
- Figs. 14-16. *Isorthis amplificata* sp. nov., Wenlock Limestone or basal Ludlovian siltstone, old quarry at Cwm, Usk inlier, Britain (Nat. Grid Ref. 33320160). 14, Internal mould of pedicle valve ($\times 2$), GSM 102213. 15, Latex impression of same specimen ($\times 2$). 16, Internal mould of brachial valve ($\times 3$), GSM 102214, Holotype.
- Figs. 17-19. *Isorthis amplificata* sp. nov., Wenlock Limestone or basal Ludlovian siltstone, bank in field, 600 yards NW. of Porth-llong, Usk inlier, Britain (Nat. Grid Ref. 34829825). 17, Internal mould of brachial valve ($\times 2$), GSM 102215. 18, Latex impression of same specimen ($\times 2$). 19, Oblique view of same latex impression showing divergence of brachiophores.
- Figs. 20-30. *Isorthis amplificata* sp. nov., Wenlock Limestone old quarry on west side of Lincoln Hill, Iron Bridge, Britain (Nat. Grid Ref. 670038). 20-24, Anterior, posterior, side, internal and external views of brachial valve ($\times 3$), GSM 102216, Paratype. 25, Interior of pedicle valve ($\times 2$), GSM 102217. 26-30, Posterior, anterior, side, pedicle valve and brachial valve ($\times 2$), GSM 102218, Paratype.
- Figs. 31-38. *Isorthis clivosa* sp. nov., 31-32, Mid Eltonian siltstone, trackside 300 yards south of Hafod-fawr, Llandoverly area, Britain (Nat. Grid Ref. 81443096), internal mould of pedicle valve ($\times 2$), GSM 102219, and latex impression ($\times 2$). 33-34, Mid-late Eltonian, 6 yards upstream of mountain fence along Nant Cwm Clyd, 1,000 yards SE. of Cwm Clyd Farm, Llandoverly area, Britain (Nat. Grid. Ref. 80152980), internal mould of brachial valve ($\times 2$), GSM 102220, and latex impression ($\times 2$). 35-38, Mid Eltonian, 50 yards up R. Gwydderig from Bont Wen, on road A. 40. 35-36, External mould of pedicle valve ($\times 2$), GSM 102221, and latex impression ($\times 2$). 37-38, External mould of brachial valve ($\times 2$), GSM 102222, and latex impression ($\times 2$).



and section and project normal to the hinge line. External to the teeth are lateral cavities roofed over by the interarea and bounded by the external face of the tooth and the floor of the valve. In large specimens these cavities may be obscured.

Interior of brachial valve. The adductor muscle field extends about four-sevenths of the distance to the anterior margin and is slightly less than one-third as wide as the greatest shell width. A rounded, median ridge (about two-fifths width of muscle field) extends from the anterior margin of the muscle field posteriorly becoming somewhat carinate as it passes between the brachiophores. Flanking the median ridge are adductor impressions, narrower than the median ridge and bounded by very faintly raised margins which are sub-parallel to the median ridge, but slightly concave towards it. Posteriorly these margins, which are directed externally to the brachiophore bases, curve sharply medially and merge with the bases of the brachiophores. Anteriorly the margins fade towards the end of the median ridge. Anterior adductor impressions are smaller than the posterior pair and when slightly more impressed are clearly separated by faint transverse ridges. In many specimens the impressions are faint, the outer margins incomplete and the appearance is of divergent margins extending from immediately outside the brachiophores, fading about mid-length where the median ridge also may fade.

The brachiophores are very long, thin, erect, pointed blades directed normal to the hinge line or only slightly divergent from each other. Their distal extremities are separated by a distance equal to one-fifth of greatest shell width. Their anterior edges are normal to the commissural plane. Proximally they are connected by short curved fulcral plates to the posterior edge of the valve floor along the hinge line. The fulcral plates floor very small sockets and roof over a much larger lateral cavity.

The cardinal process consists of a thin blade-like shaft which arises from the crest of the posterior carinate portion of the median ridge between the brachiophores and terminates in a very slightly bulbous, non-lobed myophore.

Anterior crenulations on the valve margin have a low rectangular cross-section and bear fine grooves along the mid-line of their internal faces. Interspaces are rounded. This type of anterior crenulation is very similar to that described as diagnostic of *Rhipidomelloides*.

Type specimens. This species was erected and first described by J. de C. Sowerby in Murchison's *Silurian System*, p. 611, and illustrated in pl. 3, fig. 12*d* and pl. 5, fig. 15.

Boucot (1960, p. 3) designated as 'holotype', 'The specimen figured by Salter (op. cit.)', referring to pl. 5, fig. 15.

The figure was by J. de C. Sowerby, not Salter, and comprised not one but three specimens, an internal impression of a pedicle valve, an internal impression of a brachial valve and an external impression of a pedicle valve. None of the originals of these figures has been definitely identified but they may be related to GSM 51555 in the Geological Survey Museum, London. Specimen No. GSM 51555 is from the Geological Society Collection—Murchison Collection, Oaker Quarry (near Beecher) and the old label states 'Pl. 5, fig. 15'. The impressions are all slightly distorted. Similar distortion is to be seen in specimens from Oaker Quarry (Nat. Grid reference 377816) about 5 miles east of Clun, but not in material from the Ludlow district or the inliers of Woolhope, May Hill, or Usk. Dr. Stubblefield (in correspondence) considers that this specimen is remotely eligible as the original of pl. 5, fig. 15, and is quite probably one of several syntypes. In order to clarify the situation, I designate the ringed specimen on GSM 51555 (an internal impression of a brachial valve) as lectotype and figure it Plate 65, fig. 28. It is arguable whether a specimen which is not certainly the original should be designated lectotype. However, the Geological Society Collection has been very carefully examined by the Geological Survey and it seems certain that no more likely specimen exists. To designate GSM 51555 as a neotype would hardly assign to this specimen its due significance.

Distribution. *S. lunata* ranges in the Ludlovian of Britain from the Lower Leintwardinian to the highest Whitcliffian where it is most abundant. In the inliers of Usk, May Hill, and Woolhope it has been recorded as present but very rare in the basal part of the Downtonian—immediately above the Ludlow Bone Bed. It should be noted that the original of Sowerby's pl. 3, fig. 12d, also of *S. lunata*, cannot be traced, but the tablet bearing specimens figured as 12a, b, c, e, and g is marked: 'Devonian (Tilstones) Horeb Chapel, R. I. Murchison, F.G.S.'.

In the Lower Leintwardinian, it is present at May Hill and Ludlow, rare at Usk and fairly common at Woolhope. In the Upper Leintwardinian it is fairly common at May Hill, Usk, Ludlow, and Builth, and common at Woolhope. In the Lower Whitcliffian, it is rare in the Leintwardine area, fairly common at Woolhope, Ludlow and Builth, and common at Usk and May Hill. In the Upper Whitcliffian, it is common at Usk, May Hill, Woolhope, Ludlow, the Leintwardine area, Builth, Knighton, and Kerry. It appears, therefore, to have migrated from the south-eastern part of the shelf area north-westwards to the basin area during the later part of Ludlovian time. (See also Holland and Lawson, 1963, p. 287.)

Records of *S. lunata* from localities outside Britain have been checked and cannot be authenticated. Its sudden appearance in Britain in early Leintwardinian times raises the question of its ancestry. In the Hemse Group of Gotland (early Ludlovian age, probably mid Eltonian based on associated *Pristiograptus nilssonii* and *Lobograptus scanicus*), is a shell which is considered to be conspecific with *D. conservatrix* McLearn. The latter is a salopinid and is redescribed in 'Salopinid Brachiopods of the Silurian and Lower Devonian' (Walmsley, Boucot, and Harper, in preparation). *S. conservatrix* is known from the Ross Brook Formation (late Llandovery age) of Nova Scotia. *S. conservatrix* seems to be the most likely ancestor of *S. lunata*.

A species of *Salopina* from the Stonehouse Formation (Gedinnian age) of Arisaig, Nova Scotia, (Walmsley, Boucot and Harper, in preparation) is very close to *S. [Dalmanella] missendenensis* (Straw), from the Little Missenden Bore (1913) material. Unfortunately, there is too little bore material available to establish specific identity. The age of the bore material was recorded, Straw and Woodward 1933, p. 139, as 'either late Downtonian or post-Downtonian'. It seems likely that both the Stonehouse and Little Missenden forms were derived from *S. lunata*.

Subfamily ISORTHINAE Schuchert and Cooper, 1931

Genus ISORTHIS Kozłowski, 1929, emended

Type species. *I. szajnochai* Kozłowski, 1929.

Diagnosis. Planoconvex to equally biconvex isorthinids lacking hollow costellae, having a well-developed median ridge separating elongate diductor tracks in the pedicle valve, and a well-impressed adductor muscle field in which the transverse ridges are normal to the median ridge in the brachial valve. Cardinal process commonly simple, non-lobed especially in Silurian species, bilobed in some Devonian species. Brachiophores erect or postero-laterally inclined, never convergent on to the median ridge.

Comparison. *Isorthis* is distinguished from *Schizophoria* by having the greater convexity always in the pedicle valve and by having transverse ridges in the adductor muscle field aligned normal to the median ridge whereas in *Schizophoria* they are oblique, directed antero-laterally from the median ridge and the brachial valve has the greater convexity. Schuchert and Cooper (1932, p. 149) suggested that *Isorthis* was probably derived from an early Silurian *Schizophoria*. No true *Schizophoria* is known, however, from the Silurian and it appears more likely that *Schizophoria* in the Devonian was in fact derived from *Isorthis*.

Salopina is distinguished from *Isorthis* by having hollow costellae (see Boucot *et al.* 1960, pl. 1, fig. 12) and by the distinctive flexure where the margins of the adductor muscle field meet the bases of the brachiophores (see Pl. 65, fig. 1 and contrast with Pl. 63, figs. 10 and 14). The median ridge in the pedicle valve is also less pronounced.

The distinction between *Isorthis* and both *Dalmanella* and *Onniella* as emended by Williams and Wright (1963, pp. 27, 28) lies mainly in the shorter more cordate pedicle muscle field of the latter genera and in the case of *Dalmanella* the convergence of the brachiophore bases on to the median ridge.

Levenea is distinguished from *Isorthis* by its pentagonal delthyrial cavity and muscle field in the pedicle valve.

Description. Biconvex, varying from almost planoconvex to subequally biconvex. Pedicle valve always having greater convexity. Brachial valve non-sulcate to sharply sulcate. Outline variable, sub-circular, transversely elliptical or shield shaped. Hinge line straight, usually between half and three-quarters as long as greatest shell width, which is near mid-length. Lateral commissures straight, anterior commissure recti-marginate and crenulate or unsulcate and crenulate. Pedicle valve interarea usually twice as long as brachial valve interarea, gently incurved, apsacline. Delthyrium triangular, open. Brachial valve interarea plane, anacline to orthocline. Notothyrium triangular, open, partially filled by cardinal process. Pedicle valve beak distinct but not overhanging hinge line, brachial valve beak slight. Shell multicostellate, costellae increasing by bifurcation. Pattern of bifurcation in medial region of brachial valve characterized by median pair of primary costellae branching medially very early. In some species these secondary costellae again branch medially to produce tertiary costellae. A second order of branching from the median primary may arise. The second pair of primary costellae produce secondaries and both primary and secondary costellae may again divide producing tertiaries and second order branches. At 5 mm. length the presence of tertiary and second order branching varies with species. All this branching is symmetrical as in *Salopina*, but quite different from the pattern developed in *Resserella*. The costellae are rounded, evenly spaced with rounded interspaces (striae). At 5 mm. length the number of costellae per mm. varies between three and five and is most commonly four.

Interior of pedicle valve. The delthyrial cavity is usually fairly deep, but may have a delthyrial platform on which the median ridge and diductor tracks are raised above the general floor of the valve. In some species the anterior edge of the platform makes a steep descent. Dental lamellae vary in thickness and in their inclination relative to the plane of symmetry of the shell. A pedicle callist is present in some species. Teeth, triangular in plan and cross-section project normal to the hinge line, sometimes curving slightly posteriorly. Crural fossettes are usually present and vary in depth and position on the medial surface of the tooth. A median ridge extends from the delthyrial cavity, not reaching beyond the diductor impressions. The ridge varies in length, height, and width and may be parallel sided, narrow anteriorly, or widen anteriorly. In some species sub-elliptical adductor impressions occupy the posterior end of the ridge. In others no distinct adductor impressions are visible but faint striations along the median ridge may represent an adductor track. Diductor tracks, separated by the median ridge, may be slightly or deeply impressed, narrow, elongate, sub-parallel or divergent anteriorly, rarely extending beyond mid-length. The diductor impressions have a smooth, non-flabellate outline and do not enclose the adductor impressions anteriorly.

Pallial marking rarely visible. In some species vascular trunks extend forward from the anterior limit of the diductor tracks, diverging in line with these tracks, towards the anterior margin.

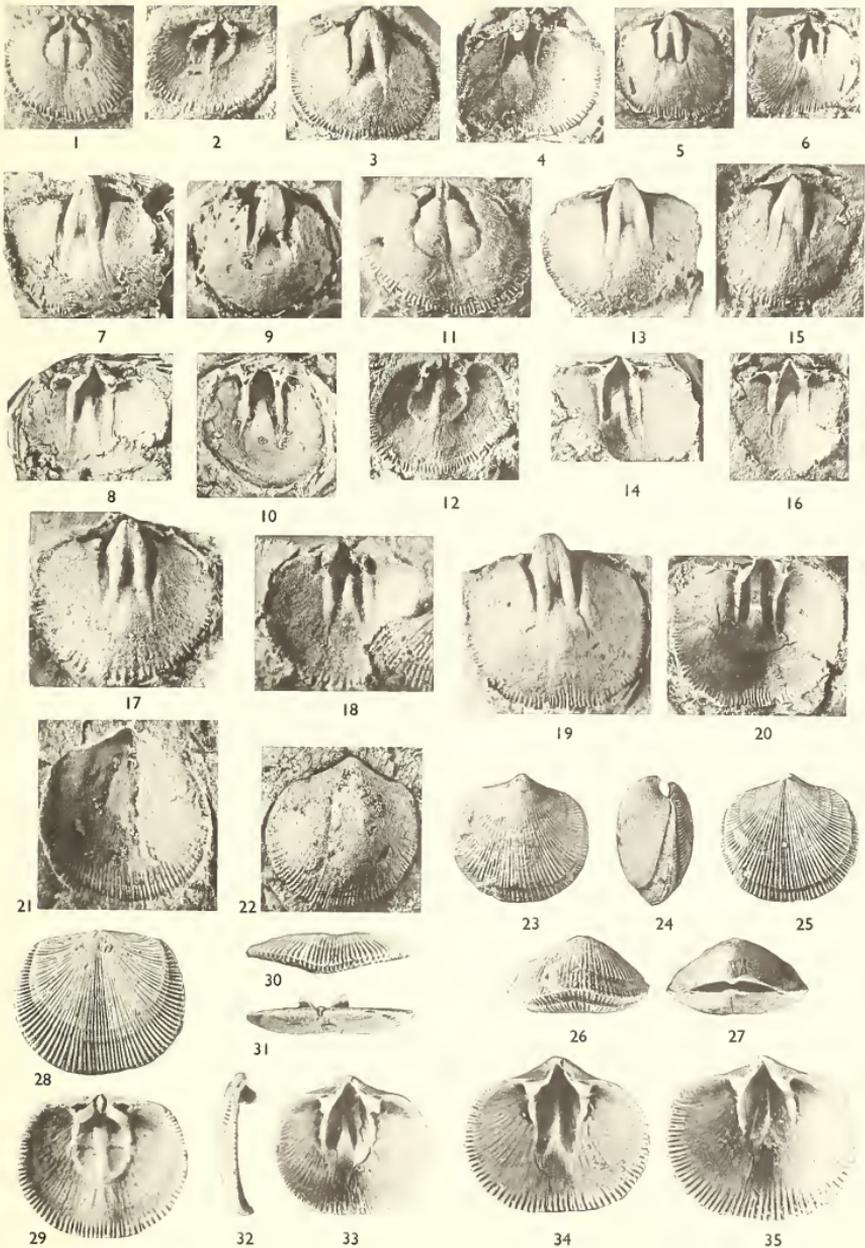
Crenulations of the anterior shell margin usually low and rounded but variable.

Interior of brachial valve. The sub-circular to elongately elliptical adductor muscle field occupies the median third of the valve, usually extending slightly anterior to mid-length. A median ridge is always present varying from one-eighth to one-quarter as wide as the muscle field, usually constant in width, rarely tapering anteriorly. The degree of impression of the muscle scars varies, resulting in some species in a distinct transverse 'step' or ridge normal to the median ridge, separating the anterior and posterior pairs of impressions and giving a clearly quadripartite appearance, with the anterior pair either equal to or larger than the posterior pair. In other species there is no sign of such transverse marking. The muscle field is bounded by a raised margin of variable outline which anteriorly converges and fades towards the median ridge and posteriorly merges smoothly with the bases of the brachiophores.

The brachiophores vary in angle of divergence, thickness, and length. In most species they are thin, flaring plates. Fulcral plates connect the lateral face of the brachiophore to the posterior margin of the valve and floor the dental sockets which vary in size. In some shells, socket pads are present instead of fulcral plates. The cardinal process

EXPLANATION OF PLATE 62

- Figs. 1–22. *Isorthis clivosa* sp. nov. 1–4, Mid Eltonian siltstone, trackside 300 yards SE. of Hafod-fawr, Llandoverly area, Britain (Nat. Grid Ref. 81443096). 1–2, Internal mould of brachial valve ($\times 2$), GSM 102223, and latex impression ($\times 2$). 3–4, Internal mould of pedicle valve ($\times 2$), GSM 102224, and latex impression ($\times 2$). 5–6, Early Leintwardinian, roadside quarry, 1,080 yards ENE. of Mary Knoll House, Ludlow area, Britain (Nat. Grid Ref. 49107399), internal mould of pedicle valve ($\times 2$), GSM 102225, and latex impression ($\times 2$). 7–8, Early Bringewoodian, roadside on A. 40, 190 yards WNW. of Ynys-y-Bont, Llandoverly area, Britain (Nat. Grid Ref. 83723225), internal mould of pedicle valve ($\times 2$), GSM 102226, and latex impression ($\times 2$). Note vascular trunks. 9–10, Early Bringewoodian, roadside, 1,000 yards east of Sluvad Farm, Usk inlier, Britain (Nat. Grid Ref. 32509920), internal mould of pedicle valve ($\times 3$), GSM 102227, and latex impression ($\times 3$). Note crural fossettes, thick dental lamellae, and wide median ridge. 11–12, Mid Eltonian, trackside, 300 yards south of Hafod-fawr, Llandoverly area, Britain (Nat. Grid Ref. 81443096), internal mould of brachial valve ($\times 2$), GSM 102228, Paratype. Note pear-shaped outline of adductor muscle field, and latex impression ($\times 2$). 13–14, Early Bringewoodian, roadside on A. 40, 190 yards WNW. of Ynys-y-Bont, Llandoverly area, Britain (Nat. Grid Ref. 83723225), internal mould of pedicle valve ($\times 2$), GSM 102229, Paratype, and latex impression ($\times 2$). Note abrupt end of median ridge. 15–18, Mid Eltonian, stream bank 600 yards SE. of Esgair Ilaethdu, Llandoverly area, Britain (Nat. Grid Ref. 79022926). 15–16, Internal mould of pedicle valve ($\times 2$), GSM 102230, Paratype, and latex impression ($\times 2$). 17–18, Internal mould of pedicle valve ($\times 3$), GSM 102231, and latex impression ($\times 3$). 19–20, Late Leintwardinian, roadside, 1,230 yards ENE. of Mary Knoll House, Ludlow area, Britain (Nat. Grid Ref. 49227407), internal mould of pedicle valve ($\times 3$), GSM 102232, Holotype, and latex impression ($\times 3$). Note flat median ridge with abrupt anterior end and also the anterior crenulations. 21–22, Mid Eltonian, trackside 300 yards south of Hafod-fawr, Llandoverly area, Britain (Nat. Grid Ref. 81443096), external mould of pedicle valve ($\times 2$), GSM 102233, and latex impression ($\times 2$).
- Figs. 23–35. *Isorthis slitensis* sp. nov. 23–27, Slite Marl (Wenlockian), Cement plant quarry at Slite, Island of Gotland (Baltic), pedicle valve, side, brachial valve, anterior and posterior views ($\times 2$), GSM 102234, Paratype. 28–32, Slite Marl, canal ditch 800 m. SW. of Alby (north of Lergravsviken), Parish of Rute, Gotland, exterior, interior, anterior, posterior, and side views of brachial valve ($\times 2$), GSM 102235, Holotype. Note relatively long adductor muscle field and vascular marks. 33–35, Slite Marl, Cement plant quarry at Slite, Gotland. 33, Interior of pedicle valve ($\times 2$), GSM 102236, Paratype. 34, Interior of pedicle valve ($\times 3$), GSM 102237. Note relatively long diductor tracks and median ridge. 35, Interior of pedicle valve ($\times 3$), GSM 102238. Note anterior crenulations.



arises as a thin laterally compressed or semi-cylindrical shaft from the median ridge between the brachiophores and expands slightly into a myophore which may be simple, non-lobed, and slightly bulbous, occupying the apical portion of the notothyrium, or may be distinctly bilobed as in several Devonian species. In well-preserved specimens the posterior face of the myophore often shows a series of chevron-shaped crenulations arranged with their apices pointing anteriorly.

Geological Range. Silurian (Lower Llandoveryan) to Devonian (Eifelian, ? Lower Givetian).

Remarks. Kozłowski (1929, pp. 29 and 75) regarded the near equality of the convexity of the two valves and the simple cardinal process as being amongst the distinguishing characteristics of *Isorthis*. Schuchert and Cooper (1932, p. 149) described the lateral profile as 'unequally to sub-equally biconvex' and stated that the cardinal process was 'small, bilobed, trilobed or multilobed'.

In the twenty species of *Isorthis* which have been studied, the biconvexity varies from almost plano-convex to sub-equally convex. Silurian species generally have a simple cardinal process. Some Devonian species have a bilobed process.

Isorthis orbicularis (J. de C. Sowerby)

Plate 63, figs 1-15; Plate 64, figs. 1-14; Plate 65, figs. 30-31

- 1839 *Orthis orbicularis* J. de C. Sowerby in Murchison, p. 611, pl. 5, fig. 16 (non fig. 15).
 non 1924 *Dalmanella orbicularis* McLearn, p. 56, pl. 4, fig. 7.
 non 1942 *Dalmanella orbicularis* Dahmer, *Senckenbergiana*, 25, p. 116, figs. 14-16.
 non 1951 *Dalmanella orbicularis* Dahmer, pp. 91-94, pl. 7, fig. 1; pl. 9, figs. 20-21; pl. 10, fig. 6;
 pl. 11, fig. 22; pl. 12, fig. 10.
 non 1960 *Isorthis orbicularis* Boucot *et al.*, p. 5, p. 1, figs. 13-20; pl. 2, figs. 1-7.

Diagnosis. Unequally biconvex, sulcate, with circular to transversely elliptical outline. Median ridge of pedicle valve narrow, rounded, extending to centre of valve and separating sub-parallel diductor tracks which do not extend into anterior half of valve. Posteriorly, the median ridge separates a pair of short semi-elliptical adductor impressions.

Brachial valve adductor muscle field well impressed, bounded by sub-circular raised margin, confined to posterior half of valve and distinctly quadripartite. Median ridge relatively wide and constant in width, posteriorly thickened between brachiophores. Muscle impressions sub-equal. Brachiophores short, divergent, and slightly flaring blades. Cardinal process non-lobed.

Comparison. The distinctions between *I. orbicularis* and the other isorthids described in this paper are given under the respective species. *I. orbicularis* has been confused with *Salopina lunata* but these are now seen to represent different genera. *I. orbicularis* has also been confused with *I. fornicatuncurvata* Fuchs. The more elongate and less distinctly, less constantly quadripartite adductor muscle field of the later species, however, together with greater convexity of the brachial valve, clearly distinguish it.

Description. Unequally biconvex to almost plano-convex, with pedicle valve at least twice as deep as brachial valve. Circular to transversely elliptical outline with well-

rounded cardinal angles. Anterior commissure crenulate and slightly sulcate, lateral commissure straight. Hinge line equal to two-thirds of greatest width, which is at mid-length. Width slightly greater than length, thickness almost half length.

Exterior of pedicle valve. Evenly convex with distinct beak projecting one-sixth total length posterior to hinge line. Delthyrium margins subtending about 60° . Lateral margins of the interarea smoothly rounded.

Exterior of brachial valve. Slightly convex with shallow median sulcus widening from umbo to anterior margin where it equals about one-third of shell width. Lateral margins of sulcus not sharply defined. Outline, sub-circular to transversely elliptical with antero-lateral margins rather more rounded than postero-lateral margins. Interarea anacline. Notothyrium enclosing about 60° .

The pattern of rib branching in the median area of the brachial valve consists of a median pair of P I, with P Is, P It and P I 2nd, and P II with P IIs. At 5 mm. length all these except sometimes P It, have appeared (see text-fig. 1).

Interior of pedicle valve. A low, rounded, narrow median ridge extends from the delthyrial cavity to almost mid-length where it fades gradually. In the posterior part of the delthyrial cavity this ridge separates short subelliptical adductor scars, often well impressed. Anterior to the adductor impressions the sub-parallel diductor tracks are separated by the median ridge and end with rounded margins at mid-length. Laterally the diductor tracks are bounded by straight sub-parallel or slightly convergent ridges which extend forward from the dental lamellae, decreasing in height to mid-length.

The teeth, which bear crural fossettes on their medial surfaces, are supported by dental lamellae which diverge slightly ventro-laterally before converging towards the floor of the delthyrial cavity. A small pedicle callist is present.

Interior of brachial valve. The well-impressed adductor muscle field is confined to the posterior half of the valve, and is bounded by a circular to slightly elongate raised margin, which merges posteriorly with the bases of the brachiophores and anteriorly fades as it curves towards the median ridge. A less well-developed pair of ridges runs antero-laterally from the junction of the anterior and posterior pairs of adductors. Four adductor impressions of sub-equal size are separated by a broad, low, rounded median ridge which is about one-quarter to one-third as wide as the muscle field and by narrower transverse ridges which are either parallel to the hinge line or directed slightly postero-laterally. This arrangement of ridges separating the muscle impressions gives a distinctive 'cross' pattern. Short, stubby, plate-like brachiophores flare antero-laterally. Antero-laterally directed sockets are supported by fulcral plates or, often in larger specimens, by socket pads.

The cardinal process has a cylindrical shaft and a conical non-lobed myophore.

Anterior crenulations are low, rounded without median grooves and are evenly spaced. Pallial marks are rarely seen but a pair of trunks running anteriorly from the adductor impressions divide before reaching the anterior margin. From the same origin a second pair run lateral to them.

Variation in muscle field. Most variation occurs in the brachial muscle field where the highly symmetrical cross pattern may be extended to an elongate, roughly elliptical outline with irregularly raised margins and transverse ridges which are obscure or faint, depending upon the degree of impression of the muscle scars. The pedicle valve shows some slight variation in the ridges bounding the diductor tracks. These ridges may be

straight and almost parallel, straight but slightly convergent anteriorly, or slightly curved (convex outwards).

Type specimens. This species was first described by J. de C. Sowerby (*in* Murchison, *Silurian System*, p. 611). It was figured pl. 5, fig. 16 which is a multiple figure. The figured specimens are in the collection of the Geological Survey and Museum of Great Britain and are believed to be related to fig. 16 as follows:

Geol. Soc. Colln. No. 6647 is taken to be the original of pl. 5, fig. 16, top left. Geol. Soc. Colln. No. 6648 is thought to be the original of fig. 16, bottom left, top right, and bottom right, but GSM 33239 may also have been used in drawing fig. 16, bottom right.

Geol. Soc. Colln. No. 6647 is a poorly preserved internal mould of a pedicle valve. Geol. Soc. Colln. No. 6648 is a complete shell and GSM 33239 is a poorly preserved exterior of a brachial valve.

In his brief description of *O. orbicularis*, J. de C. Sowerby (*Silurian System*, p. 611) mentions many localities in the Welsh Borderlands, but does not state the horizon or localities from which his specimens figured in pl. 5, fig. 16 were obtained.

Davidson (1869, pp. 215 and 218) included this species in *O. lunata*. McLearn (1924, p. 56) records *D. orbicularis* (J. de C. Sowerby) as occurring rarely in boulders in Stonehouse field at Arisaig, Nova Scotia—'probably from zone D of the Stonehouse Formation'. From his illustration pl. 4, fig. 7, it is not possible to say whether this is *I. orbicularis* but examination of a large collection of material from the Stonehouse Formation has failed to reveal a single specimen of *I. orbicularis*. *I. cf. fornicatumcurvata* Fuchs, however, not referred to by McLearn is fairly abundant—and it seems likely that this record of *I. orbicularis* from Arisaig is mistaken.

Dahmer (1951, p. 91) stated that the type was the specimen figured in *Silurian System*, pl. 5, fig. 16, but quoted two specimen numbers, 6647 and 6648, and referred to 'the figured ventral valve'. No. 6647 is a pedicle valve but 6648 is a complete shell. His selection of a type is thus not clear and in order to clarify the situation, Geol. Soc. Colln. No. 6647 is here selected as the lectotype. Geol. Soc. Colln. No. 6648 and GSM 33239 are figured syntypes. Specimens numbers 6647 and 6648 are refigured, pl. 65, figs. 30 and 31. It should be noted, however, that the species from the Ebbe Sattel of Germany described and figured by Dahmer as *D. orbicularis* is a different species, *I. fornicatumcurvata* (Fuchs). Despite the fact that Dahmer put this latter species in synonymy with *I. orbicularis*, the two species are quite distinct, as detailed under Comparison, above p. 465.

Boucot, *et al.* (1960, p. 5, pl. 1, figs. 13–20 and pl. 2, figs. 1–7) described a species from the Sutherland River Formation of Devon Island (Canadian Arctic Archipelago), as *I. orbicularis* and recorded the occurrence as the first known from North America. Examination of these silicified shells has revealed, however, that they differ in a number of important characteristics from *I. orbicularis*. In particular, the absence of a sulcus; the lack of transverse ridges and the faintness of the median ridge in the brachial muscle field, which is thus not distinctly quadripartite and is only weakly impressed; the relatively shorter hinge line and the narrow double median ridge in the pedicle valve (see Boucot, pl. 2, fig. 3).

Distribution. *I. orbicularis* is a common shell in the shelly facies of the Ludlovian of the Welsh Borderland. It ranges from the base of the Ludlovian (lowest Eltonian) to the lower part of the Whitcliffian but is most abundant in the lower Leintwardinian. In the basin facies of the Ludlovian in Central Wales, it has been recorded as common in the 'lower siltstone group' (see Lawson, 1960, p. 121), and rare or absent above the zone of *Monograptus leintwardinensis*.

It has been recorded from several places outside Britain but examination of Boucot's collections from Gotland, Germany, Podolia, New Brunswick, Nova Scotia, Quebec and Maine reveals that the isorthids in these areas are different species from *I. orbicularis*, several of them being new species which are being described in a separate paper. So far, no specimens of *I. orbicularis* (J. de C. Sowerby) have been seen by the author from localities outside the Welsh Borderland.

Isorthis slitensis sp. nov.

Plate 62, figs. 23–35.

Diagnosis. Unequally biconvex, faintly sulcate, sub-circular outline with only slightly rounded cardinal angles. Median ridge of pedicle valve narrow, carinate to rounded,

extending into anterior half of valve and separating wide parallel diductor tracks. Brachial valve adductor muscle field moderately well impressed, bounded by circular raised margin, extending into anterior half of valve, distinctly quadripartite, muscle impressions of equal size. Median ridge of constant width, thickened posteriorly between brachiophores. Brachiophores moderately thick, straight, divergent blades.

Comparison. This species is very close to *I. orbicularis*, but is distinguished by having the following: (i) less circular outline with less rounded cardinal angles, (ii) sulcus less defined, (iii) the valves of almost equal length, (iv) both pedicle and brachial valve muscle fields relatively longer, extending into the anterior half of the shell.

Description. Unequally biconvex to almost plano-convex with pedicle valve at least twice as deep as the brachial valve. Circular to sub-quadrate outline with cardinal angles only slightly rounded and antero-lateral margins well rounded. Anterior commissure crenulate, slightly sulcate, lateral commissures straight. Hinge line equal to two-thirds of greatest width which is at mid-length. Width slightly greater than length, thickness slightly more than half of the length.

Exterior of pedicle valve. Evenly convex with distinct beak which barely projects posterior to the brachial valve. Lateral margins of the interarea smoothly rounded. Margins of delthyrium enclosing 60°.

Exterior of brachial valve. Slightly convex with faint median sulcus widening anteriorly. Outline somewhat shield-shaped with cardinal angles only slightly rounded. Interarea anacline. Notothyrium enclosing about 70°, partially filled by the cardinal process which protrudes slightly. The branching of the costellae in the median area of the brachial valve results in P I and P II having P Is and P IIs at 5 mm. length. Tertiary and second order branches appear only at or after this stage.

Interior of pedicle valve. A median ridge, carinate in small forms, becoming rounded in larger shells, extends from the delthyrial cavity to about mid-length of the valve where it ends in a gradual slope. In one large shell the median ridge bears a very faint median groove on its posterior two-thirds. No separate adductor impressions are seen. Parallel diductor tracks which extend beyond the anterior end of the median ridge and are separated by it, terminate imperceptibly just anterior to mid-length. Laterally the diductor tracks are defined by low ridges extending forward from the bases of the dental

EXPLANATION OF PLATE 63

Figs. 1-15. *Isorthis orbicularis* (J. de C. Sowerby). 1-4, Early Leintwardinian, south end of old quarry, behind Darran Farm, Usk inlier, Britain (Nat. Grid Ref. 32759795). 1, Internal mould of pedicle valve ($\times 3$), GSM 102239. Note impressions of adductor and diductor muscles. 2, Latex impression ($\times 3$) of same specimen. Note diductor tracks confined to posterior half of valve. 3, Enlarged view ($\times 5$) showing adductor and diductor impressions and subparallel dental lamellae. 4, Side view of specimen in fig. 1, showing absence of delthyrial platform. 5-8, Early Bringewoodian, roadside quarry at Porth-llong, Usk inlier, Britain (Nat. Grid Ref. 35209780), posterior view ($\times 3$), internal mould of pedicle valve ($\times 2$), GSM 102240, latex impression ($\times 2$) and enlarged ($\times 5$). Note adductor scars in relation to the narrow median ridge. 9-15, Early Leintwardinian, south end of old quarry behind Darran Farm, Usk inlier, Britain (Nat. Grid Ref. 32759795). 9-10, Internal mould of brachial valve ($\times 2$), GSM 102241, and latex impression ($\times 2$). 11-12, External mould of brachial valve ($\times 2$), GSM 102242, and latex impression ($\times 2$). 13-15, Internal mould of brachial valve ($\times 2$), GSM 102243, latex impression ($\times 2$) and enlarged view of mould ($\times 5$). Note adductor muscle field confined to posterior half of valve and also vascular trunks.



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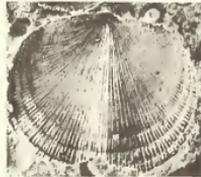
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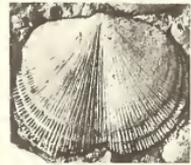
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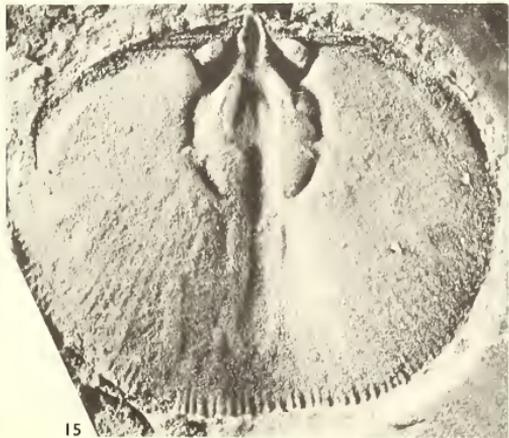
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lamellae. The ridges terminate opposite the anterior end of the median ridge. The teeth are strong, have a rounded lateral profile, and deeply incised crural fossettes on the anterior edges of their medial faces. Dental lamellae diverge slightly outwards before converging slightly towards the floor of the delthyrial cavity. A small pedicle callist is present.

Interior of brachial valve. Well-impressed adductor muscle scars form a distinct quadripartite pattern surrounded by a circular to slightly elongate raised margin, the lateral portions of which fuse with the brachiophore bases. Anteriorly the raised margin decreases as it curves in towards the median ridge. The median ridge, which is broad and low, equals about one-quarter of the width of the muscle field. Transverse ridges caused by the deeper impressions of the anterior pair of muscle scars are parallel to the hinge line. The muscle scars are of equal size.

The brachiophores diverge from the inner margins of the notothyrium, with a slight flare, at about 74° from each other. They are fairly thick stubby plates with a carinate posterior edge and bluntly rounded extremities. The postero-lateral faces of the brachiophores merge into fuleral plates which floor the sockets or into socket pads. The triangular sockets widen antero-laterally and are slightly roofed over at the posterior end by the interarea. The cardinal process, which arises from a posterior thickened and raised portion of the median ridge (notothyrial platform), has a short, thick cylindrical shaft and a conical myophore which largely fills the notothyrium from which it protrudes slightly. This projecting posterior portion of the myophore bears five or six fine crenulations arranged in a chevron pattern with apices directed anteriorly. Along the anterior margin of the valve, the crenulations are low and rounded with narrower interspaces.

Holotype. GSM 102235, brachial valve (figured Pl. 62, figs. 28–32). Slite Marl (Wenlockian). Canal ditch 800 m. south-west of Alby (north of Lergravsviken), parish of Rute, Gotland.

Paratypes. GSM 102234, whole shell (figured Pl. 62, figs. 23–27); GSM 102236, pedicle valve (figured Pl. 62, fig. 33); GSM 102237, pedicle valve (figured Pl. 62, fig. 34); and GSM 102238, pedicle valve (figured Pl. 62, fig. 35). Slite Marl (Wenlockian). Cement plant Quarry at Slite, Gotland.

Distribution. This species has only been seen in material collected by Boucot from the Slite Marl of Gotland. Additional material was kindly provided by Dr. Hede from the same beds but from a different locality. It is not present in collections available from other horizons in Gotland, nor is it present in collections from other areas. The age of the Slite Marl is given (Regnell and Hede, 1960, p. 49) as Wenlockian. According to Boucot (verbal communication) it is probably—but not certainly—Upper Wenlockian. The close similarity between *I. slitensis* of Wenlockian age and *I. orbicularis* of Ludlovian age suggests that the latter may have been derived from the former. It is also the reason for including a Gotland shell in this paper as comparisons are thereby made easier.

Isorthis amplificata sp. nov

Plate 61, figs. 1–30

1869 *Orthis crassa* Lindstrom; Davidson, p. 213, pl. 27, figs. 18 and 19a (non fig. 17).

Diagnosis. Unequally biconvex, faintly sulcate with circular to transversely elliptical outline. Median ridge of pedicle valve low, flat, moderately wide for about one-third of the valve length then tapering gently; separating diductor tracks which do not reach mid-length.

Brachial valve adductor muscle field well impressed, bounded by circular raised margin extending well into anterior half of valve; distinctly quadripartite. Median ridge

narrows between larger anterior pair of impressions, and posteriorly thickens between the brachiophores. Brachiophores distinctive, very thick, straight, erect, only slightly divergent; their posterior edges separated only by the width of the cardinal process. Sockets large and deep; teeth massive.

Comparison. This species is fairly close to *I. orbicularis* but is distinguished by the following:

(i) Unusually thick non-flaring brachiophores which almost meet at their bases and which have a posterior edge aligned normal to the commissure plane, whereas in *I. orbicularis* the posterior edge is only slightly oblique to this plane and the brachiophores are thinner and flare outwards as they diverge.

(ii) More massive teeth with deeper crural fossettes and larger sockets.

(iii) The wider median ridge and absence of distinct adductor scars in the pedicle valve.

(iv) Pear-shaped outline of the muscle field in the brachial valve.

There is an amplification, especially of teeth and brachiophores, to which the name refers.

Description. Unequally biconvex, with pedicle valve twice as deep as brachial valve. Outline sub-circular to transversely elliptical with rounded cardinal angles. Anterior commissure crenulate and gently sulcate, lateral commissure straight. Hinge line slightly greater than half the greatest width which is slightly posterior to mid-length. Width slightly greater than length, thickness almost half the length.

Exterior of pedicle valve. Evenly convex with well-developed beak which overhangs the pedicle interarea and is almost in contact with the beak of the brachial valve. The pedicle beak projects one-tenth of total length beyond the hinge line. Lateral margins of interarea sharp.

Exterior of brachial valve. Slightly convex with a very shallow sulcus widening from the umbo to the anterior margin. Lateral margins of sulcus indefinite. Outline transversely elliptical. Cardinal angles rounded. Interarea orthocline. Notothyrium having margins which diverge only slightly, partly filled by myophore of the cardinal process which protrudes slightly. The pattern of branching of the costellae in the median area of the brachial valve is P I + P Is + P It + P I 2nd and P II + P IIs, all of which have been produced at the 5 mm. stage.

Interior of pedicle valve. A low, rounded median ridge extends from the delthyrial cavity to the centre of the valve where it ends in a gentle slope. The posterior extremity of the delthyrial cavity is flat. Adductor scars are not seen. Parallel, well impressed, narrow diductor tracks separated by the median ridge, extend to the anterior end of the ridge where they terminate with rounded margins. Low extensions of the dental lamellae bound the diductor tracks laterally. The thick vertical dental lamellae support massive teeth, whose anterior extremities are ridge-like, directed antero-laterally. The medial faces of the teeth bear deeply cut crural fossettes which are straight and inclined antero-ventrally. The posterior faces of the teeth bear accessory sockets directed antero-laterally. No pedicle callist seen.

Interior of brachial valve. Well impressed, pear-shaped adductor muscle field defined by raised margins which posteriorly fuse with the anterior edges of the brachiophore bases and anteriorly decrease towards the median ridge. In one specimen, short, low

oblique ridges extend outwards from the central part of each margin in an antero-lateral direction (see Pl. 61, fig. 18).

Muscle field equals almost two-thirds shell length and over one-third greatest width. The median ridge is narrow and rounded between anterior pair of impressions but becomes wider and flatter between posterior pair. The anterior pair is larger and sub-elliptical, posterior pair trigonal and not always clearly separated. The anterior pair well impressed. When the posterior pair is also well impressed, the transverse ridge, normal to the median ridge, emphasizes the quadripartite character.

The brachiophores are very thick, straight, erect, and proximally are separated posteriorly only by the width of the cardinal process. Distally they diverge slightly, their bases merging with the raised margin of the muscle field. In some specimens fulcral plates are visible, joining the postero-lateral surface of the brachiophore to the posterior edge of the valve and flooring the sockets which are partially excavated beneath the interarea. Sockets are large and widely divergent and sometimes crenulated. The cardinal process arises as a short shaft between the posterior edges of the brachiophores and expands to a bulbous non-lobed myophore which partially protrudes from the notothyrium.

Crenulations of the anterior shell margin are low and evenly rounded with rounded interspaces.

Holotype. GSM 102214, internal mould of brachial valve (figured Pl. 61, fig. 16). Siltstone immediately above Wenlock Limestone (? latest Wenlockian/earliest Ludlovian). Old Quarry, at Cwm, Usk inlier, Britain (Nat. Grid Ref. 33320160).

Paratypes. GSM 102207, internal mould of pedicle valve (figured Pl. 61, fig. 3). Siltstone immediately above Wenlock Limestone (? latest Wenlockian/earliest Ludlovian). Bank in field, 600 yards north-west of Porth-llong, Usk inlier, Britain (Nat. Grid Ref. 34829825).

GSM 102216, brachial valve (figured Pl. 61, figs. 20–24) and GSM 102218, whole shell (figured Pl. 61, figs. 26–30). Wenlock Limestone (Wenlockian). Old Quarry on west side of Lincoln Hill, Iron Bridge, Britain (Nat. Grid Ref. 670038).

Distribution. This species occurs commonly in the four to six feet of buff and rust-coloured decalcified siltstones immediately overlying the Wenlock limestone in the Usk inlier. In these beds the shells have been dissolved and very clear internal and external moulds were collected, the majority being moulds of the brachial valve. Boucot collected shells, here considered to be conspecific, from the Wenlock limestone at Iron Bridge, Shrewsbury (Grid Ref. 670038 Old Quarry on west side of Lincoln Hill). So far, these are the only known occurrences of this species, the age of which is Wenlockian and possibly earliest Ludlovian. (See Walmsley, 1959, pp. 487 and 506–7 for discussion of the age of the beds at Usk).

Isorthis clivosa sp. nov.

Plate 61, figs. 31–38; Plate 62, figs. 1–22

Diagnosis. Unequally biconvex, nonsulcate to faintly sulcate with circular to transversely elliptical outline.

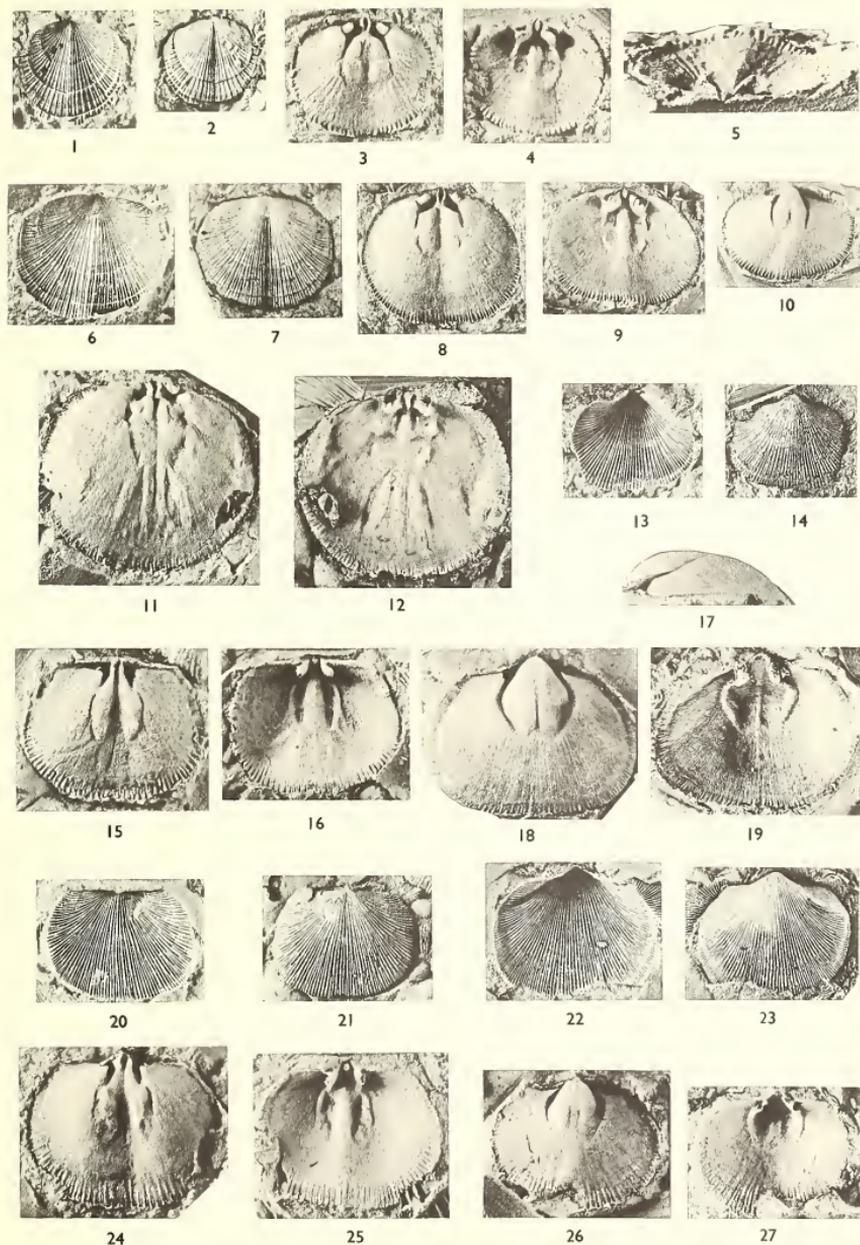
Median ridge of pedicle valve wide, ending in broad slope and separating narrow deeply impressed diductor tracks. Well marked vascular grooves diverge from anterior ends of diductor tracts toward anterior margin. Brachial valve has distinctly quadripartite adductor muscle field bounded by circular raised margin not extending into anterior half of valve. Median ridge narrows between larger anterior pair of impressions. Dental lamellae thick with flattened anterior edges. Brachiophores, divergent thin blades.

Comparison. This species is distinct from all other isorthids described here because of the pedicle valve's wide median ridge with its broad anterior slope, to which the name refers. In this respect it resembles *I. arcuvia* (Hall and Clarke) but differs from it in having a distinctly quadripartite muscle field in the brachial valve. In the combination of these two characters it resembles *I. szajnochai* Kozłowski, the type species of *Isorthis* but may be easily distinguished by its less convex brachial valve, the narrowing of the brachial valve median ridge anteriorly, the much lower pedicle valve median ridge, the shorter more curved pedicle valve interarea and the thinner brachiophores. It is possible that *I. szajnochai* was derived from *I. clivosa*, or a form close to it. *I. neocrassa* (Nikiforova) from the lower, (?) middle, Llandovery of the Siberian Platform appears to be very close to *I. clivosa* (see Nikiforova and Andreeva 1961, pp. 113–16 and pl. 18, figs. 1–21) but there are apparent differences in the muscle fields and cardinalia. *I. neocrassa* is possibly ancestral to *I. clivosa*.

Description. Unequally biconvex with pedicle valve having greater convexity. Outline sub-circular to transversely elliptical. Cardinal angles rounded. Anterior commissure crenulate and rectimarginate to faintly sulcate. Lateral commissure straight. Hinge line equal to half greatest width of shell which is at mid-length. Width equal to or slightly greater than length.

EXPLANATION OF PLATE 64

- Figs. 1–14. *Isorthis orbicularis* (J. de C. Sowerby). 1–2, Early Bringewoodian siltstone, roadside quarry at Porth-llong, Usk inlier, Britain (Nat. Grid Ref. 35209780), external mould of brachial valve ($\times 2$), GSM 102244, and latex impression ($\times 2$). Note sulcus and costellae. 3–5, Early Bringewoodian, bank in yard at Coed-y-paen Farm, Usk inlier, Britain (Nat. Grid Ref. 33479825), internal mould of brachial valve ($\times 3$), GSM 102245, latex impression ($\times 3$) and enlarged posterior view ($\times 5$) of impression showing flaring brachiophores and small myophore. 6–7, Early Leintwardinian, south end of old quarry behind Darran Farm, Usk inlier, Britain (Nat. Grid Ref. 32759795), external mould of brachial valve ($\times 2$), GSM 102246, and latex impression ($\times 2$). 8–9, Early Leintwardinian, roadside 1,000 yards west of Dinham Bridge, Ludlow area, Britain (Nat. Grid Ref. 49817441), internal mould of brachial valve ($\times 2$), GSM 102247, and latex impression ($\times 2$). 10, Early Bringewoodian, roadside quarry at Porth-llong, Usk inlier, Britain (Nat. Grid Ref. 35209780), internal mould of pedicle valve ($\times 2$), GSM 102248. Note transverse form and slightly curved dental lamellae. 11–14, Early Leintwardinian, south end of old quarry behind Darran Farm, Usk inlier, Britain (Nat. Grid Ref. 32759795). 11–12, Internal mould of brachial valve of large gerontic specimen ($\times 2$), GSM 102249, and latex impression ($\times 2$). Note vascular trunks. 13–14, External mould of pedicle valve ($\times 2$), GSM 102250, and latex impression ($\times 2$).
- Figs. 15–27. *Salopina lunata* (J. de C. Sowerby). 15–19, Early Leintwardinian siltstone, south end of old quarry behind Darran Farm, Usk inlier, Britain (Nat. Grid Ref. 32759795). 15–16, Internal mould of brachial valve ($\times 3$), GSM 102251, and latex impression ($\times 3$). 17, Side view of specimen in fig. 18 ($\times 3$). 18–19, Internal mould of pedicle valve ($\times 3$), GSM 102252, and latex impression ($\times 3$). 20–23, Late Whitcliffian, 700 yards north of Mary Knoll House, Ludlow area, Britain (Nat. Grid Ref. 48217429). 20–21, External mould of brachial valve ($\times 2$), GSM 102253, and latex impression ($\times 2$). Note posterior costellae, subparallel to hinge line. 22–23, External mould of pedicle valve ($\times 2$), GSM 102254, and latex impression ($\times 2$). 24–25, Whitcliffian, trackside 220 yards NNW. of Upper Berthlwyd Farm, Usk inlier, Britain (Nat. Grid Ref. 37470600), internal mould of brachial valve ($\times 3$), GSM 102255, and latex impression ($\times 3$). Note wide median ridge and anterior crenulations. 26–27, Early Leintwardinian, south end of old quarry behind Darran Farm, Usk inlier, Britain (Nat. Grid Ref. 32759795), internal mould of pedicle valve ($\times 3$), GSM 102256, and latex impression ($\times 3$). Note slightly raised median area and medially concave dental lamellae.



Exterior of pedicle valve. Evenly convex with beak projecting about one-seventh shell length posterior to hinge line. Margins of delthyrium subtending about 50°. Lateral margins of interarea sharp.

Exterior of brachial valve. Convex, with very faint wide median sulcus in some specimens. Outline transversely subelliptical, interarea one-third as long as in pedicle valve, anacline.

Interior of pedicle valve. A wide, long median ridge arising in the posterior part of the delthyrial cavity, extends forward to the centre of the valve where it descends in a broad slope to the valve floor. In the posterior half of the delthyrial cavity, faint, narrow adductor tracks flank the median ridge which anteriorly separates narrow, deeply impressed, slightly divergent diductor tracks extending to the end of the median ridge. Beyond this point vascular grooves continue in the line of the diductor tracks, diverging and fading towards the anterior margin. Laterally the diductor tracks are defined by forward extensions of the vertical dental lamellae which are fairly thick and have flattened anterior edges. In some specimens they extend well beyond the end of the median ridge, lateral to the vascular grooves. Teeth moderately large, with blunt extremities, laterally directed accessory sockets and shallow crural fossettes in the commissural plane. A small pedicle callist is present.

Interior of brachial valve. A well-impressed brachial adductor muscle field confined to the central third of the posterior half of the valve, is bounded by sub-circular raised margins which posteriorly fuse with the bases of the brachiophores and anteriorly decrease towards the median ridge. The median ridge is rounded and narrow—equal to one-seventh of the width of muscle field—between the larger anterior pair of impressions and wider between the posterior pair. The anterior pair is more deeply impressed than the posterior impressions, resulting in a marked step across the muscle field normal to the median ridge, and a quadripartite aspect.

The brachiophores are thin blades with vertical anterior edges, diverging at 60°. They bound the moderately large sockets which are raised on socket pads. The cardinal process arises with a very short shaft from the posteriorly thickened median ridge between the brachiophores. The myophore is bulbous and non-lobed.

Holotype. GSM 102232, internal mould of pedicle valve (figured Pl. 62, fig. 19). Late Leintwardinian. Roadside exposure 1,230 yards east-north-east of Mary Knoll House, Ludlow area (Nat. Grid Ref. 49227407).

Paratypes. GSM 102228, internal mould of brachial valve (figured Pl. 62, fig. 11). Mid Eltonian. Trackside, 300 yards south of Hafod-Fawr, Llandovery area (Nat. Grid Ref. 81443096).

GSM 102229, internal mould of pedicle valve (figured Pl. 62, fig. 13). Early Bringewoodian. Roadside on A. 40, 190 yards west-north-west of Ynys-y-Bont, Llandovery area (Nat. Grid. Ref. 83723225).

GSM 102230, internal mould of pedicle valve (figured Pl. 62, fig. 15). Mid Eltonian. Stream bank 600 yards south-east of Esgair Ilaethdu, Llandovery area (Nat. Grid Ref. 79022926).

Distribution. *I. clivosa* associated with *I. orbicularis* occurs fairly commonly in material presented to the writer by Dr. J. Price from the Black Cock Beds (= middle and upper Eltonian) and the lower Cwm Clŷd Beds (= lower Bringewoodian) of the Llandovery area in Wales. Material collected by Dr. Boucot from the Rhumney River section, Cardiff, S. Wales (Nat. Grid Ref. 200794) also contains both species. In the writer's collections from the Welsh Borderland *I. clivosa* occurs extremely rarely in Upper Forest Beds (lower Bringewoodian) of Usk and the Lower and Upper Leintwardine Beds of the Ludlow anticline, in all cases associated with abundant *I. orbicularis*. In a small collection from the Lower Leintwardine Beds of Oreleton, presented by Dr. Lawson, two specimens of *I. clivosa* were found. Poorly located material from the Ludlovian of the Denbigh Moors (N. Wales) also contained two specimens of *I. clivosa*. In the British Ludlovian, therefore, the known range is from middle

Eltonian to upper Leintwardinian and this species seems to have been more common in the basin facies, rarely moving into the shelf area. The writer has identified this species, however, in collections made by Boucot from the upper Wenlockian of Golden Grove, near Llandeilo (Wales), and from the Canaston Beds (Upper Llandovery) of Pembrokeshire (Wales).

It also occurs in New Brunswick, Canada, in beds believed to be of Upper Llandovery age and also in beds of Ludlovian age. (Boucot, Johnson, Harper, and Walmsley—in press).

Collections from various localities in Maine—determined by Boucot as Upper Llandovery (C₁)—Lower Wenlock and Lower Ludlow in age, and a collection of Upper Llandovery (C₃)—Ludlow age from the Merida Andes of Venezuela also contain *I. clivosa*. An account of these occurrences is in preparation.

The total known range to date, therefore, is from Upper Llandovery to Upper Leintwardinian.

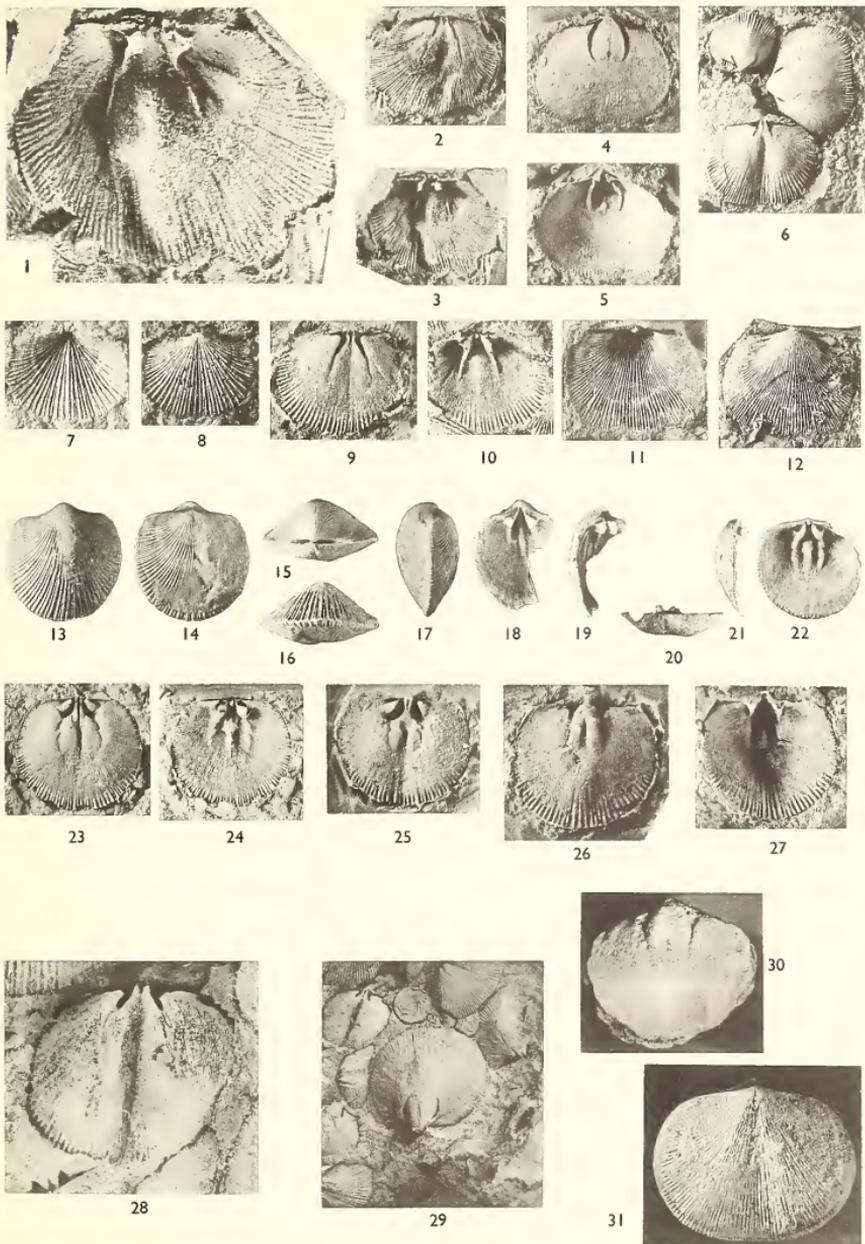
Isorthis scuteformis, sp. nov.

Plate 65, figs. 13–27

Diagnosis. Unequally biconvex isorthis, non-sulcate to faintly sulcate, with shield-shaped outline and lacking a delthyrial platform in the pedicle valve.

EXPLANATION OF PLATE 65

- Figs. 1–12. *Salopina lunata* (J. de C. Sowerby). 1–3, Late Whitcliffian siltstone, 700 yards north of Mary Knoll House, Ludlow area, Britain (Nat. Grid Ref. 48217429). 2–3, Internal mould of brachial valve ($\times 2$), GSM 102257, and latex impression ($\times 2$). 1, is enlarged view of latter ($\times 5$) to show flexure where the muscle field margin joins the base of the brachiophore. 4–5, Late Whitcliffian, trackside 100 yards north of Brook Farm, Usk inlier, Britain (Nat. Grid Ref. 32329768), internal mould of pedicle valve ($\times 2$), GSM 102258, and latex impression ($\times 2$). 6, Early Leintwardinian, trackside 200 yards NNE. of Hilla Farm, Uskin lier, Britain (Nat. Grid Ref. 37770688), internal moulds of brachial and pedicle valves ($\times 2$), GSM 102259, showing common preservation. 7–8, Late Leintwardinian, small quarry 400 yards NW. of Walnut Tree Farm, Usk inlier, Britain (Nat. Grid Ref. 33059680), external mould of brachial valve ($\times 3$), GSM 102260, and latex impression ($\times 3$). 9–12, Late Whitcliffian 700 yards north of Mary Knoll House, Usk inlier, Britain (Nat. Grid Ref. 48217429). 9–10, Internal mould of brachial valve ($\times 3$), GSM 102261, and latex impression ($\times 3$). 11–12, External mould of pedicle valve ($\times 2$), GSM 102262, and latex impression ($\times 2$).
- Figs. 13–22. *Isorthis scuteformis scuteformis* subsp. nov. Early Eltonian mudstone, railway cutting, eastern entrance to Ledbury Tunnel, Malvern area, Britain (Nat. Grid Ref. 386724). 13–17, Pedicle valve, brachial valve, posterior, anterior, and side views ($\times 2$), GSM 102263, Paratype. Note shield-shaped outline. 18–19, Interior of pedicle valve ($\times 2$), GSM 102264, Paratype, and oblique view of same specimen ($\times 2$) to show teeth. 20–22, Posterior, side, and interior views ($\times 3$), GSM 102265, Holotype. Note constant width of median ridge and continuous, fairly straight margins of adductor muscle field.
- Figs. 23–27. *Isorthis scuteformis uskensis* subsp. nov. 23–24, Eltonian siltstone, 150 yards SE of Prescoed Farm, Usk inlier, Britain (Nat. Grid Ref. 34959962), internal mould of brachial valve ($\times 2$), GSM 102266, Holotype, and latex impression ($\times 2$). Note larger anterior pair of adductor impressions, disjunct curved margins of muscle field, and anteriorly narrowed median ridge. 25–27, Late Eltonian, trackside 1,000 yards north of Llangibby Castle, Usk inlier, Britain (Nat. Grid Ref. 36509825). 25, Internal mould of brachial valve ($\times 3$), GSM 102267, Paratype. 26–27, Internal mould of pedicle valve ($\times 3$), GSM 102268, Paratype, and latex impression ($\times 3$). Note shield-shaped outline, pedicle callist, and short median ridge, small pointed teeth and anterior crenulations.
- Figs. 28–29. *Salopina lunata* (J. de C. Sowerby), GSM 51555. 28, Internal mould of brachial valve ($\times 5$), Lectotype. Same specimen shown top left (left of round spot) ($\times 1\frac{1}{2}$) in order to define the position of lectotype on the slab GSM 51555. Note, specimens on this slab all somewhat distorted (see p. 461). Museum label on this specimen states 'Oaker Quarry'.
- Figs. 30–31. *Isorthis orbicularis* (J. de C. Sowerby). Horizons and localities not known. 30, Internal mould of pedicle valve ($\times 2$), Lectotype. GSC 6647 (see p. 467). 31, Brachial valve of whole shell ($\times 2$). GSC 6648.



Comparison. *I. scuteformis* is distinguished from *I. orbicularis* by its shield-shaped outline and general absence of a sulcus in the brachial valve which is relatively more elongate. *I. arcuaria* (Hall and Clarke) also has a shield-shaped outline and a non-sulcate brachial valve in which the adductor muscle field is not distinctly quadripartite but the pedicle valves of these two species are quite distinct in that *I. arcuaria* has a wide median ridge raised on a delthyrial platform which ends in a steep anterior slope.

Description. Unequally biconvex, with the pedicle valve having greater convexity. Distinctly shield-shaped outline with relatively straight lateral margins, only slightly rounded cardinal angles and antero-lateral margins which curve smoothly round to the anterior margin. Anterior commissure crenulate and rectimarginate, lateral commissures straight. Hinge line half as long as greatest width of shell, which is at mid-length. Thickness equal to half length.

Exterior of pedicle valve. Convex, slightly arched along mid-line. Beak distinct, projecting one-tenth total length beyond hinge line. Interarea with sharp lateral margins.

Exterior of brachial valve. Gently convex, non-sulcate or faintly sulcate. Outline distinctly shield-shaped. Interarea, anacline. Notothyrium with only slightly divergent margins.

Interior of pedicle valve. A relatively short, low, rounded median ridge extends from the delthyrial cavity to mid-length, where it fades gradually. It separates well-impressed sub-parallel elongate adductor tracks. Sub-parallel, low, forward extensions of the short dental lamellae bound the diductor tracks laterally and end opposite the anterior limit of the median ridge.

Interior of brachial valve. The well-impressed adductor muscle field occupies the median third of the posterior half of the valve and is bounded by raised margins which posteriorly fuse with the bases of the brachiophores and anteriorly terminate opposite the end of the median ridge.

The brachiophores are short, thin, flaring plates. Sockets are raised on socket pads. The cardinal process has a bulbous, non-lobed myophore which occupies the notothyrium.

Isorthis scuteformis scuteformis, subsp. nov.

Plate 65, figs. 13–22

This sub-species of *I. scuteformis* is characterized by the following: Pedicle valve: incurved beak, comparatively massive blunt teeth, which lack crural fossettes, and the absence of a pedicle callist. Brachial valve: adductor muscle field not distinctly quadripartite, bounded by continuous, almost straight, lateral margins. The median ridge is uniformly wide. The brachiophores, at the hinge line, are separated only by the width of the cardinal process which has a very short shaft. The sockets are short.

Holotype. GSM 102265, brachial valve (figured Pl. 65, figs. 20–22). Early Eltonian. Railway cutting at eastern entrance to Ledbury Tunnel, Malvern area (Nat. Grid Ref. 386724).

Paratypes. GSM 102263, whole shell (figured Pl. 65, figs. 13–17) and GSM 102264, pedicle valve (figured Pl. 65, figs. 18–19). Early Eltonian. Railway cutting at eastern entrance to Ledbury Tunnel, Malvern area (Nat. Grid Ref. 386724).

Distribution. This sub-species is present in material collected by Boucot from the Ludlovian (Eltonian) of the Malvern area, Britain (railway cutting near eastern entrance of Ledbury railway tunnel. Grid

Ref. 386724). It has not yet been seen in equivalent beds of the Ludlow area or in the other Welsh Borderland Eltonian localities, nor from other Ludlovian areas.

Isorthis scuteformis uskensis, subsp. nov.

Plate 65, figs. 23–27

This sub-species differs from *I. scuteformis scuteformis* by the following: Pedicle valve: beak is not incurved and the small, very pointed teeth bear deep crural fossettes. A pedicle callist is present. Brachial valve: adductor muscle field is distinctly quadripartite with the anterior pair of impressions considerably larger than the posterior pair. The margins of the muscle field are curved and disjunct. The median ridge narrows sharply where it passes between the anterior pair of impressions. The brachiophores are more widely separated from each other at the hinge line, the cardinal process has a long slender shaft and the sockets are deep.

Holotype. GSM 102266, internal mould of brachial valve (figured Pl. 65, fig. 23). Basal Lower Forest Beds (early Eltonian). 150 yards south-east of Prescoed Farm, Usk inlier (Nat. Grid Ref. 34959962).

Paratypes. GSM 102267, internal mould of brachial valve (figured Pl. 65, fig. 25) and GSM 102268, internal mould of pedicle valve (figured Pl. 65, fig. 26). Lower Forest Beds (late Eltonian). Trackside, 1,000 yards north of Llangibby Castle, Usk inlier (Nat. Grid Ref. 36509825).

Distribution. So far, this subspecies is known only from the Lower Forest Beds (Eltonian) of the Usk inlier. It is possible that it occurs elsewhere in the Eltonian but has been determined as '*Dalmanella orbicularis*'.

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All the specimens figured in this paper have now been deposited in the Geological Survey Museum, London, and bear GSM numbers.

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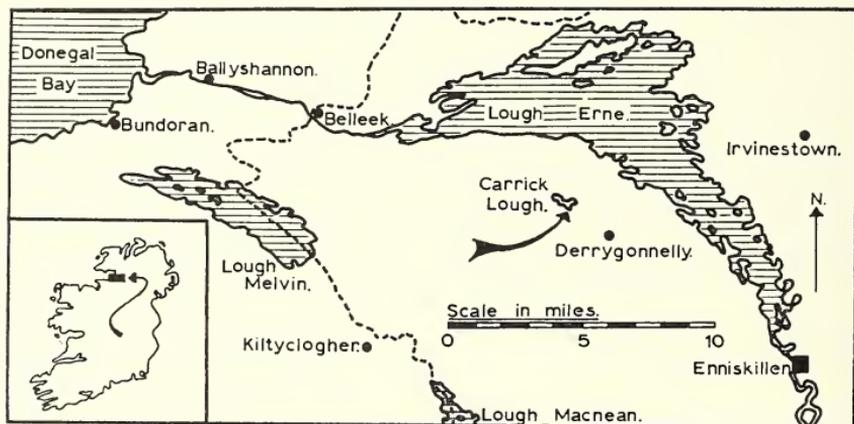
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A NEW FENESTRATE BRYOZOAN FROM THE LOWER CARBONIFEROUS OF COUNTY FERMANAGH

by R. TAVENER-SMITH

ABSTRACT. Collections of bryozoa made recently in south Fermanagh include numbers of small but complete *Fenestella*-like colonies. These show considerable morphological variation, but careful examination indicates that they all belong to a single homogeneous population. The sample is described, and it is considered that the distinctive pattern of branching shown by the colonies and the presence in each of a strongly developed proximal spine places them in a new genus, for which the name *Ptilofenestella* is proposed.

A COLLECTION of bryozoa has been made from thin beds of muddy limestone on the south side of Carrick Lough (text-fig. 1), County Fermanagh, Northern Ireland. The



TEXT-FIG. 1. The geographical situation of Carrick Lough.

strata occur not far below the local top of the Carboniferous Limestone and are probably of D_1 age, corresponding stratigraphically with the lower part of the Dartry Limestone (Oswald 1955) of the Leitrim-Sligo area. They are highly fossiliferous, and because the original fossil material has been to some extent replaced by silica, treatment of blocks with dilute hydrochloric acid has yielded a considerable fauna. This is characterized by the presence of large numbers of finely preserved bryozoan fragments of varying size and shape. Brachiopods, lamellibranchs, gastropods, trilobites, and sponges are also present but constitute only minor elements of the fauna. Representatives of the first three groups are usually of small size, serving still further to emphasize the predominantly bryozoan nature of the assemblage. Among the bryozoa,

fenestrate cryptostomes are most numerous and a preliminary examination of these showed the common presence of a distinctively shaped form that is the subject of this paper.

The colonies in question are quite small. Though varying considerably in size, they do not exceed a centimetre in length or 6 mm. in diameter. The zoarial shape is very characteristic, being hemispherical proximally but cylindrical distally, at which extremity it is open. The reticulate meshwork of branches and dissepiments forming the colonial skeleton thus presents the appearance of an elongate basket open at one end. The framework is strong, and this, coupled with its small size, probably accounts for the preservation of a large number of specimens.

Zoaria of this sort are associated in the collections with fenestellid fragments of many kinds, and it was at first thought that they represent the broken-off proximal extremities of larger funnel-shaped colonies of *Fenestella*. Closer examination showed that this is not so, because the ends of branches forming the zoarial baskets are usually not fractured, but are quite undamaged (Pl. 66, fig. 11). The specimens are therefore complete colonies, but the possibility remains that they are immature forms that were killed off at an early stage in development and segregated by current action. This is unlikely for several reasons. First, fossil material from the locality concerned is in general poorly sorted and shows no sign of having been carried far. Delicate structures like long, spiny outgrowths are commonly preserved without damage, for example. Again, if the basket-shaped colonies are all young forms the associated fauna would be expected to yield fragments with a comparable meshwork and appearance representing broken parts of larger, adult expansions. None satisfying this requirement was found in the course of examining more than 5,000 fenestellid fragments from the same locality and horizon. Finally, the arrangement of branches in the distal part of some of the longer zoaria suggests that these are in a late stage of development. A branch thus situated may in some cases be seen to terminate abruptly while the pair on either side of it grow more closely together beyond, so that the normal dissepimental length is soon re-established. When two or three branches fail in this way at several points round the periphery of the cylinder the diameter is reduced so that it begins to close in distally (Pl. 66, fig. 4). Branch failure of this kind, though by no means universal, is not uncommon among the larger specimens and similar occurrences in other stocks have been attributed by Elias and Condra (1957, p. 56) to a decline in the vigour of growth during the later, or gerontastic phase of colonial development. For these reasons it seems likely that the specimens are complete, fully developed zoaria which, by reason of their compact shape and structure, have been preserved without damage in considerable numbers.

EXAMINATION OF SPECIMENS

External features. Although all the colonies are basically alike in that they have a basket-like shape, they are quite variable in several respects, as even a cursory examination shows. The most obvious differences relate to the length of the basket (from 3 to 10 mm.), its diameter ($1\frac{1}{2}$ to 6 mm.), and the number of branches composing it (13–34). There is also considerable variation in the texture of the meshwork of branches and dissepiments forming the basket. Some colonies, not always the smallest, have a fine mesh in which the usual fenestrule size is about 0.22×0.57 mm., while in others, not always the largest,

the mesh is much coarser and fenestrules may be up to 0.44×0.88 mm. Less noticeable differences affect the spacing of zooecial apertures and carinal nodes, the size of apertures, and width of branches. In view of these differences an examination was carried out to determine the limits of morphological variation in the assemblage, and to ascertain whether more than one taxonomic group was represented.

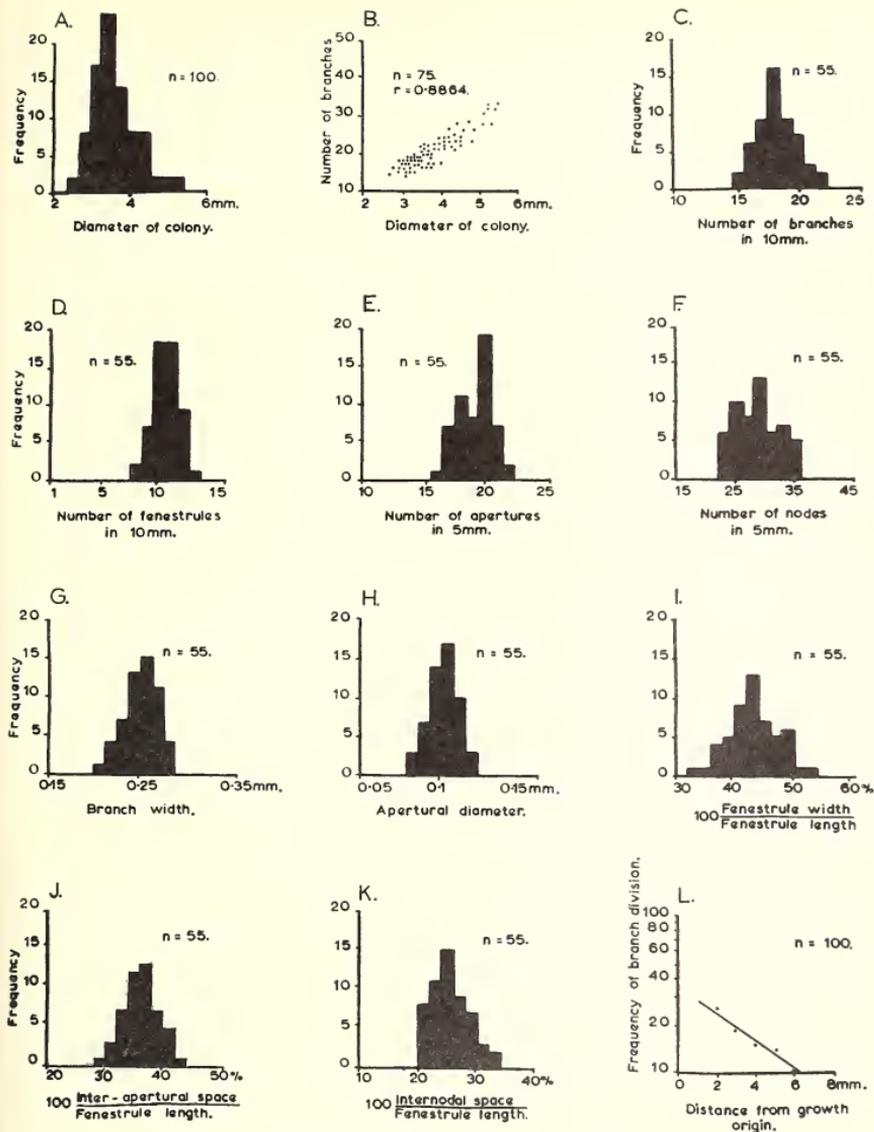
It seemed reasonable to examine at the outset the grosser differences of zoarial size and structure, with the exception of the length of colonies which is a function of age and therefore of no immediate interest. The range of zoarial diameter was determined by measuring this feature at a standard distance of 3 mm. from the growth origin (to eliminate possible effects due to age differences) in a hundred colonies chosen to be fairly representative of the collection. The resultant data were used to construct the histogram of text-fig. 2A. Next the diameter of seventy-five colonies was plotted against the number of branches composing them (text-fig. 2B), all readings being taken at the same distance from the proximal end as before. The two graphs demonstrate the existence of a continuous series in each case, and it is evident that differences in these respects noticed in the collection are those between end members of the series which, when viewed together, may differ considerably from one another. The second graph also shows that a fairly constant proportional relationship exists between the number of branches in a colony and its diameter. This explains why the meshwork of large and small colonies is often (though not always) of similar texture.

In order to examine the nature and extent of structural variability in greater detail a sample of fifty-five of the best preserved colonies was chosen so as to present as far as possible an adequate cross-section of the collection. Each of these was then measured for twelve variables, between ten and twenty readings being taken in every case, depending on the size and state of preservation of the specimen. Nearly 9,000 measurements were made, all being taken from the mature, cylindrical parts of zoaria, the short proximal ends being avoided because of the difficulty of making accurate measurements there due to the strong curvature of the meshwork. The dimensions recorded were as follows:

(a) Those regarded as standard in systematic work on fenestrate bryozoans, namely the number of branches in 10 mm. measured transversely to the branch axes; the number of fenestrules in the same distance measured parallel to the branch axes; the number of zooecial apertures in one row per 5 mm., and the number of carinal nodes, also in 5 mm. The procedure used in recording these data was that recommended by Condra and Elias (1944, pp. 54-57).

(b) In some circumstances continuous variables are more useful than discontinuous ones, and measurements were therefore made of fenestrule length, fenestrule width (each measured between the mid-points of opposite sides), inter-apertural distance, and internodal distance (the distance between adjacent centres in both cases—see text-fig. 3). These were the continuous variables most nearly equivalent to the discontinuous ones mentioned above.

(c) Branch width and apertural diameter. Measurements of the first were made at right angles to the branch axis midway along the length of a fenestrule, so as to obtain the normal width, unaffected by branch-dissepiment junctions or branch division. In these colonies there are no notable differences in branch width immediately before and after branch division, and so such measurements were not taken. In recording branch

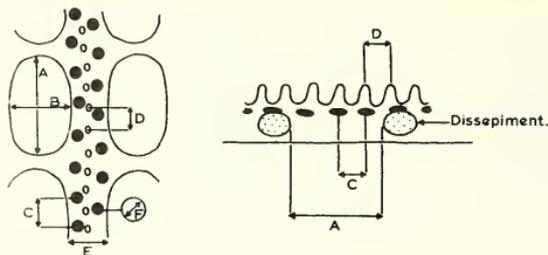


TEXT-FIG. 2. Graphs of structural data from the sample. A, distribution of the diameters of 100 colonies. B, a bivariate plot showing the relationship between zoarial diameter and number of branches in each of 75 colonies. C-F, distributions of the modal values of 55 colonies for each of the characters named. G-H, other distributions utilizing the mean values of the same number of colonies. I-K, percentage ratios between mean values of the features named in 55 zoaria. L, incidence of branch division in relation to distance from growth origin in 100 colonies.

width and apertural diameter care was taken to avoid parts of zoaria showing excessive secondary skeletal material, so that the effects of this complication should, as far as possible, be excluded from the data.

(d) The number of zooecial apertures per fenestrule was considered by Elias and Condra (1957, p. 63) to be of great taxonomic importance. This dimension was therefore recorded, and measurements were also made of the number of carinal nodes per fenestrule.

From these measurements histograms were constructed to illustrate the pattern of morphological variation. They were based on the central values (mean or mode, depending on whether a variable was continuous or not) of each of the zoaria in the sample.



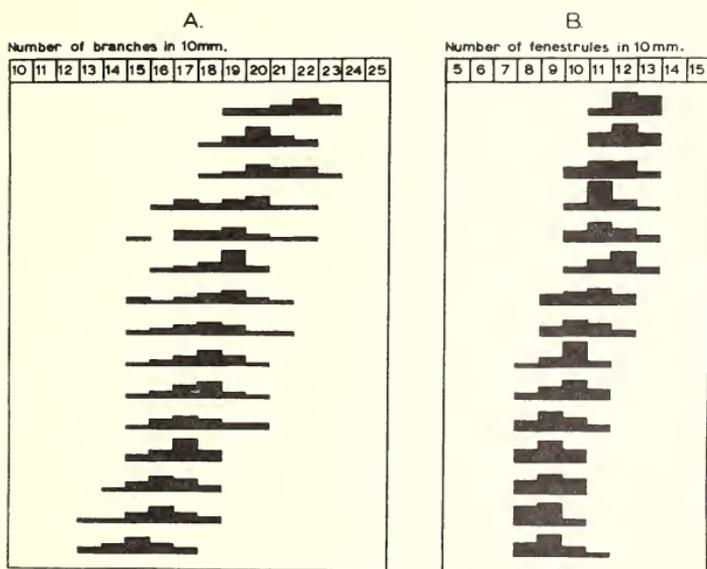
TEXT-FIG. 3. Method of making measurements. A, fenestrule length. B, fenestrule width. C, inter-apertural space. D, internodal space. E, branch width. F, apertural diameter.

These graphs (text-figs. 2C-H) show that for every feature considered the distribution of data is unimodal, with no marked bi- or polymodality such as would be expected if the sample was inhomogeneous in any respect. It is therefore clear that morphological differences between zoaria in these respects relate not to the presence of more than one taxon in the sample, but to the existence of a continuum of forms, the end members of which when seen together show distinct structural dissimilarities.

The histograms utilize only one value for each zoarium, however, and give no indication of the degree of intra-colonial variation that is present. In order to remedy this, and also to provide an idea of the amount of overlap between colonies, text-figs. 4A and B show the distribution of counts of the number of branches and fenestrules per 10 mm. in fifteen zoaria (listed in the same order in both diagrams) covering the range of variation observed in the sample. It is seen that there is substantial overlap between the ranges of different colonies, and the impression of continuous variation given by text-figs. 2C and D is reinforced. A similar pattern exists for each of the other variables examined.

A further suggestion implicit in text-fig. 4 is that a zoarium with many branches per 10 mm. also tends to have a high fenestrule count in that distance, and vice versa. In other words, there appears to be a correlation between these two variables that would seem likely to determine the texture of the meshwork, and hence the size of fenestrules. This possibility can be tested by plotting the mean width of fenestrules against their mean length in a number of zoaria. When this was done for the fifty-five colonies of the

sample it was found that the coefficient of correlation (r) was 0.6886, showing that a significant positive correlation does exist. This means that in spite of variation in the size of fenestrules from one colony to another (according to the texture of the mesh-work) there is a definite tendency for their shape (i.e. the ratio between length and breadth in this case) to remain fairly constant. Nevertheless the correlation is not a particularly strong one, and room is left for a certain amount of fluctuation, as specimens in

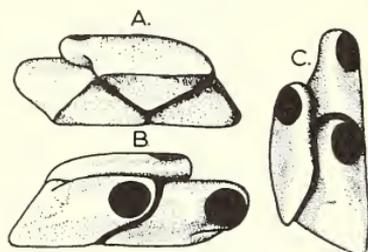


TEXT-FIG. 4. Graphs of the number of branches per 10 mm. (A), and of fenestrules per 10 mm. (B) in colonies chosen to illustrate the range of variation observed in the sample. Fifteen counts were made of each feature in every colony, and the order of arrangement is the same in both diagrams.

the collection show. This aspect of variation was explored by expressing the mean fenestrule width of each colony as a percentage of mean fenestrule length (thus giving a statistic for fenestrule shape) and arranging the resulting data in histogram form (text-fig. 2i). The distribution is seen to be a normal one with a well-developed mode reflecting the correlation between the two dimensions involved. In more than half the colonies average fenestrule width is between 40 and 45 per cent. of the length, while in only about one case in ten is it less than 35 per cent. or more than 50 per cent. It is again apparent that the observed differences do not indicate the existence of separate distinctive groups within the sample, but only of a continuous series, of which those colonies showing the greatest differences are the end members. The ratios inter-apertural space to fenestrule length (text-fig. 2j), and internodal space to fenestrule length (text-fig. 2k) were treated in the same way and the resultant graphs, which reflect the number of

zoecial apertures and carinal nodes per fenestrule, once more demonstrate the homogeneity of the data.

Internal structure. Following the work of Nekhoroshev (1932, pp. 35–41) and his colleagues in Russia it has been generally realized that internal features, particularly the shape of the zoecial chamber, are of taxonomic importance. Examination of these in colonies of the present assemblage is not easy, however, for the internal structure has in many cases been extensively destroyed during silicification. Another difficulty is due to the basket shape of the zoaria which makes it almost impossible to cut more than two branches lengthways in the same section. The branches are, in any case, quite short, so that even in the most favourable circumstances only a small number of chambers are seen. Twenty colonies were mounted in resin blocks and serially sectioned at intervals of 0.05 mm. Six showed well-preserved internal structures, a further eight showed vestigial structures on which some measurements could be made, and the rest were unproductive.



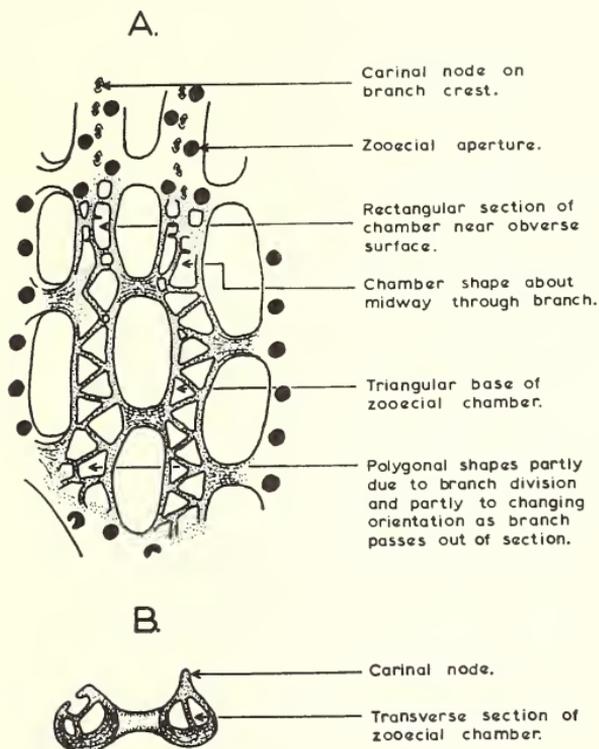
TEXT-FIG. 5. The shape of the zoecial chamber: drawings of a model based on serial sections. A, dorso-lateral view showing the triangular base-shape. B, ventro-lateral view. C, ventral view to illustrate the arrangement of chambers within a branch.

As is commonly the case in fenestellids, the plan of the zoecial chamber was found to differ according to the level at which the section was taken. This is because the chambers are not simple, box-like structures but have rather more complex shapes often bounded by curved surfaces (text-fig. 5). For this reason the plan of a chamber near the obverse surface of a branch approaches a rectangle, though in its lower part it is triangular (text-fig. 6A). The latter is the zoecial base shape that is often referred to in systematic descriptions and it is to this feature that the following discussion relates.

Although a triangular base shape is the commonest, colonies that were sectioned showed that there is some variation in this feature. Minor differences are apparent between neighbouring triangles along the same branch, certain of which may be slightly broader, narrower, higher, or lower than others (text-fig. 6A). Variation of this kind is ubiquitous, and appears to be random not systematic, no doubt reflecting the differing growth potential of individual zooids. More marked irregularities of chamber plan are commonly found where branch division takes place, probably due to the more complex budding pattern in such situations. Here chambers may have three, four, or five-sided base shapes, the decisive factor in the matter perhaps being the availability of space. A remark by Larwood (1962, p. 24) in connexion with the variation of zoecial shape in a group of Cretaceous cheilostomes seems relevant here. He says that '... if only a limited amount of space is available for development, a zoecium tends to fill that space, and its shape is to some extent controlled by it'.

Measurements of zoecial base shapes showed the average length (i.e. the side parallel with the branch axis) to be 0.18 mm., and width (perpendicular to the branch axis) to be 0.17 mm. The extremes of variation recorded were represented by chambers that measured 0.26 mm. \times 0.15 mm., and 0.15 \times 0.19 mm., the last figure being the

width in each case. It is noteworthy that Larwood (though admittedly working on an entirely different group of bryozoa) does not consider the size of the chamber to be as important taxonomically as its shape. He states (1962, p. 24) that: 'For a given species there may be considerable differences in size between the zoecia of different zoaria.



TEXT-FIG. 6. Internal structure. A, tangential section of branches showing the plan of the zoecial chamber at different levels. B, transverse section of branches with a dissepiment.

Zoecial size, therefore, should seldom be used as a basis for differentiating species.' Perhaps similar views are held by the Russian workers, for although they have used zoecial shape for systematic purposes for many years, they rarely give the dimensions of these structures and as far as the author is aware, do not use zoecial size for discriminatory purposes.

The results of the morphological examination may be summarized as follows. Samples of 55-100 zoaria from a single locality and horizon in the Carboniferous Limestone have been measured for all features that are normally considered to be of taxonomic

importance. With respect to each it has been found that continuous variation exists in the sample. Homogeneous distributions of this kind are customarily taken to indicate the presence of a single species, and it is therefore concluded that the collection represents one stock in which, to judge by the dispersion of the data, there was a considerable degree of morphological variation.

An idea of the relative variability of the data for each of the main features measured may be gained by comparing their coefficients of variation $\left(\frac{100\sqrt{\text{variance}}}{\text{mean}}\right)$. These are given below, each figure being based directly on the mean or modal values of 55 colonies, and indirectly on between 550 and 775 measurements.

Branches per 10 mm.	9.57	Apertures per 5 mm.	7.13
Fenestrules per 100 mm.	8.87	Nodes per 5 mm.	12.08
Branch width	6.40	Apertural diameter	9.41

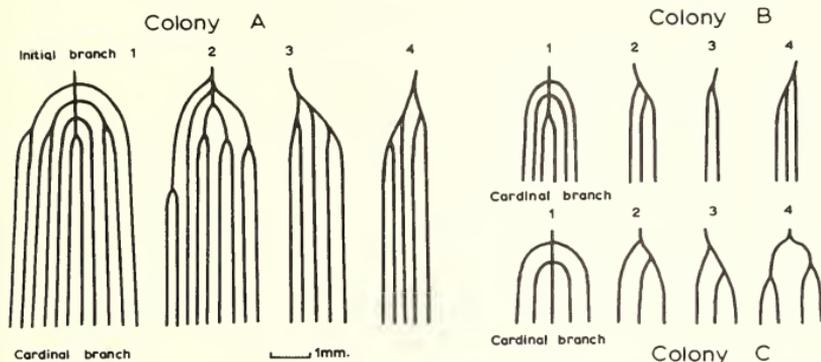
Variation is least marked in branch width and the spacing of zooecial apertures, and since these features bear a direct relationship to the shape and size of the chamber, it follows that these also will be relatively stable. On the other hand, the distribution of branches and fenestrules (the characters governing meshwork texture) and of carinal nodes is notably more variable, and it is possible for two colonies to differ considerably in these respects and yet belong to the same species. The figures therefore suggest that, because they show less fluctuation, data relating to the dimensions and spacing of zooecia might be more useful taxonomically than those concerned with the meshwork texture in the strict sense. With regard to the latter they also show that the number of fenestrules per 10 mm. is rather less variable than that of branches in the same distance, thus supporting the contention of Elias and Condra (1957, p. 63) on this point. The high coefficient of variation for the spacing of carinal nodes is noteworthy: this feature was consistently the least regularly distributed of all those measured on the sample.

MORPHOLOGICAL DESCRIPTION

The following description is based on an examination of more than two hundred colonies, each of which has the characteristic conico-cylindrical, basket-like shape. The dimensions of the baskets vary appreciably, some being long, narrow cylinders whereas others are shorter and relatively broader. While differences in length are largely a function of age, and therefore of only incidental interest, those of diameter are more important and are illustrated in text-fig. 2A. Although the number of branches in the cylindrical part of a colony is generally correlated quite highly with the diameter (text-fig. 2B), there is enough variation to permit observable differences of meshwork texture and fenestrule shape from one colony to another.

The characteristic shape of each zoarium results from the mode of growth of its branches, which is as follows. From the proximal extremity a small number of initial branches diverge. These are almost always four or five in number (conforming to the 'initial circle' of eight or ten zooecia in *Fenestella* described by Cumings 1904, p. 61) though rarely there may be three or six. They branch and dichotomize at close intervals, and the proliferation of branches on a radial pattern, coupled with the necessity for them to remain interconnected by relatively short dissepiments, induces the initially

hemispherical or conical shape of the zoarium. Once this has been attained the incidence of branch division falls sharply (text-fig. 2L) and the number of branches is virtually stabilized. They continue to grow in length, lying approximately parallel to one another, so that the distal part of the zoarium is cylindrical. Failure of branches during the later stages of growth may cause the diameter of the cylinder to decrease distally, as already mentioned. The number of branches composing the cylindrical part of the zoarium may be from ten to thirty-six, depending on the diameter of the basket and texture of the meshwork. A distinctive feature shown by all specimens is that one of the initial branches



TEXT-FIG. 7. The pattern of branching in three representative zoaria. Dissepiments are omitted for greater clarity. Initial branches are numbered in order of occurrence clockwise from the cardinal branch in each case.

always divides more vigorously than the rest, and gives rise to a correspondingly larger part of the meshwork. This strongly developed branch system always has a pinnate growth pattern and is invariably easy to distinguish from the others. It is as if a colony of *Ptylopora* had been incorporated into the meshwork of an otherwise orthodox funnel-shaped *Fenestella*. For this structure it is proposed to introduce the name cardinal branch. Text-fig. 7 illustrates diagrammatically the branching pattern of three representative colonies from the collection, and in each of them the position and importance of the cardinal branch is apparent.

Another feature that characterizes the assemblage is the presence in all colonies of a spinose process extending back from the proximal extremity (Plate 66, fig. 9). Generally this is broken off near the base, but it is sometimes complete and may measure up to 8.5 mm. long and 0.2 mm. in diameter. Occasionally such spines are seen to divide into two at some point along their length, but this is uncommon. Where it happens the subsidiary spine usually branches off at a wide angle, as if the division was the result of new growth following breakage of the original. Other spines, of comparable length or shorter, may originate at random from the obverse surface of the curved initial part of a zoarium. There may be three or four of these. It is proposed to refer to the spine originating at the proximal extremity as the proximal spine and the others as lateral spines.

The writer is in agreement with Likharev (1924, pp. 1019-21) in regarding these

structures as means of attachment and support, though the proximal spine differs greatly from the relatively stout basal 'holdfast' often seen in *Fenestella*. It seems improbable that these spines fulfilled their function by growing downwards into loose sediment of the sea-bed and thereby stabilizing the zoarial basket as it extended in the opposite direction. Had this been the case, the earliest zooids of the colony would have faced directly downwards into the substratum, an unlikely situation. A more acceptable explanation may be that the habit was pendant, and that the proximal spine provided an attachment from which the zoarium was suspended. It is possible that the colonies grew within the interstices of an open framework of accumulating debris on the sea-bed, and that the spines served as rigid anchoring processes to maintain them in position. Such an environment might also help to account for the small size of these colonies, and for the fact that they are often perfectly preserved, though associated with large amounts of broken fossil material.

The branches of which the zoarium is composed have their obverse (or celluliferous) surfaces on the exterior of the basket. This face of each branch is divided longitudinally by a median crest, on either side of which (text-fig. 6B) the surface slopes rather sharply away to the branch margin. Along the crest there is a single row of closely spaced carinal nodes which, although presenting a superficial appearance of uniformity, are seen on closer inspection to differ to some extent in shape and development. Some of them are relatively tall (up to 0.2 mm.) and slender (being more suitably described as spines than nodes) while others are only half as high but are wider at the base, with a broadly conical

EXPLANATION OF PLATE 66

Ptilofenestella carrickensis from the Carboniferous Limestone at Carrick Lough, Co. Fermanagh, Ireland. Registration numbers refer to the collections of the British Museum (Natural History), London, where the specimens are kept.

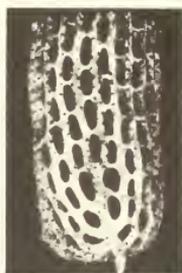
- Fig. 1. A small colony with well-preserved proximal and lateral attachment spines. The proximal spine is broken and a curved subsidiary has developed from the stump. PD 4484. Paratype. $\times 5.2$.
- Fig. 2. A colony of intermediate size showing prominent carinal nodes which are long and slender proximally, but less well-developed distally. PD 4479. Paratype. $\times 7.0$.
- Fig. 3. Lateral view of a zoarium to show the growth pattern of the cardinal branch. PD 4478. Paratype. $\times 6.8$.
- Fig. 4. The termination of several branches has resulted in a progressive decrease in diameter towards the distal end of this colony. PD 4480. Paratype. $\times 7.3$.
- Figs. 5-7. Proximal views of three colonies of different size and shape. The cardinal branch is towards the top of the page in each case. PD 4485-PD 4487. Paratypes. $\times 6.7$, $\times 6.7$, and $\times 7.2$ respectively.
- Fig. 8. Part of a large, open-textured colony showing the structural features in greater detail. PD 4474. Paratype. $\times 15.8$.
- Fig. 9. A small colony with large fenestrules, relatively thin branches and a slender proximal spine. PD 4476. Paratype. $\times 7.5$.
- Fig. 10. The unbroken tips of some branches are visible in this small zoarium which also has unusually long and slender carinal nodes in the proximal region. PD 4477. Paratype. $\times 8.0$.
- Fig. 11. An oblique view of the distal end of a zoarial basket showing the unbroken ends of the branches. PD 4481. Paratype. $\times 8.0$.
- Fig. 12. A large, many-branched colony with close meshwork. The rows of carinal nodes are easily seen. PD 4475. Paratype. $\times 5.2$.
- Fig. 13. A typical example of the most commonly occurring form in the collection. PD 4473. Holotype. $\times 8.0$.
- Fig. 14. The interior of a zoarial basket broken lengthways to show the spines on the reverse side of branches. PD 4482. Paratype. $\times 8.0$.



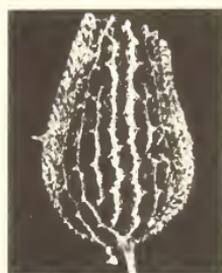
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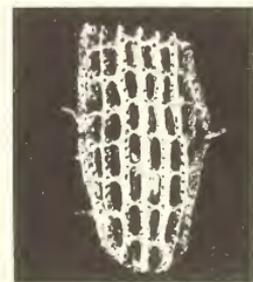
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11



14

profile. These differences do not appear to follow a regular pattern and it is not uncommon to find taller and shorter nodes in juxtaposition. Nevertheless the taller kind are commoner in the proximal region while lower, wider ones predominate distally.

Zooecial apertures are situated in two longitudinal rows alternating with one another on either side of the median crest. They are circular and when well preserved are surrounded by low, thin, unornamented peristomes. The apertures do not overlap the branch margin and the latter, bordering the fenestrule, is therefore straight.

Zooecial chambers are located in two longitudinal rows within branches, corresponding to the arrangement of the apertures (each of which is at the distal end of its cell). Chambers are rather irregularly shaped (text-fig. 5), and appear rectangular in longitudinal sections near the obverse surface of a branch, but triangular in those near the base.

The reverse side of branches is invariably smooth and well-rounded, and a curious feature shown by some colonies (fifteen out of twenty-seven examined) is the sporadic presence of small nodes or spines on this surface. These are irregularly developed even in a single zoarium, being more numerous on some branches than others. They often occur singly in the middle of a branch opposite the junction with a dissepiment, but may also be present between such positions. These protruberances vary in size and shape: they may approximate in these respects to carinal nodes, or be so small as to be hardly visible. They are usually confined to the proximal part of a colony and are rarely seen in the cylindrical region.

Branch division occurs most commonly in the proximal part of a zoarium (text-fig. 2L), and is not attended by any notable preliminary increase in branch width or by the appearance of an incipient third row of zooecia, as has been reported in some species of *Fenestella*. Dissepiments vary in length from one colony to another according to the spacing of branches. Fenestrules are rectangular or oblong-oval in shape, depending on the amount of flare at each end of a dissepiment. The spacing of apertures does not bear a simple relationship to that of the dissepiments (i.e. they are not 'stabilized' in the sense of Elias and Condra, 1957), and the dissepiments are depressed below the branch surface on both sides, though to a slightly greater extent on the obverse (text-fig. 6B).

The micrometric formula of this species, constructed in the orthodox manner (Miller 1961, p. 222) is $13-23/8-13//17-24/21-38$. The additional figures given below relate to the distribution of the modal values of fifty-five zoaria for the named variables. They could be used as a basis for biometrical comparisons utilizing the χ^2 test or a comparable technique. Each mode is based on fifteen measurements.

1. Number of branches in 10 mm.	15	16	17	18	19	20	21	22
Frequency in sample	2	6	9	16	9	7	3	2
2. Number of fenestrules in 10 mm.	8	9	10	11	12		13	
Frequency in sample	2	7	18	18	9		1	
3. Number of apertures in 5 mm.	16	17	18	19	20		21	22
Frequency in sample	1	7	11	8	19		7	2
4. Number of carinal nodes in 5 mm.	22-23	24-25	26-27	28-29	30-31		32-33	34-35
Frequency in sample	6	10	8	13	6		7	5
5. Number of apertures per fenestrule	2	3						
Frequency in sample	31	24						

Further quantitative data are as follows (in every case the mean value for fifty-five specimens is followed by the variance in parenthesis):

<i>Fenestrule length</i>	0.072 (0.223) mm.	<i>Internodal space</i>	0.18 (0.020) mm.
<i>Fenestrule width</i>	0.030 (0.065) mm.	<i>Branch width</i>	0.24 (0.009) mm.
<i>Inter-apertural space</i>	0.025 (0.011) mm.	<i>Apertural diameter</i>	0.10 (0.004) mm.

DISCUSSION

Colonies of the Fermanagh sample exhibit most of the characters of *Fenestella*, to which genus they were at first thought to belong. They also have other features which render their inclusion in that genus difficult. The first of these is the universal presence of the cardinal branch, a structure without parallel in *Fenestella*. A somewhat similar branch arrangement occurs in *Ptiloporella* Hall, but in that genus the pinnate pattern of growth recurs many times in a zoarium, whereas in colonies of the present assemblage it is restricted to one of the initial branches only, the others showing the usual pattern seen in *Fenestella*. Furthermore, except near the growth origin, the cardinal branch is no thicker than the subsidiaries to which it gives rise; traced into the cylindrical part of a zoarium it soon loses its identity and cannot be distinguished from any other branch (text-fig. 7). This is not so in *Ptiloporella*, where the thicker primary and thinner secondary branches remain quite distinct throughout their length (Hall 1885, p. 36).

Another unusual feature of the present collection is the development of a strong, backwardly directed proximal spine in each colony. This is often accompanied by others of a similar nature arising from the obverse surface of the curved part of the zoarium. The latter have counterparts in *Fenestella*, but the proximal spine has none, and is in marked contrast to the stout, encrusting 'holdfast' that is generally seen when the basal part of a colony of that genus is preserved.

In view of these distinctive structures it is considered better to erect a new genus for the reception of the Fermanagh specimens, than to include them in one of the existing genera. Because the distinctive branch arrangement shown by the sample has features in common with that of *Ptylopora* M'Coy, *Ptiloporella* Hall, and *Fenestella* Lonsdale, the name *Ptilofenestella* seems appropriate for the new genus.

Order CRYPTOSTOMATA Shrubsole and Vine 1882

Family FENESTELLIDAE King 1850

Genus PTILOFENESTELLA gen. nov.

Diagnosis. Funnel or basket-shaped zoarium consisting of a meshwork structurally similar to that of *Fenestella* but with a cardinal branch. This has a pinnate growth pattern and gives rise to a considerably larger part of the zoarial expanse than any of the other initial branches. There is also a well-developed proximal spine that appears to have served as an attachment structure for the colony.

Type species. *Ptilofenestella carrickensis* sp. nov.

Horizon and locality. Viséan limestone, probably of D₁ age, south side of Carrick Lough near Derrygonnelly, Fermanagh, Ireland.

Ptilofenestella carrickensis sp. nov.

Diagnosis. *Ptilofenestella* up to 10 mm. long and 6 mm. in diameter, with 4 or 5 initial branches and between 10 and 36 branches in the cylindrical part of a colony. There are 2 or 3 circular zoecial apertures per fenestrule, and the chamber shape is rectangular above and triangular below. Meshwork formula: 13-23/8-13//17-24/21-38.

Holotype. British Museum (Natural History) No. PD 4473.

Paratypes. Nos. PD 4474 to PD 4485. All are figured in Plate 66.

Discussion. It is difficult to choose one or two specimens to represent a variable assemblage, and the procedure adopted here was as follows. A well-preserved example of the most commonly occurring form (PD 4473) was chosen as the holotype, and three others (PD 4474-PD 4476) were selected as paratypes to indicate the extremes of diversity in zoarial size and diffuseness of meshwork, the features in which morphological variation is usually most evident. Further paratypes (PD 4477-PD 4485) were then chosen to illustrate various other morphological characteristics mentioned in the text.

Acknowledgements. I would like to thank Professor Alwyn Williams for suggesting the subject for research and for guidance in the preparation of this paper. Also my colleague, Mr. R. E. H. Reid, who kindly furnished the first of the fossil material together with information as to the collecting locality. Finally, I am indebted to my wife for translating relevant parts from the work of Russian authors.

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DIONELLA GEN. NOV. (SUPERFAMILY MEMBRANIPORACEA) FROM THE UPPER CRETACEOUS OF EUROPE

by A. W. MEDD

ABSTRACT. The new genus *Dionella* is proposed for membraniform Polyzoa from the Upper Cretaceous of Europe having slightly calcified frontal walls, diatellae, hyperstomial ovicells, and small interzoecial avicularia, which, when present, are distal to the ovicells. The type material of the seven species assigned to this genus is redescribed with the establishment of lectotypes, a neotype, and many synonymies. A possible evolutionary pattern for the group has also been given.

THE material, which forms the basis of this paper, is part of the large collection of Chalk Polyzoa made by R. M. Brydone and lodged in the Sedgwick Museum, Cambridge. With this material Brydone established numerous species of Cretaceous membraniform Polyzoa, and those which had encrusting zoaria he placed in the genus *Membranipora*. However, an encrusting zoarium is no longer accepted as the major diagnostic feature of this genus (Borg, 1931, p. 4) and all of the species, assigned by Brydone to this genus, must be transferred to other genera. The present paper is the first of a series attempting such a systematic revision, and is one of the topics studied for a thesis at the University of Cambridge.

The terminology and stratigraphy adopted in this paper follow that used by Larwood (1962). The text-figures are based on drawings made with the aid of a squared graticule and the measurements have been made with the aid of a micrometer scale.

Measurements are given below in an abbreviated form (text-fig. 1) for many of the type specimens, and they are all in hundredths of a millimetre. These measurements are given only for those autozoecia which occur in a longitudinal row and do not give rise to a new row. *N* represents the number of observations made for each character. The autozoecial measurements comprise three sets of figures for each character (for example: 54-67/60/4), which correspond to the observed range, the mean, and the standard deviation respectively. The standard deviation has not been calculated for the ovicells and so only the observed range and the mean are given (for example: 54-67/60).

SYSTEMATIC DESCRIPTIONS

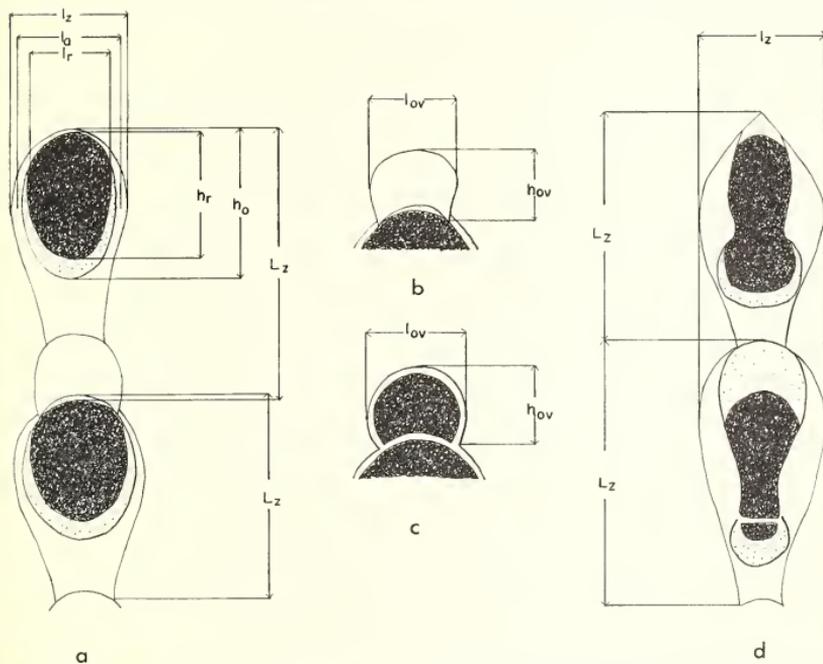
Superfamily MEMBRANIPORACEA Busk 1854

Genus DIONELLA gen. nov.

- 1846 *Cellepora*: von Hagenow, p. 617 [*partim*]
- 1887 *Membranipora*: Marsson, p. 58 [*partim*]
- 1906 *Membranipora*: Brydone, pp. 293, 294 [*partim*]
- 1910 *Membranipora*: Brydone, pp. 5, 76 [*partim*]
- 1910 *Cellepora*: Brydone, p. 5.
- 1914 *Membranipora*: Brydone, pp. 345-7.
- 1916 *Membranipora*: Brydone, p. 338.

- 1917 *Membranipora*: Brydone, p. 49.
 1920 *Tegella* (*Membranipora*): Canu and Bassler, p. 166.
 1925 *Membranipora*: Levisen, pp. 332-3.
 1930 *Membranipora*: Voigt, p. 421 [*partim*]; p. 434 [*?partim*]
 1930 *Membranipora* (*Callopora*): Voigt, p. 443 [*?partim*]; p. 444 [*partim*]
 1936 *Membranipora*: Brydone, p. 65 [*partim*]
 1949 *Membranipora*: Voigt, pp. 16 [*partim*], 18-19.
 1959 *Membranipora*: Voigt, p. 55.
 1962 *Membranipora*: Voigt, p. 30 [*partim*]

Type species. *Cellepora trifaria* von Hagenow, 1846, p. 617. Lower Maastrichtian. Rügen, Germany.



TEXT-FIG. 1. Explanation of the abbreviations used in the measurements of: (a) autozoecia; (b) complete or (c) broken ovicells; (d) avicularia. L_z = length of the zooecium; l_z = width of zooecium; h_a = length of aperture; l_a = width of aperture; h_r = length of opesium; l_r = width of opesium; h_{ov} = length of ovicell; l_{ov} = width of ovicell.

Diagnosis. Membraniporacea with rounded-rhomboidal zooecia, usually budded multi-serially; zooecia with well-defined mural-rims; aperture more or less restricted by cryptocyst; gymnocyst variably developed, both proximally and laterally; mural-rim more or less spinose, with 0-12 pairs of spine-bases; dietellae present, often arranged asymmetrically; avicularia of two kinds of interzoecial, either of which may be absent, one type is small, distally rounded or acuminate, distal to the autozoecium; the other

type is solitary, elongate spatulate, and may grade into vicarious; ovicell hyperstomial, prominent.

Remarks. It has been found necessary to designate a new genus for those membraniporine Polyzoa which possess autozoecia with dietellae, a hyperstomial ovicell, and a single associated interzoecial avicularium at their distal margins. These avicularia are directed away from the autozoecial distal margins and their presence or absence is not influenced by the ovicell of the associated autozoecium. All of the species belonging to this genus have, until now, been placed in *Cellepora* (*sensu lato*) and *Membranipora* (*sensu lato*). There has been no previous attempt to group these species into a single taxonomic unit.

Voigt's use of *Membranipora* (*Callopora*) for some of the species [Voigt, 1930, pp. 443 ff.] is rejected, as this places such species in the subgenus *Callopora* and within the genus *Membranipora*. The group, which he regarded as comprising the genus *Membranipora*, is here considered to be the superfamily Membraniporacea. Voigt considered species placed under the subgenus *Callopora* to have zooecia with an ovicell, a spinose mural-rim and avicularia which vary in structure and position. This group is also regarded as being supra-generic.

The genus *Callopora* Gray *sensu stricto* is not available for these species, as its diagnosis requires the presence of adventitious avicularia on the autozoecial gymnocyst. Autozoecial spinosity of the mural-rim is here regarded as being, at the most, of specific importance. Also, the closely similar species *D. surculus* (Brydone) has spine-bases which are so large and numerous as to suggest cribrimorph affinities.

Dionella is closely similar to *Callopora sensu stricto*, however, as is seen when specimens of *D. suffragista* (Brydone) from various horizons of the Chalk are compared. A gymnocystal pore is occasionally present in this species and is reminiscent of those pores seen in *Callopora bipunctata* (Goldfuss); these are associated with adventitious avicularia in the latter species. However, the pore is not always present in *D. suffragista* and is never associated with an adventitious avicularium.

The avicularia of *Dionella* species differ from those of *Tegella* Levinsen. They are adventitious in the case of *Tegella*, and are placed on a hyperstomial ovicell. The writer disagrees with Waters (1924, p. 608), who did not consider *Tegella* to be of generic importance. Although there are several intermediate forms between these two genera, a very large proportion of specimens can be referred unambiguously to one or the other of them.

Dionella is similar to *Chaperia* Jullien, particularly in the shape and general structure of the zooecia, and in the presence of distal interzoecial avicularia; compare, for example, *D. trigonopora* (Marsson) with *Chaperia galeata* (Busk) figured by Canu and Bassler (1923, pl. 34, figs. 9-10). However, the presence of occlusor laminae in the zooecia of *Chaperia* species is here considered to be of at least generic diagnostic importance (Brown 1952). Brown has established the genus *Patsyella* (Brown 1948, p. 112) for species in which the occlusor laminae are vestigial or absent, but in which there are entozoecial ovicells. The zooecial structures of species referred to this genus, however, are different from those occurring in *Dionella*, but the loss of occlusor laminae in *Chaperia galeata* would render its generic diagnosis very difficult.

Dionella differs from *Copidozoum* Harmer by the greater consistency of occurrence,

and a different position of emplacement, of the interzoecial avicularia. The species of *Dionella* have a different autozoecial structure to those of *Ellisina* Norman, *Periporosella* Canu and Bassler, and *Parellisina* Osburn.

Stratigraphical Distribution. Senonian, zones of *M. cortestudinarium* to *B. mucronata*; Maastrichtian of Europe. Eocene (Middle Jacksonian) of Carolina, U.S.A.

KEY TO THE SPECIES OF *DIONELLA* GEN. NOV.

- (I) *Dionella* with well-developed cryptocyst; avicularia of two structural types, a small, acuminate, interzoecial, distal to most, or all, of the autozoecia and a large solitary, elongate spatulate, interzoecial or vicarious, which can also be distal to the autozoecia.
- (A) Mural-rim spinose, but not interrupted by the spine-bases; ovicell with distal flattening; dietellae asymmetrically arranged
1. *D. trifaria* (von Hagenow)
- (B) Mural-rim extremely spinose, interrupted by the spine-bases; ovicell distally flattened; dietellae symmetrically arranged
2. *D. surculus* (Brydone)
- (C) Mural-rim interrupted by the single pair of very large oral spine-bases; ovicell not distally flattened; dietellae impersistent; zooecia often ogival
3. *D. trigonopora* (Marsson)
- (II) *Dionella* with little cryptocyst; avicularia of three structural types, a small, distally rounded or elongate-spatulate, interzoecial, distal to most of the autozoecia, and a large, solitary, spatulate vicarious; ovicell not distally flattened.
- (A) Small, distally rounded, interzoecial avicularia.
- (1) Large vicarious avicularia present or absent; mural-rim spinose but not interrupted by the spine-bases; dietellae asymmetrically arranged
4. *D. simulacrum* (Brydone)
- (2) Large vicarious avicularia absent; dietellae symmetrically arranged.
- (a) Mural-rim extremely spinose, slightly interrupted by the spine-bases; dietellae large
5. *D. tringhamensis* (Brydone)
- (b) Mural-rim interrupted by the single pair of very large oral spine-bases; dietellae small
6. *D. flacilla* (Brydone)
- (B) Small, elongate-spatulate, interzoecial avicularia; large vicarious avicularia absent; mural-rim spinose, slightly interrupted by the spine-bases; dietellae small, symmetrically arranged; gymnocystal pore occasionally developed
7. *D. suffragista* (Brydone)

SUMMARY OF THE CHARACTERS COMMON TO ALL *DIONELLA* SPECIES

Description. Zoarium unilamellar, locally multilamellar, encrusting. Initial zoarial development either regular or irregular. Zooecial budding multiserial, generally with a regular arrangement of alternating longitudinal rows, developing from ordinary or wide

autozoecia or from vicarious avicularia when these are present; a second zoecial layer is developed over irregular patches of the zoarium, occasionally round the ancestrula.

Adult zoecia usually rounded rhomboidal, but may be irregularly so, because of an uneven substrate. Interzoecial furrows distinct. The basal wall is thin and often im-persistent. Gymnocyst is smooth, variably exposed proximally and extremely so later-ally. Cryptocyst descends steeply into the aperture, which is oval to irregularly so. Opesia oval, occasionally pear-shaped, or irregularly round. Mural-rim thin, usually well defined.

Ovicells hyperstomial, prominent and smooth, with a complete and differentiated ectooecium and endooecium. There is usually even distribution throughout the zoarium. Ancestrula and young zoecia like adult zoecia but smaller. The ancestrula has no associated avicularium. Regenerated zoecia: autozoecia occasionally regenerate autozoecia, singly; very occasionally forming a new zoecial layer.

When present, the large solitary avicularia occur at random throughout the zoarium. They are spatulate, with an elongate-oval aperture. Lateral constrictions infold within the proximal-central portion of the aperture. A small distal and one pair of distal-lateral dietellae are usually present. The flat palette is recessed, usually broad and can extend to the proximal-central portion of the aperture. The cryptocyst forms a flat, finely granular, narrow, U-shaped strip along the proximal quarter of the aperture. Smooth gymnocyst is commonly well developed laterally and variably so proximally.

A single interzoecial avicularium is found distal to most of the autozoecia, directed away from the autozoecial aperture. Occasionally at the distal zoarial margins, and rarely within the zoarium, several avicularia of this type may be found around a single zoecium. They are small, but exceptionally can attain autozoecial dimensions. Granular cryptocyst is a U-shaped strip of variable width and is confined to the sub-opercular portion of the aperture. A straight transverse-bar, or condyles, bisect the opesium. The lateral and distal walls are often well developed.

1. *Dionella trifaria* (Von Hagenow)

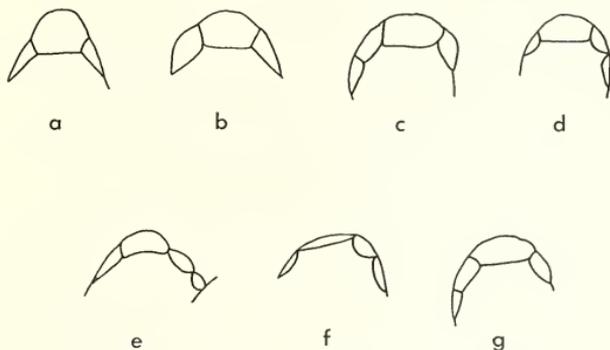
Plate 67, figs. 1-6; Plate 68, figs. 1-6

- 1846 *Cellepora trifaria* von Hagenow, p. 617, pl. 23b, fig. 40.
- 1906 *Membranipora griffithi* Brydone, p. 293, text-fig. 1.
- 1910 *Membranipora griffithi* Brydone: Brydone, p. 5.
- 1910 *Cellepora trifaria* von Hagenow: Brydone, p. 5.
- 1914 *Membranipora boletiformis* Brydone, p. 346, pl. 26, figs. 5-6.
- 1914 *Membranipora griffithii* Brydone: Brydone, p. 347, pl. 26, figs. 7-8.
- 1920 *Tegella (Membranipora) griffithii* (Brydone) Canu and Bassler, p. 166.
- 1925 *Membranipora trifaria sic* (von Hagenow) Levinsen, p. 333, pl. 3, fig. 27.
- 1929 *Membranipora bradingensis* Brydone, p. 29, pl. 9, fig. 4.
- 1929 *Membranipora retrorsa* Brydone, p. 29, pl. 9, fig. 5.
- 1930 *Membranipora griffithi* Brydone: Voigt, p. 421, pl. 10, fig. 13.
- 1949 *Membranipora griffithi* Brydone: Voigt, p. 18.
- ?1949 *Membranipora boletiformis* Brydone *subboletiformis* Voigt, p. 18, pl. 2, figs. 2-3.
- 1949 *Membranipora boletiformis* Brydone: Voigt, p. 18.
- 1959 *Membranipora trifaria* (von Hagenow): Voigt, p. 55, pl. 6, fig. 2.
- 1962 *Membranipora trifaria* (von Hagenow): Voigt, p. 30, pl. 12, fig. 3.

Neotype (designated by Voigt, 1959, p. 72). A zoarial fragment. Lower Maastrichtian. Rügen, East Germany. Von Hagenow Collection, Hamburg.

Emended Diagnosis. *Dionella* with the aperture restricted by a band of cryptocyst; mural-rim spinose, with one to four pairs of spine-bases distal and three distal-lateral dietellae present, asymmetrically arranged; avicularia either small, interzoecial, distal to each autozooecium, or large vicarious, the latter also occasionally distal interzoecial.

Description. Adult zooecia slightly shallow or deep. Either a large distal and one pair of distal-lateral dietellae occur, or often three asymmetrically arranged distal-lateral dietellae are present (text-fig. 2). A small distal and three or four lateral pairs of septula occur. Cryptocyst a granular or coarsely granular band, widest proximally and proximal-laterally and narrowing distal-laterally, with occasional slight distal development.



TEXT-FIG. 2. *Dionella trifaria* (von Hagenow). $\times 40$. The range in variation of the autozooecial dietellae of: a, B36287, figured by Brydane as *M. griffithi* Brydane; b, B36288, figured by Brydane as *M. griffithi* Brydane; c, B36108, holotype of *M. griffithi* Brydane, distal-lateral dietellae occurring asymmetrically; d, B36496, holotype of *M. bradingsis* Brydane; e, B36286, lectotype of *M. boletiformis* Brydane; f, g, B36497, holotype of *M. retrorsa* Brydane.

Mural-rim not broken up by the one to four pairs of spine-bases, which are large. The number of spine-bases on adult zooecia varies in a single zoarium; they may rarely be absent.

Ovicells with proximal-lateral grooves, and occasional distal flattening extending V-shaped proximally. Half to nearly all of the adult zooecia possess ovicells; usually there are nought to one, occasionally two, rings of adult zooecia prior to their appearance.

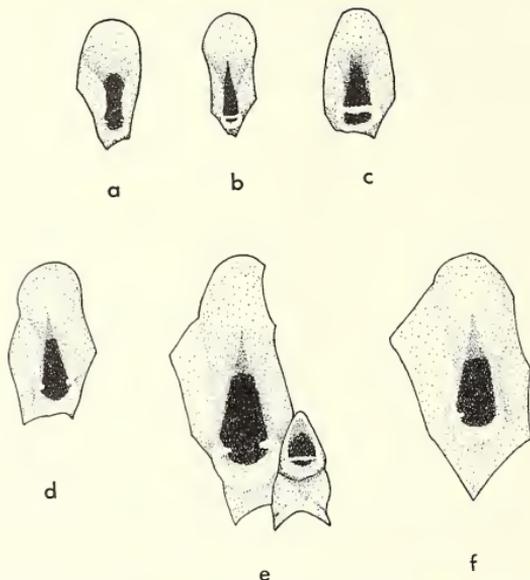
The ancestrula possesses 5 pairs of spine-bases, the primary zooecia have 4-5 pairs, the secondary zooecia 3 pairs, and the tertiary zooecia 2-3 pairs, with the reduction in pairs occurring along the proximal margins of the mural-rim.

Regenerated zooecia: vicarious avicularia occasionally regenerate from either autozoocia or other vicarious avicularia. Small interzoecial avicularia regenerated rarely from vicarious avicularia.

Avicularia are of two kinds:

(1) Vicarious, with occasional concentration at the distal zoarial margins; rarely they may be absent in a zoarium. This type can also be interzoecial, when it is found

distal to the autozoecium, ovicelled or not, and directed away from the autozoecial aperture. The aperture may be extremely laterally expanded distally; length is very variable (text-fig. 3). The flat palette variable in shape; it may have a proximal-central triangular area which is, itself, further recessed. A transverse-bar or prominent condyles are situated within the proximal-central quarter of the aperture.

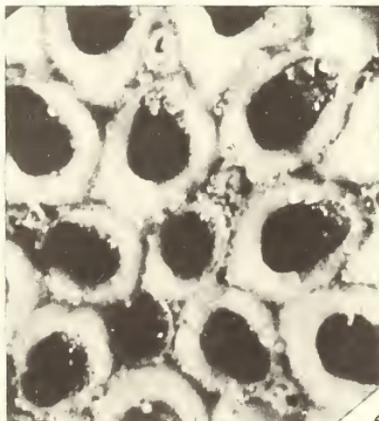
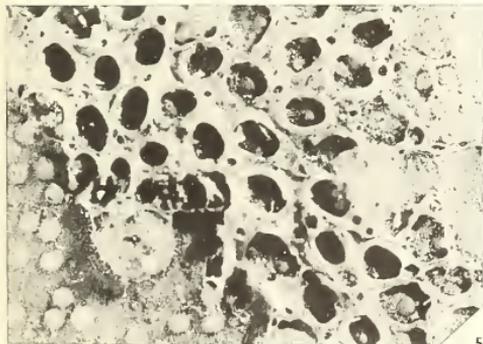
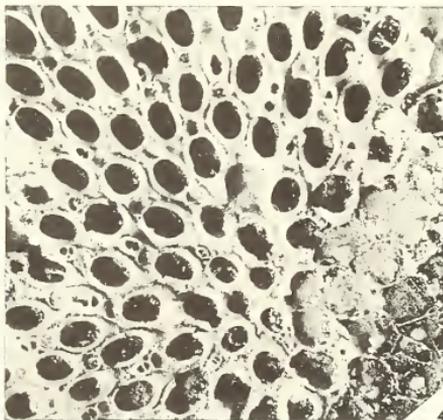
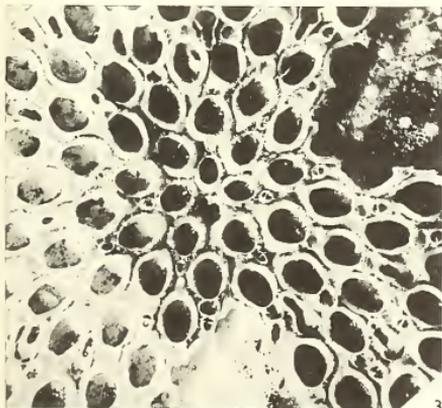
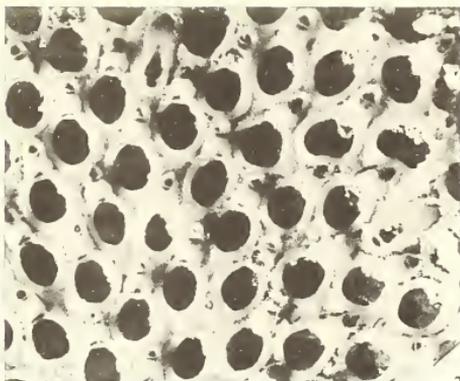
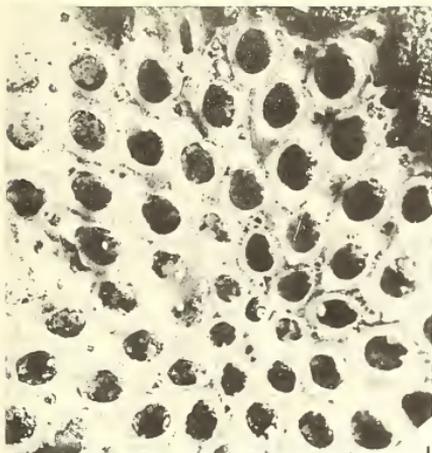


TEXT-FIG. 3. *Dionella trifaria* (von Hagenow). The range in variation of the large avicularia. *a*, B36285, syntype of *M. boletiformis* Brydone. Small, interzoecial, can be found distal to an ovicelled zoecium; aperture expanded distally. *b*, B36286, lectotype of *M. boletiformis* Brydone. Opesium much restricted by lateral development of palette. *c*, B36496, holotype of *M. bradingensis* Brydone. Variation in the extent and nature of the palette seen in a single zoarium. The proximal-central portion of the palette more deeply recessed than the rest. *d*, B36288, a specimen figured by Brydone as *M. griffithi* Brydone. Large vicarious avicularium, and a small interzoecial avicularium distal to an ovicell. The distal flattening and the lateral constrictions on the ovicell also shown. *f*, B36108, holotype of *M. griffithi* Brydone. A typical vicarious avicularium.

EXPLANATION OF PLATE 67

Figs. 1-6. *Dionella trifaria* (von Hagenow). 1, [Holotype of *M. griffithi* Brydone]; incomplete zoarium with ancestrula and young zoecia. B36108. 2, Zoarial fragment showing the avicularia. B36287. 3, [Syntype of *M. boletiformis* Brydone]; incomplete zoarium with ancestrula, young zoecia and two types of interzoecial avicularia. B36285. 4, [Holotype of *M. bradingensis* Brydone]; incomplete zoarium with either of the two types of interzoecial avicularia distal to the autozoecium. B36496. 5, [Holotype of *M. retrorsa* Brydone]; incomplete zoarium with the ancestrula and young zoecia obscured by the superposition of a second zoecial layer. B36497. 6, [Lectotype of *M. boletiformis* Brydone]; ancestrula and a regular initial zoarial development. B36286, $\times 50$.

All figures $\times 20$ unless otherwise specified; from unretouched negatives.



MEDD, Cretaceous membraniform Polyzoa

(2) The single interzoecial avicularium is acuminate, with the aperture generally level with the zoarial surface. A slight, recessed palette is present and granular cryptocyst almost fills the sub-opercular portion of the aperture. Gymnocyst absent. The transverse-bar can also have a shallow V-shape. A small distal and a single distal-lateral diatella are present.

Measurements. (For explanation of the abbreviations, see text-fig. 1.)

<i>N</i>	1	2	3	4
	8	10	8	4
<i>L_z</i>	50-64/55/4	45-64/57/6	46-64/55/5	45-49/47/2
<i>l_z</i>	38-60/45/7	28-38/33/2	40-51/45/3	32-42/38/4
<i>h_a</i>	35-41/37/1	35-42/39/2	35-41/38/2	32-38/36/2
<i>l_b</i>	28-41/33/4	26-30/28/1	32-38/35/2	27-32/30/2
<i>h_r</i>	28-33/30/2	29-36/33/3	27-35/31/3	27-32/29/2
<i>l_r</i>	22-29/24/2	20-26/23/1	26-29/27/1	19-24/21/2
<i>h_{ov}</i>		16-19/17	19-20/20	
<i>l_{ov}</i>		17-19/18	19-22/20	

1 = B36286, the lectotype (here chosen) of *M. boletiformis* Brydone; 2 = B36496, the holotype of *M. bradingensis* Brydone; 3 = B36108, the holotype of *M. griffithi* Brydone; 4 = B36497, the holotype of *M. retrorsa* Brydone.

Remarks. *Cellepora trifaria* was clearly established by von Hagenow. The type, however, was destroyed during World War II (Voigt, 1959, p. 4). The neotype, designated by Voigt (1959, p. 72), completely corresponds to von Hagenow's species. Voigt's figure also shows regeneration of autozoecia by the small interzoecial avicularia.

M. griffithi, *M. boletiformis*, *M. bradingensis*, and *M. retrorsa*, all species established by Brydone, and probably *M. boletiformis* Brydone *subboletiformis* Voigt, are here regarded as synonymous with *Dionella trifaria* (von Hagenow).

All the available specimens, including Brydone's types, have been re-examined. *M. griffithi* was established by Brydone (1906, p. 293), who differentiated it from *C. trifaria* (1910, p. 5) by having 'symmetrical' vicarious avicularia, whereas he considered those of *C. trifaria* to be 'decidedly unsymmetrical'. There is no difference between the avicularia of *M. griffithi* and *C. trifaria* and the writer follows Voigt (1959, p. 55) in regarding these two species as synonymous. The 'triangular incision' of the ovicell that he mentioned (1906, p. 293) is the distal flattening referred to above.

Voigt (1930, p. 421) placed *M. griffithi* in his 'Gruppe der Membranipora sacerdotalis Brydone', but later (1949, p. 18) altered his opinion 'as it (*M. griffithi*) forms its own group' [translation]. He (1959, p. 55) redescribed *C. trifaria*, with *M. griffithi* as a junior synonym, and recently (1962, p. 30), in a description of Russian specimens, has noted that the specimens lacked spine-bases.

Brydone considered *M. boletiformis* to be 'ancestral to *M. griffithi*'. In the R. M. Brydone Collection, the maximum number of specimens of *M. boletiformis* and *M. griffithi* are from the *Gonioteuthis quadrata* and the *Belemmella lanceolata* zones respectively. However, the earliest specimens of *M. griffithi* come from the *G. quadrata* zone, and some of these were found in the same quarry as one-third of all of the specimens of *M. boletiformis* collected from that zone. Examination of all of the specimens of these two Brydone species shows that they differ only in the nature and position of the large, spatulate avicularium. These are vicarious in *M. griffithi* and their apertures are

only slightly expanded distally; and are vicarious or interzoecial in *M. boletiformis*, often distal to an autozoecium, and their apertures are expanded distally. However, there are many intermediate forms of both characters and the variation in shape and position of avicularia in this species is a systematic unit of great subjectivity and is not sufficiently important to warrant continued separation of these two species. Also Voigt (1962, p. 30) states 'on both zoaria [of *M. trifaria*], there are no larger avicularia, but these are not always developed: they are also absent on some Rügen examples' [translation].

Voigt (1949, p. 18) established *M. boletiformis* Brydone *subboletiformis*, which he diagnosed as having a greater number of apertural spines than the Brydone species, and also by having 'larger zoecia'. These 'larger zoecia' have the same measurements as the lectotype of *M. boletiformis* (B36286). Also the number of spine-bases is not excessive for this species, particularly for the young zoecia, and subspecific discrimination is not considered justifiable.

Brydone considered *M. boletiformis* to be ancestral or an early form of *M. griffithi*, differing 'only by a general slimness and narrowness, and by the small avicularia' having a different shape. As the species occurs in the *Bellefmitella mucronata* zone, it is not stratigraphically distinct from *M. griffithi*. The autozoecial and apertural width is smaller than *M. griffithi*, but is not so great as to be of statistical significance and to be used as a systematic discriminant. The final difference, a lack of acumination of the small avicularium, is not considered to be of sufficient systematic importance to warrant the continued separation of these two species. Thus this species is a synonym of *D. trifaria* (von Hagenow).

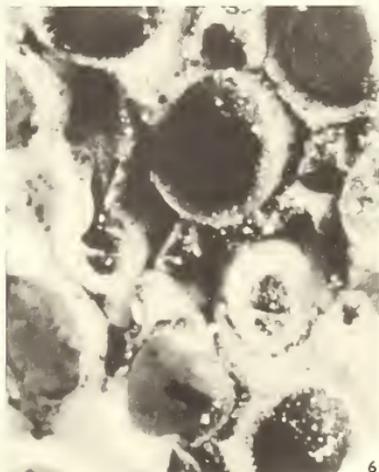
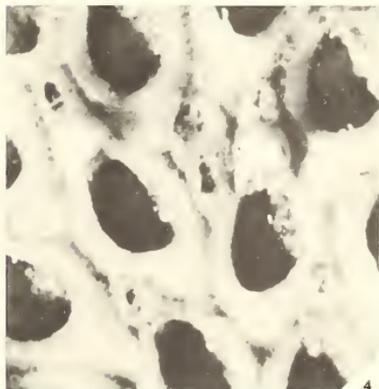
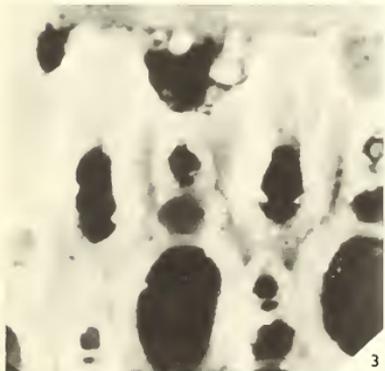
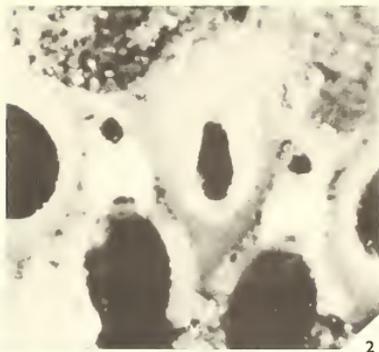
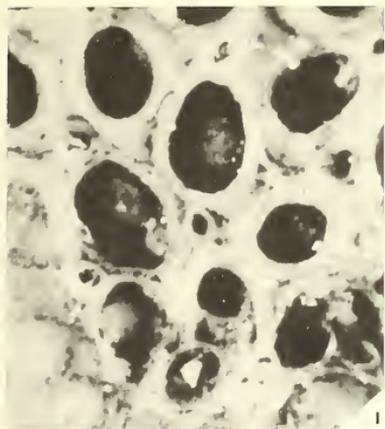
M. retrorsa was established by Brydone on the basis of a unique specimen, which is a small incomplete zoarium of fourteen zoecia. There is one possible vicarious avicularium present, and the mural-rim bears fairly large spine-bases which are typical of *D. trifaria*. The 'rounded' avicularia are considered to be a result of weathering, and so *M. retrorsa* is synonymous with *D. trifaria*.

D. trifaria, therefore, is a species with a relatively wider range of morphological variation, especially in the nature and the position of the avicularia of both types, than has been previously stated, and includes the four species, and probably the one subspecies, discussed above. *D. trifaria* is distinguished from *D. simulacrum* (Brydone) by its greater development of cryptocyst, the structures on the ovicell, and in the slight differences in both types of avicularia. *D. trifaria* is distinguished from *D. triminghamensis* (Brydone) by its mural-rim which is not indented by the spine-bases, by a slightly different type of avicularium; and by a different arrangement and number of the die-

EXPLANATION OF PLATE 68

- Figs. 1-6. *Dionella trifaria* (von Hagenow). 1, [Holotype of *M. retrorsa* Brydone]; ancestrula and initial regular zoarial development obscured by overgrowth of a second zoecial layer. B36497. 2, [Holotype of *M. griffithi* Brydone]; ovicelled autozoecia with associated distal interzoecial avicularia; subvicarious avicularium with the proximal-central portion of the palette more deeply recessed. B36108. 3, Distal margin of a zoarium. B36287. 4, [Lectotype of *M. boletiformis* Brydone]; ovicelled autozoecia and two types of interzoecial avicularia. B36286. 5, Distal margin of a zoarium with clusters of avicularia. B70237. 6, Regeneration of an avicularium by an autozoecium. B36288.

All figures $\times 50$; from unretouched negatives.



tellae. *D. trifaria* is distinguished from *D. trigonopora* (Marsson) by a different type of autozoecium, spine-base structure, and a slightly different type of avicularium. These species, however, are all characterized by having an interzoecial avicularium distal to most, or all, autozoecia. Many other specimens from the R. M. Brydone Collection have been assigned to *D. trifaria*, as here revised.

Stratigraphical Distribution. Senonian, zones of *M. cortestudinarium* to *B. mucronata*; Maastrichtian, including the zone of *Belemmella lanceolata* of Europe.

Specimens. B36108. Holotype of *M. griffithi* Brydone. Incomplete zoarium. Maastrichtian, zone of *B. lanceolata*. Trimmingham, Norfolk. B36285. Syntype of *M. boletiformis* Brydone. Incomplete zoarium. Senonian, zone of *G. quadrata*. Locality 1086 of Brydone (1912, p. 100). B36286. Lectotype (here chosen) of *M. boletiformis* Brydone. Incomplete zoarium. Senonian, zone of *G. quadrata*. Cliff at Seaford, Sussex. B36287-8. Two incomplete zoaria, figured by Brydone as *M. griffithi* (1914, pl. 26, figs. 5-6). Horizon and locality as for B36108. B36496. Holotype (by original configuration) of *M. bradingensis* Brydone. Incomplete zoarium. Senonian, lower part of the zone of *B. mucronata*. Near Brading, Isle of Wight. B36497. Holotype (by monotypy) of *M. retrorsa* Brydone. Zoarial fragment. Horizon and locality as for B36108.

Other specimens. England: from numerous localities in south-east and east England, ranging from Dorset and the Isle of Wight to Norfolk. Sedgwick Museum: (a) zone of *B. lanceolata*—B60522-4, B69557-612, B84569. (b) zone of *B. mucronata*—B63603-17, B70264-8, B85348-56, B85372-3, B85597-601, B65611-27, B85646. (c) zone of *G. quadrata*—B70225-33, B70235-63, B82289-91, B85567-96, B85603, B85605, B85607-10. (d) zone of *O. pilula*: subzone of *E. scutata* var. *cincta*—B70208-24, B85556-66; subzone of *E. scutata* var. *depressula*—B70177-207, B82286-8, B85538-55. (e) zone and subzone of *M. testudinarium*—B70175-6, B72299-300, B85519-37. (f) zone of *M. coranquium*—B69908, B85518. France: Fecamp. Zone of *M. cortestudinarium*—F16111.

2. *Dionella surculus* (Brydone)

Plate 69, figs. 3, 5

1929 *Membranipora surculus* Brydone, p. 29, pl. 9, figs. 6-9.

1949 *Membranipora surculus* Brydone: Voigt, p. 19.

Lectotype (here chosen), SM, B36499. An incomplete zoarium, with the ancestrula obscured by a second zoecial layer. Maastrichtian, zone of *B. lanceolata*. Trimmingham, Norfolk.

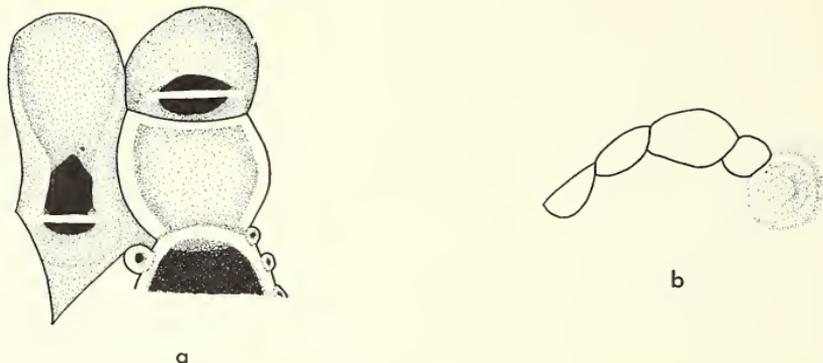
Emended Diagnosis. *Dionella* with the aperture restricted by a band of cryptocyst; mural-rim extremely spinose with ten to eleven pairs of spine-bases, crenulated; distal and two pairs distal-lateral dietellae present; avicularia of two types of interzoecial, solitary, spatulate, occurring at random, and single, acuminate, distal to each autozoecium.

Description. Adult zoecia of average depth. A distal and two pairs of distal-lateral dietellae occur, usually large. A small distal, and two lateral pair of septula are present. Gymnocyst can be extensively developed. Cryptocyst a coarse-granular band, variable in width, widest proximally and proximal-laterally, narrowing distal-laterally to a granular lining of the inner part of the mural-rim, also slight distal development. Mural-rim broken up by the ten to eleven pairs of large spine-bases; the number of spine-bases varies within a single zoarium. Where the stumps of spines are seen, they are found to be laterally fused and to curve over the aperture.

Ovicells with deep proximal-lateral grooves and a flattened triangular area on the distal dorsal surface (text-fig. 4). Nearly all of the adult zoecia possess ovicells; usually there is either nought or one ring of adult zoecia prior to their appearance.

The ancestrula possesses six pairs of spine-bases, the primary zooecia have seven to eight pairs, with the increase in numbers along the proximal portion of the mural rim. The ancestrula is usually obscured by overgrowth of a later zoecial development.

Regenerated zooecia: both the large, solitary, and the small, interzoecial avicularia commonly regenerate from autozoocia, and the small avicularium very rarely regenerates from the large, solitary type.



TEXT-FIG. 4. *Dionella surculus* (Brydone). $\times 150$. *a*, B36499, lectotype, showing two types of avicularia and distal portion of an autozoecium, with a broken ovicell. *b*, B36498, syntype, with a large echinoid boss interfering with the autozoecial dieltellae arrangement.

Avicularia are of two kinds.

(1) Interzoecial, solitary, with some tendency towards a concentration at the zoarial distal margins and to be formed by a regeneration from an autozoecium. The aperture is expanded distally. A transverse-bar is situated within the proximal-terminal quarter of the aperture. Smooth gymnocyst is slightly developed both proximally and laterally (text-fig. 4).

(2) The small interzoecial avicularia are in the case of a few young zooecia, directed distal-laterally away from the aperture. They are acuminate, with the aperture raised

EXPLANATION OF PLATE 69

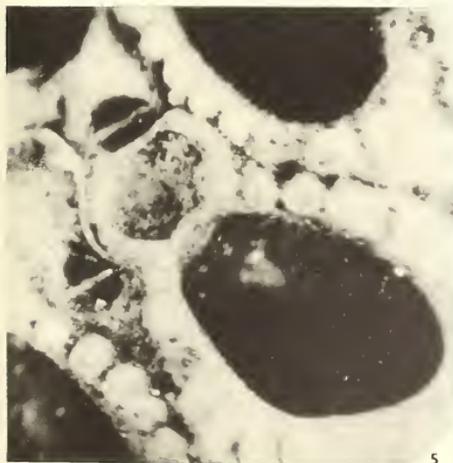
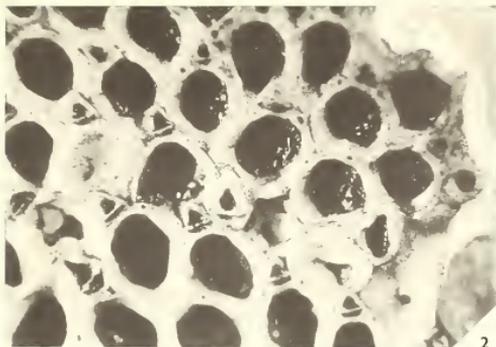
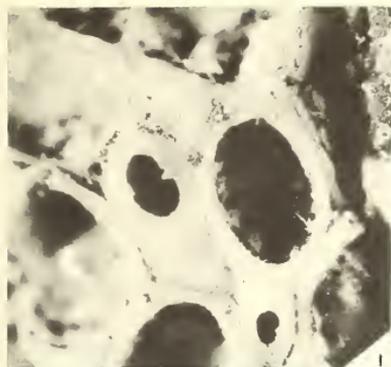
Fig. 1. *Dionella flacilla* (Brydone). Holotype; zoarial fragment with typical adult autozoecia and an enlarged interzoecial avicularium. B36319. $\times 40$.

Figs. 2, 4, 6. *Dionella trigonopora* (Marsson). 2, Neotype; zoarial fragment with calcified autozoecia and a kenozoecium, which terminates the preceding longitudinal zoecial row. F16071. $\times 20$.

4. [Lectotype of *M. crateroides* Brydone]; ancestrular region, the ancestrula without an associated interzoecial avicularium. B36333. $\times 40$. 6, [Syntype of *M. crateroides* Brydone]; a typical elongate spatulate interzoecial avicularium; to the left of it is an enlarged acuminate type of avicularium, which has regenerated from an autozoecium. B36332. $\times 80$.

Figs. 3, 5. *Dionella surculus* (Brydone). 3, Lectotype; zoarial fragment with an avicularium regenerated from an autozoecium. B36499. $\times 40$. 5, Lectotype; autozoecium and both types of avicularium; the distal wall of the broken ovicell is concave. B36499. $\times 120$.

All figures from unretouched negatives.





distally and sunken proximally, with respect to the zoarial surface; there is practically no palette. Gymnocyst is rarely seen due to the sunken nature of the proximal region of the avicularium. The septula are occasionally externally visible. A small distal, and one pair distal-lateral, dietellae are present.

Measurements. (For explanation of the abbreviations used, see text-fig. 1.)

N	1	2	N	1	2
	10	10		10	10
L_z	49-57/51/2	46-55/51/2	h_r	26-31/29/1	29-33/31/1
l_z	32-41/36/3	37-45/39/3	l_r	18-20/19/1	18-24/22/2
h_a	32-38/35/3	37-38/38/0	h_{ov}	17-19/18	18-22/19
l_a	23-29/26/2	26-31/28/2	l_{ov}	18-20/19	19-22/20

1 = B36498, the syntype of *D. surculus* (Brydone); 2 = B36499, the lectotype of *D. surculus* (Brydone).

Remarks. The syntype and specimens B69420-9 have been re-examined.

Brydone (1929, p. 29) considered *M. surculus* to have a 'very distinct place of its own in the group of *M. griffithi*'. *D. surculus* is differentiated from all other members of this group in the increased number and size of the spine-bases. These form an unbroken crenulation of the lateral gymnocyst, which is a characteristic cribrimorph arrangement. However, no case of complete solid spines, overarching the aperture, has been found. Also, *D. surculus* is similar to *D. trifaria* (von Hagenow), particularly in the slight structural variation of the large interzoecial avicularia; and so *D. surculus* is retained in the group as Brydone suggested.

Voigt (1949, p. 18) considered *M. boletiformis* Brydone *subboletiformis* to be intermediate to *M. boletiformis* Brydone and to *M. surculus*. Although the spine-base occurrence in *D. trifaria* (von Hagenow) is very variable, they are inconspicuous and do not crenulate the autozoecial mural-rim. Hence *D. trifaria* (von Hagenow) and *D. surculus* are retained as separate species.

Stratigraphical Distribution. Senonian, zone of *B. mucronata* and Maastrichtian, zone of *B. lanceolata*.

Specimens. B36499. Lectotype—see above. B36498. Syntype of *M. surculus* Brydone. Incomplete zoarium. Horizon and locality as for the lectotype. Other specimens: (a) zone of *Belemnitella lanceolata*—B69420-9; (b) zone of *Belemnitella mucronata*—B85714-16.

3. *Dionella trigonopora* (Marsson)

Plate 69, figs. 2, 4, 6

- 1887 *Membranipora trigonopora* Marsson, p. 58, pl. 5, fig. 16.
 1910 *Membranipora trigonopora* Marsson: Brydone, p. 76.
 1917 *Membranipora crateroides* Brydone, p. 49, pl. 3, figs. 1-2.
 1925 *Membranipora trigonopora* Marsson: Levensen, p. 332, pl. 3, fig. 26.
 1929 *Membranipora trigonopora* Marsson: Brydone, p. 25.
 1930 *Membranipora (Callopora) trigonopora* Marsson: Voigt, p. 444, pl. 9, fig. 6.
 1936 *Membranipora trigonopora* Marsson: Brydone, p. 61.
 1936 *Membranipora crateroides* Brydone: Brydone, p. 65.
 ?1949 *Membranipora flammula* Voigt, p. 16, pl. 3, figs. 2-3.
 1963 *Membranipora trigonopora* Marsson: Veenstra, p. 101, pl. 2, fig. 6.

Neotype (here designated), SM, F16071. A zoarial fragment. Lower Maastrichtian, zone of *Belemnella lanceolata*. Rügen, East Germany.

Emended Diagnosis. *Dionella* with deep zooecia; aperture restricted by a broad band of cryptocyst; mural-rim spinose with two to three pairs of spine-bases the oral spine-base pair being very large; one pair small, impersistent, distal-lateral dietellae; avicularia of two kinds of interzoocelial, either of which may be absent, and vicarious: small, acuminate, distal to the autozoecium, and elongate spatulate, solitary, occurring at random throughout the zoarium, including distally to an autozoecium.

Description. Zoarium occasionally now unattached. Adult zooecia wide and deep, occasionally ogival in shape. One pair of small, impersistent, distal-lateral dietellae present (text-fig. 5). A distal and two lateral pair of septula occur. The basal wall is thin and continuous, often with a central depressed area. Gymnocyst very slightly developed proximally only. Cryptocyst a coarsely granular, variably developed band, widest proximally and proximal-laterally, narrowing distal-laterally, but with good distal development. The distal part of the cryptocyst bears two small pits. Opesia oval to very irregularly rounded-rectangular. One pair of very large oral spine-bases occurs at the distal-lateral termination of the mural-rim, and there is one, occasionally two, pair of very small apertural spine-bases.

Ovicells occur on about one-tenth of the adult zooecia, with patchy distribution throughout the zoarium; usually there are one to three rings of adult zooecia prior to their appearance.

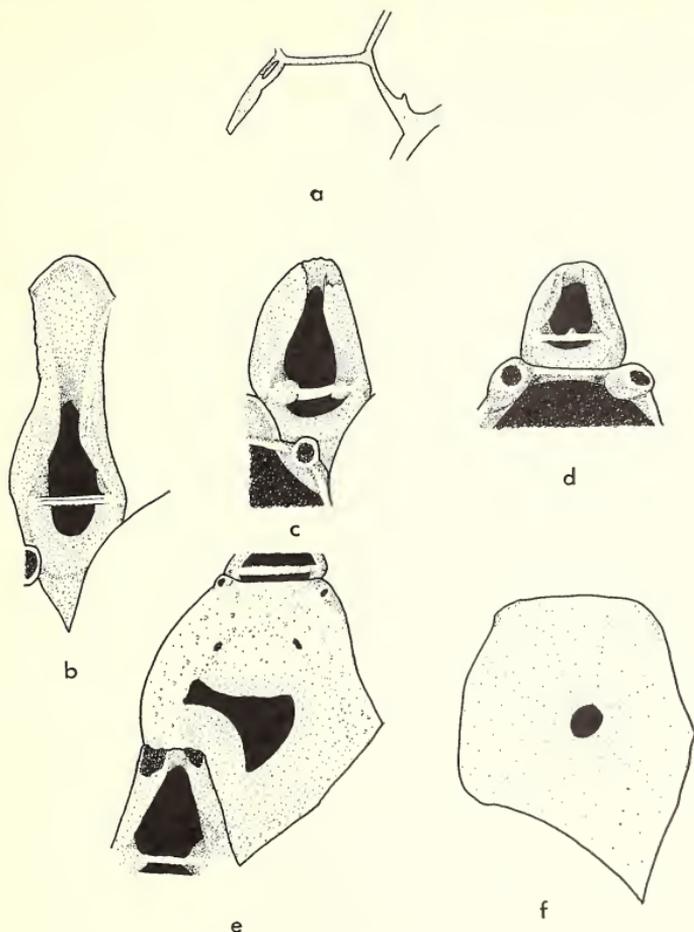
Ancestrula and young zooecia rounded-rhomboidal in shape and possess little cryptocyst. The oral pair of spine-bases is not dominant before the tertiary, or even the quaternary, ring of zooecia. The ancestrula possesses five pairs of spine-bases, all of equal size; the primary zooecia have four pairs, with the oral and the oral-apertural pairs larger than the others; the secondary zooecia have a persistent, large or small pair of oral spine-bases, an impersistent, large or small, oral-apertural pair, and one or two, impersistent, small apertural pair, thus the secondary zooecia possess one to three pairs of spine-bases; the tertiary zooecia have the same spine-base arrangement as those on the adult zooecia, with only an occasional absence of dominance of the oral pair. Occasionally the central primary zoecium also has no associated avicularium.

Regenerated zooecia: vicarious avicularia commonly regenerate from normal, or calcified, autozoecia, either singly or repeatedly. Calcified zooecia: occasionally the autozoecial aperture is partially or completely closed by coarsely granular secondary calcareous tissue (text-fig. 5). Kenozoecia occasionally present; are of the simple type, with granular cryptocyst and a circular opesium.

Avicularia are of two kinds:

(1) Vicarious or interzoecial, solitary. When interzoecial, they occur singly, distal to an autozoecium. Their size is very variable, the largest being those that regenerate from autozoecia. Dietellae are absent. A transverse-bar of variable structure, or prominent condyles are situated within the proximal-terminal quarter of the aperture (fig. 5). Gymnocyst is practically absent.

(2) When the autozoecium is ovicelled, the small interzoecial avicularium is absent; occasionally none of the zooecia possess this type. It is directed distally away from the aperture, not tangential to it, as with the first type of avicularium occurring in this



TEXT-FIG. 5. *Dionella trigonopora* (Marrson). *a*, F16071, neotype, showing impermanent nature of the autozooeccial dietellae. $\times 100$. *b*, B36332, lectotype of *M. crateroides* Brydone, showing the large characteristic interzooeccial avicularium. $\times 60$. *c*, *d*, F16071, $\times 60$: *c*, large interzooeccial avicularium with broken distal part of the aperture; *d*, small interzooeccial avicularium with a small boss in the centre of the transverse-bar, found at the distal end of the autozooeccium, which has very large oral spine-bases. *e*, *f*, F16071, $\times 70$: *e*, autozooeccium calcified from the base of the cryptocyst; *f*, autozooeccium calcified from the inner edges of the mural-rim.

position. They are acuminate, with the distal half of the aperture raised above the zoarial surface, and the proximal half sunk below it. A slight, recessed palette is present. Gymnocyst is absent (fig. 5). Dietellae are absent.

Measurements. (For an explanation of the abbreviations, see text-fig. 1.)

	1	2	3		1	2	3
<i>N</i>	7	10	10	<i>N</i>	7	10	10
<i>L_z</i>	57-81/71/10	67-90/77/7	67-80/73/6	<i>h_r</i>	35-54/45/7	40-55/49/5	40-53/47/4
<i>l_z</i>	52-67/62/5	67-80/70/4	65-90/74/9	<i>l_r</i>	30-46/40/5	37-43/40/1	37-57/45/7
<i>h_a</i>	51-74/61/7	57-70/63/4	50-73/60/6	<i>h_{ov}</i>		38-40/39	
<i>l_a</i>	40-60/54/6	50-70/58/5	50-73/60/7	<i>l_{ov}</i>		40-41/40	

1 = F16071, the neotype of *D. trigonopora* (Marsson); 2 = B36332, the lectotype of *M. crateroides* Brydone; 3 = B36333, the syntype of *M. crateroides* Brydone.

Remarks. *M. trigonopora* was established by Marsson and subsequently revised by Levensen. Marsson's collection of Rügen Chalk Polyzoa, including the type specimens of *D. trigonopora*, was destroyed during World War II (Voigt, 1949, p. 6; 1959, p. 7). The neotype, here designated, completely corresponds with the description and figure of Marsson.

M. crateroides Brydone and probably *M. flammula* Voigt are here regarded as being synonymous with *D. trigonopora* (Marsson).

Marsson considered *D. trigonopora* to be a species with deep zooecia, raised mural-rims, and triangular or quadrilateral opesia. He ended his description: 'a triangular avicularium is found above the opesium, which may be absent. On the anterior part of the mural-rim is a pair of pores' [translation]; his 'pores' are here regarded as being spine-bases. Levensen (1925, p. 332) said that the gymnocyst was weakly developed due to the projection of the older (proximal) zooecia on to it. He also noted the presence of the rare large avicularia that could attain autozooecial length and half the width. His specimens were 'free, lamellar plates with irregularly arranged zooecia'. Voigt (1930, p. 444) placed *M. trigonopora* in his group of *Membranipora* (*Callopora*).

Brydone (1929, p. 25; 1936, p. 61) established a (sub) group of *M. trigonopora* containing several species which he had established. There is, however, no similarity between these species, and the (sub) group is here rejected.

Brydone (1917, p. 49), in his original description of *M. crateroides*, said that this species was distinguishable from *M. trigonopora* Marsson by its subvicarious avicularia and perhaps its ovicells, as none were recorded for Marsson's species. Notwithstanding Brydone's later comments on the merging of these two species (1936, p. 65), the writer agrees with Voigt (1930, p. 444) and considers *M. crateroides* to be a synonym of *D. trigonopora*.

Voigt (1949, p. 16) established *M. flammula*, 'distinguished by having zooecia with a completely open area, two pairs of apertural spines and subvicarious avicularia of medium size, approximately spatulate in shape. Dietellae absent. . . . Ovicells small, hyperstomial. . . . Occurs only in the "quadratenkalk" of Lägerdorf' [translation]. An examination of his figures, however, indicates the presence of a thin band of cryptocyst and the autozooecia are identical with those of the type specimens of *M. crateroides* Brydone. Only in the absence of the distal interzooecial avicularium does *M. flammula* differ from *D. trigonopora*. This type of avicularium does not always occur within a zoarium and within a population it is probable that a few zoaria may lack them. Hence *M. flammula* is a probable synonym of *D. trigonopora*.

D. trigonopora is, therefore, a species with a wider range of morphological variation,

especially in the position of the avicularia, than has been previously stated, and comprises the two species, and probably a third, discussed above.

D. trigonopora is distinguished from all other members of the *D. simulacrum* group in having a different type of autozoecium and distal, interzoecial avicularium; and, with the exception of *D. flacilla* (Brydone), also in a different spine-base arrangement.

Stratigraphical distribution. Senonian, zones of *G. quadrata* to *B. mucronata* in England. The type specimen, from Rügen, Germany, was labelled 'mucronata zone' but is probably Maastrichtian, zone of *B. lanceolata*.

Specimens. F16071. Neotype—see above. B36332. Lectotype (here chosen) of *M. crateroides* Brydone. Incomplete zoarium. Senonian, zone of *B. mucronata*. Weybourne, Norfolk. B36333. Syntype of *M. crateroides* Brydone. Incomplete zoarium. Senonian, zone of *B. mucronata*. Whitlingham, Norfolk. Other specimens. England. (a) B68422, B68424–8. Horizon and locality as for B36332. (b) Zone of *G. quadrata*—B70234.

4. *Dionella simulacrum* (Brydone)

Plate 70, figs. 1–6

- 1914 *Membranipora simulacrum* Brydone, p. 345, pl. 26, figs. 1–21.
 1916 *Membranipora feronia* Brydone, p. 338, pl. 14, fig. 4.
 ?1920 *Tegella nicklesi* Canu and Bassler, p. 167, pl. 30, figs. 9–10.
 1930 *non Membranipora simulacrum* Brydone: Voigt, p. 421, pl. 10, fig. 12.
 ?1930 *non Membranipora (Callopora) feronia* Brydone: Voigt, p. 443, pl. 10, fig. 1.
 1949 *non Membranipora simulacrum* Brydone: Voigt, p. 18.

Lectotype (here chosen), SM, B36281. An incomplete zoarium. Senonian, zone of *Micraster coran-giumm*. Gravesend, Kent.

Emended Diagnosis. *Dionella* with the opesium occupying almost all of the aperture, there being little cryptocyst; mural-rim spinose, with one to four pairs of spine-base; large distal and three distal-lateral dietellae present, asymmetrically arranged; avicularia of one or two types, a single interzoecial distal to each autozoecium, and a large vicarious.

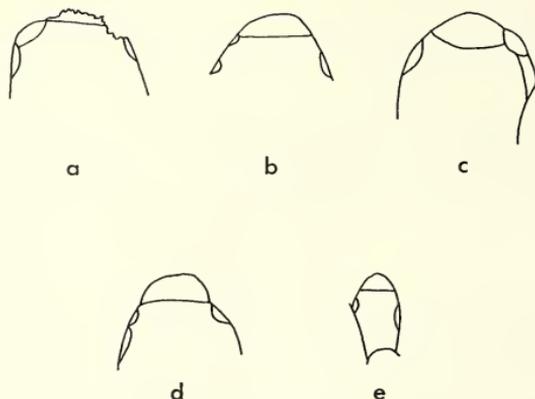
Description. Adult zoecia slightly shallow or deep. A large distal and three asymmetrically arranged distal-lateral dietellae occur (text-fig. 6). A small distal and three to four lateral pairs of septula occur. Cryptocyst a thin granular band on the proximal and proximal-lateral margins of the mural-rim, tapering distally to a granulation of the wall, the spine-base occurrence on the adult zoecia being variable within a single zoarium. Half to nearly all of the adult zoecia possess ovicells; usually there are nought to one, occasionally two, rings on adult zoecia prior to their appearance.

The ancestrula possess 5 pairs of spine-bases, the primary zoecia have 4–5 pairs, the secondary zoecia, 3 pairs and the tertiary zoecia 2–3 pairs, with the reduction in number occurring along the proximal region of the mural-rim.

Avicularia of two kinds:

(1) Vicarious, solitary, not present in all zoaria considered to belong to this species (text-fig. 7), usually a crescentic band, confined to the distal half of the aperture; rarely it is more extensive, occupying the whole of the distal half of the aperture. Prominent condyles occur within the proximal quarter of the aperture (text-fig. 7). The small

inter-zooecial avicularia are distally round, with the aperture either level with the zoarial surface or with the distal half raised. There is no true palette, but the granular cryptocyst, which may almost fill the sub-opercular region of the aperture, continues into the opercular region and thins out distal-laterally. Gymnocyst is absent. A small distal and a single distal-lateral dietella are present.



TEXT-FIG. 6. *Dionella simulacrum* (Brydone). $\times 40$. a-d, the range in variation of the autozooccal dietellae: a, B36281, lectotype, with a broken distal dietella and asymmetrical distal-lateral dietellae; b, c, B36282, syntype; d, B36318, holotype of *M. feronia* Brydone. e, B26282, the dietella arrangement of a distal inter-zooecial avicularium.

Measurements. (For an explanation of the abbreviations, see text-fig. 1.)

	1	2	3		1	2	3
N	10	8	10	N	10	8	10
L_z	64-87/76/6	68-81/72/5	67-84/73/7	h_r	43-59/51/4	47-57/51/3	53-67/57/4
l_z	38-45/42/2	40-50/44/3	39-60/49/6	l_r	28-36/32/2	28-37/31/3	30-42/36/4
h_a	46-61/56/3	51-61/54/3	57-70/61/5	h_{ov}		17-20/19	16-19/18
l_a	33-41/38/2	33-42/37/2	33-47/41/4	l_{ov}		19-22/20	18-23/21

1 = B36318, the holotype of *Menibranipora feronia* Brydone; 2 = B36281, the lectotype of *D. simulacrum* (Brydone); 3 = B36282, the syntype of *D. simulacrum* (Brydone).

EXPLANATION OF PLATE 70

Figs. 1-6. *Dionella simulacrum* (Brydone). 1, Lectotype; incomplete zoarium showing the ancestrula and young zooecia. B36281. $\times 20$. 2, [Holotype of *M. feronia* Brydone]; incomplete zoarium, including an enlarged interzooccal avicularium. B36318. $\times 20$. 3, Autozoocium and both types of avicularia present. B85477. $\times 50$. 4, Syntype; showing autozooccal and interzooccal avicularian dietellae. B36282. $\times 20$. 5, Lectotype; autozoocia with, and without, associated distal interzooccal avicularia; the subvicarious avicularium present has a slightly distally expanded aperture. B69885. $\times 50$.

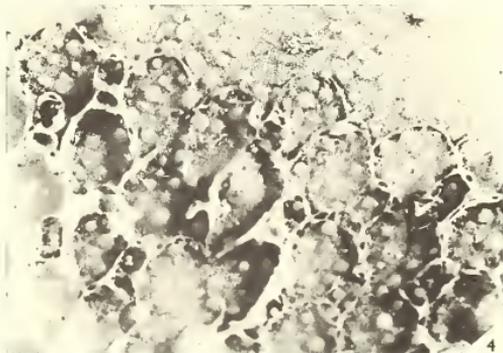
All figures from unretouched negatives.



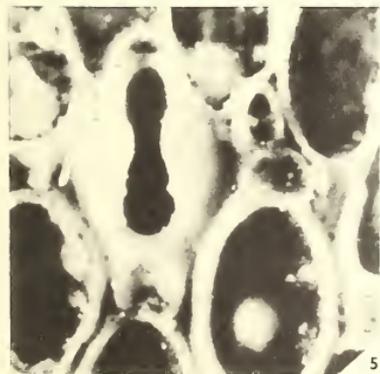
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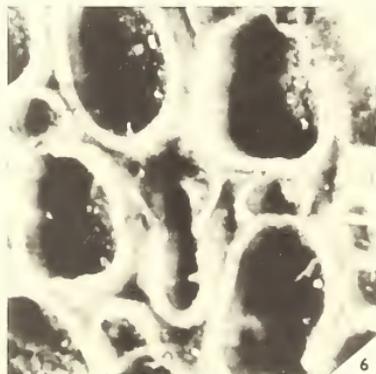
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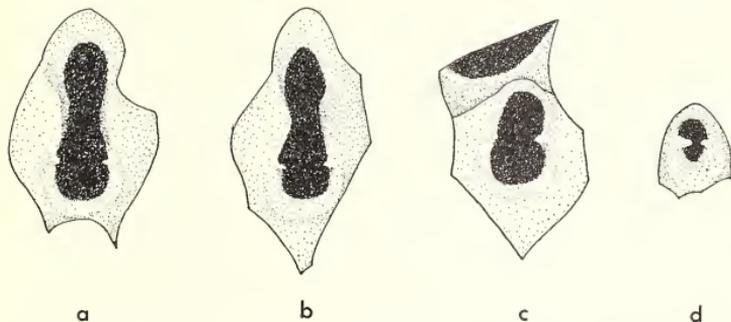
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6

Remarks. The types and all available specimens, identified by Brydone as *M. simulacrum* and *M. feronia*, have been re-examined. *M. feronia* Brydone and probably *T. nicklesi* Canu and Bassler are synonymous with *D. simulacrum* Brydone.

Brydone established *M. simulacrum* as a species with 'slender side-walls' and with both adventitious and vicarious avicularia. Referring to the adventitious type, he said that 'this type seems to separate the species from the *M. griffithi* line and ally it to *M. triminghamensis*'. He considered that vicarious avicularia 'occur very capriciously'.



TEXT-FIG. 7. *Dionella simulacrum* (Brydone). $\times 50$. Vicarious and interzoocial avicularia of: a, B36281, lectotype, vicarious avicularium with a crescentic palette; b, B36282, syntype; c, B36318, holotype of *M. feronia* Brydone, vicarious avicularium with a typical sub-opercular region of the aperture, but with the opercular region truncated and reminiscent of the small interzoocial avicularia; d, B36281, typical small interzoocial avicularium, occurring distally to the autozoocium.

Finally he stated that he had found specimens only in the *Micraster coranginum* zone of Kent and Hampshire, and once in the *Uintacrinus* band of Hampshire. Voigt (1930, p. 421) identified a specimen from the 'Quadraten oder Mukronatenkreide bei Misburg', although he (1949, p. 18) later doubted this identification, but was unable to prove it as the specimen had been destroyed. It is not possible to decide the systematic position of the specimen from his figure (1930, pl. 10, fig. 12).

There are several specimens in the collection of *Membranipora feronia* labelled by Brydone, but he only positively identified the holotype. He defined the species as having very slender zoecia with a tapering front-wall; ovicells not numerous and avicularia much like those of '*Membranipora fascelis* Brydone 'even to the occasional vicarious specimen'. He considered it to be 'rare in the zones of *A. quadratus* (restricted) and *B. mucronata* in Hampshire', and that it 'closely resembles *Reptoflustrella ovalis* d'Orbigny (1852, p. 571, pl. 731, figs. 17-18)'. The avicularia, however, bear little, if any, resemblance to those of '*M. fascelis*, whilst the presence of an occasional enlarged avicularium of an otherwise small type is a character met with throughout the membraniforms. No specimens have been recorded from any zone higher than *Goniot euthis quadrata* and there is no resemblance to *R. ovalis* d'Orbigny. The autozoecia are identical with those typical of *D. simulacrum* and the absence of true vicarious avicularia is not of sufficient systematic importance to warrant the continued separation of these species.

Voigt (1930, p. 443) identified a specimen as *M. (Callopora) feronia* Brydone from the 'Mammillatensenon Ifo/Schonen'; his figure, however, shows a form without the characteristic distal interzoecial avicularia, but with occasional scattered interzoecial avicularia, and with a slightly different type of autozoecium, there being a greater development of both gymnocyst and cryptocyst. These differences are too great for this specimen to be identified as *M. feronia*.

An examination of the figures and descriptions of *Tegella nicklesi*, established by Canu and Bassler, indicates that this species is probably synonymous with *D. simulacrum*. Examination of all specimens assigned to *D. simulacrum* shows that the large vicarious avicularia are absent in specimens from zones higher than *Micraster coranguinum*.

Stratigraphical Distribution. Senonian, zones of *M. coranguinum* to *G. quadrata* in England. Probably Eocene (Middle Jacksonian) of Carolina, U.S.A.

Specimens. Lectotype—see above. B36282: Syntype of *D. simulacrum* (Brydone). Incomplete zoarium. Horizon and locality as for the lectotype. B36318: Holotype (by monotypy) of *M. feronia* Brydone. Incomplete zoarium. Senonian, zone of *O. pilula*, subzone of *E. scutata* var. *depressula*. Locality 914 of Brydone (1912, p. 90). Other specimens. England, from numerous localities in the south-east. (a) Zone of *G. quadrata*—B36592-4, B72358, B81962-4, B85602, B85604, B85606. (b) Zone of *O. pilula*: subzone of *E. scutata* var. *cineta*—B36591; subzone of *E. scutata* var. *depressula*—B85632. (c) Zone of *M. testudinarius*: subzone of *M. testudinarius*—B36590; subzone of *U. socialis*—B69886-9. (d) Zone of *M. coranguinum*—B69863-85, B85477, B85629-31.

5. *Dionella triminghamensis* (Brydone)

Plate 71, figs. 1-3

- 1906 *Membranipora triminghamensis* Brydone, p. 294, text-fig. 2.
 1910 *Membranipora triminghamensis* Brydone: Brydone, p. 5.
 1910 *Membranipora triminghamensis* (*nom. emend.*) Brydone, p. 5, pl. 3, figs. 7-8.
 1914 *Membranipora triminghamensis* Brydone: Brydone, p. 345.
 1920 *Tegella (Membranipora) triminghamensis* (Brydone) Canu and Bassler, p. 166.

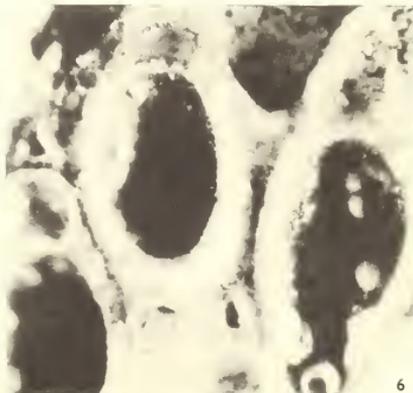
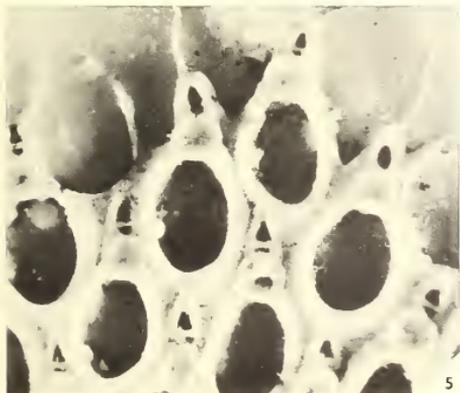
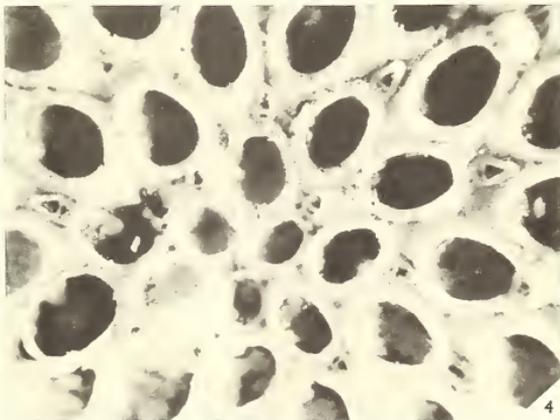
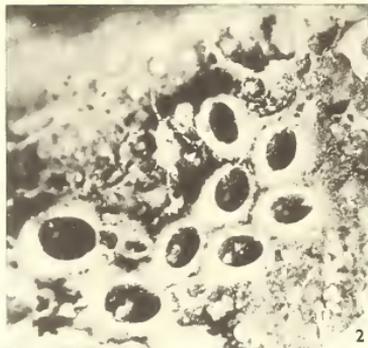
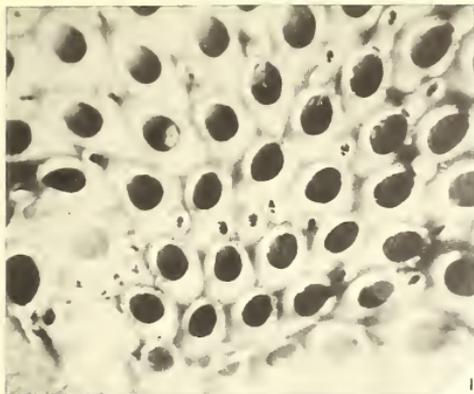
Holotype. SM, B36109. An incomplete zoarium. Maastrichtian, zone of *Belemella lanceolata*. Trimmingham, Norfolk.

Emended Diagnosis. A multiserial, or pleuriserial *Dionella*; aperture restricted by a band of cryptocyst; mural-rim spinose, with seven to ten pairs of spine-bases; distal and one, or two, pair distal-lateral diatellae present; avicularia interzoecial, distal to each autozoecium, aperture distally round.

Description. Zoarium rarely pleuriserial. Adult zoecia of average depth, occasionally slightly deep. A distal and two to four distal-lateral diatellae occur, which may be large or

EXPLANATION OF PLATE 71

- Figs. 1-3. *Dionella triminghamensis* (Brydone). 1, Holotype; initial stages of the development of a large zoarium; the incoming of ovicells is shown, as is a 'ring' of small, interzoecial avicularia. B36109. $\times 20$. 2, The distal margin of a zoarium having pleuriserial growth. B69455. $\times 20$. 3, Holotype; typical adult autozoecia and avicularia. B36109. $\times 40$.
 Figs. 4-6. *Dionella suffragista* (Brydone). 4, Lectotype; the ancestral region of the zoarium with irregular initial zoarial development. B36284. $\times 40$. 5, Lectotype; the zoarial distal margin. B36284. $\times 40$. 6, Adult autozoecium with a large gymnocystal pore. B69937. $\times 80$.
 All figures from unretouched negatives.



small (text-fig. 8), and may be symmetrically or asymmetrically arranged. A small distal and one, generally two, lateral pairs of septula are present. Cryptocyst a granular band, variable in width, widest proximally and proximal-laterally, narrowing distal-laterally to a granular lining of the inner part of the mural-rim, with slight distal development. Mural-rim variably defined, often slightly broken up by the large seven to ten pairs of spine-bases, the number of spine-bases varies within a single zoarium. Where the stumps of the spines are seen, they are found to be distinct and not laterally fused, and curve over the aperture.

Ovicells with prominent proximal-lateral grooves and occasional, slight distal flattening. Nearly all of the adult zooecia possess ovicells; usually there is nought or one ring of adult zooecia prior to their appearance. The ancestrula possesses 6 pairs spine-bases, the primary zooecia have 6-9 pairs, the secondary zooecia 7 pairs with an increase in numbers along the proximal region of the mural-rim. The central primary zooecium also usually lacks an associated avicularium.

Regenerated zooecia: the small interzoecial avicularia very rarely regenerate from autozooecia or from other such avicularia.

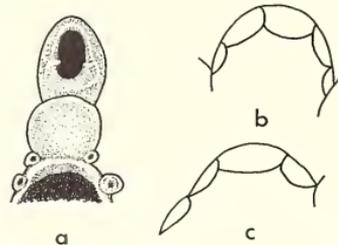
Avicularia of one kind only: small, interzoecial. They are distally and sunken proximally, with respect to the zoarial surface. A small recessed palette is usually present. Variable development of proximal and proximal-lateral gymnocyst occurs, and may be extensive (text-fig. 8). A small distal and one pair distal lateral dietellae are present.

Measurements. (For an explanation of the abbreviations, see text-fig. 1.) B36109, the holotype of *D. trininghamensis* (Brydone).

<i>N</i>	12	<i>N</i>	12
L_z	57-83/68/8	h_r	35-41/38/2
l_z	38-57/48/6	l_r	24-31/28/2
h_a	42-47/44/2	h_{ov}	19-20/319
l_a	28-37/34/2	l_{ov}	19-20/20

Remarks. The holotype and all available specimens identified by Brydone as *M. trininghamensis* have been re-examined.

M. trininghamensis was established by Brydone (1906, p. 294), who noted that it could 'be constructed from . . . [*M. griffithi*] by rounding and smoothing all sharp angles and corners'. Later (1910, p. 5) he discussed the differences between these two species and *Cellepora trifaria* von Hagenow, considering *M. trininghamensis* to be the species possessing 'no large avicularia'. He also said (1914, p. 346) that the 'accessory type' of avicularia separated *M. simulacrum* from the *M. griffithi* line and allied it to *M. trininghamensis*. The writer agrees with Brydone in there being a morphological break between *D. trifaria* (von Hagenow) on the one hand, and *D. trininghamensis* and *D. simulacrum* on the other. The two latter species are similar in their zooecial shape, but *D. trininghamensis* has a greater development of lateral gymnocyst and an increased spinous nature of



TEXT-FIG. 8. *Dionella trininghamensis* (Brydone) B36109, holotype. $\times 60$. a, General view of the distal end of an autozooecium, with a broken ovicell. b, c, dietella variation in a single zoarium.

the mural-rim. These two characters are of sufficient systematic importance to warrant the separation of these two species.

Stratigraphical Distribution. Maastrichtian, zone of *Belemnella lanceolata*.

Specimens. B36109. Holotype—see above. Other specimens. B50826, B69455-79, B69481-3. Horizon and locality as for the holotype.

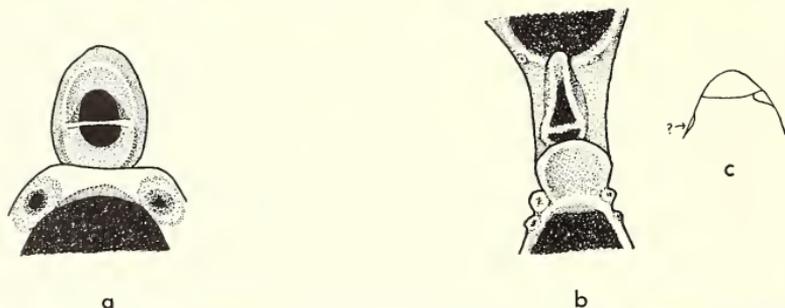
6. *Dionella flacilla* (Brydone)

Plate 69, fig. 1

1916 *Membranipora flacilla* Brydone, p. 338, pl. 14, fig. 5.

?1930 *Membranipora* (*Callopora*) aff. *flacilla* Brydone: Voigt, p. 443, pl. 9, fig. 3.

Holotype (by monotypy), SM, B36319. A zoarial fragment. The only specimen. Senonian, zone of *Belemnitella mucronata*. Weybourne, Norfolk.



TEXT-FIG 9. *a*, *Dionella flacilla* (Brydone), B36319, holotype, non-ovicelled autozoecium with very large oral spine-bases, and a distal interzoecial avicularium. $\times 70$. *b*, *c*, *D. suffragista* (Brydone). B36284, lectotype. $\times 70$. *b*, Distal interzoecial avicularium surrounded by the proximal autozoecial gymnocyst; *c*, autozoecial dietellae.

Emended Diagnosis. *Dionella* with slightly shallow zoecia; opesium occupying almost all of the aperture, there being little cryptocyst; mural-rim with only one pair of very large oral spine-bases; one pair small, distal-lateral dietellae; avicularia interzoecial, distal to most of the autozoecia, with distally rounded aperture.

Description. Adult zoecia wide and shallow. One pair of small impersistent distal-lateral dietellae present. A distal and three lateral pair of septula occur. Cryptocyst a thin granular band on the proximal and proximal-lateral margins of the mural-rim, tapering distally to a granulation of the wall. One pair of oral spine-bases only occurs, very large with a diameter of 0.08 mm. (text-fig. 9).

Ovicells apparently globular, prominent, and overlapping on to the distally adjacent zoecium; seen only in the broken state. One-third of the adult zoecia possess them, with irregular distribution throughout the zoarium.

Ancestrula and young zoecia not seen.

Avicularia of one kind only: small, interzoecial; they are absent if the autozoecium is ovicelled and occasionally if not. Rarely at the distal margins a second such avicularium, distal-lateral in position, is associated with the autozoecium. Distally

round, with the aperture either level with the zoarial surface or with the distal half raised. A small recessed palette is present. Variable development of smooth, proximal, and proximal-lateral gymnocyst occurs, usually not extensive (text-fig. 9). Dietellae absent.

Measurements. (For an explanation of the abbreviations, see text-fig. 1). B36319 the holotype of *D. flacilla* (Brydone).

	N	10		N	10
L_z	77-97/86/6		h_r	59-70/63/3	
l_z	53-67/58/4		l_r	39-50/42/4	
h_a	63-77/68/4		h_{ov}	19-26/22	
l_a	45-57/49/4		l_{ov}	22-24/23	

Remarks. The only known specimen of *D. flacilla*, the holotype, has been re-examined. Brydone slightly under-estimated the dimensions of the aperture, and so the difference between these measurements and those of the specimen referred by Voigt (1930, p. 443) to this species is even greater and Voigt's identification remains uncertain.

D. flacilla Brydone differs from *D. simulacrum* Brydone only in the absence of a vicarious avicularium and in the presence of the very large pair of oral spine-bases. These spine-bases are of sufficient importance to warrant the continued separation of these two species.

Stratigraphical Distribution. Senonian, zone of *B. mucronata*.

Specimen. B36319. Holotype—see above.

7. *Dionella suffragista* (Brydone)

Plate 71, figs. 4-6

- 1914 *Membranipora suffragista* Brydone, p. 346, pl. 26, figs. 3-4.
 ?1920 *Tegella aculeata* Canu and Bassler, p. 166, pl. 30, fig. 11.
 ?1930 *Membranipora suffragista* Brydone: Voigt, p. 434, pl. 6, figs. 13-14.

Lectotype. (Here chosen), SM, B36284. An incomplete zoarium. Senonian, zone of *Micraster coranquinum*. Gravesend, Kent.

Emended Diagnosis. *Dionella* with the aperture restricted by a thin band of cryptocyst; mural-rim spinose, with 8 pairs of spine-bases; distal and one pair distal-lateral dietellae present; avicularia interzoecial, distal to each autozoecium, elongate, spatulate; autozoecial gymnocystal pore and associated secondary calcareous tissue may occur.

Description. Adult zoecia of average depth, occasionally slightly deep. A distal and one, very rarely two, pairs of distal-lateral dietellae are present, variable in size and position (text-fig. 10). A small distal and one, generally two, lateral pairs of septula occur. A gymnocystal pore occasionally present with associated secondary calcareous tissue. Cryptocyst a thin granular band, variable in width, widest proximally and proximal-laterally, narrowing distal-laterally to a granular lining of the inner part of the mural-rim, with very slight distal development. Often slightly broken up by the eight pairs of large spine-bases.

Ovicells with slight proximal-lateral grooves and occasional, very slight, distal flattening. Nearly all of the adult zoecia possess ovicells; usually there are nought or one, occasionally up to three, rings of adult zoecia prior to their appearance. The

ancestrula possesses 6 pairs of spine-bases, the primary zooecia have 5-7 pairs, the secondary zooecia 7-9 pairs, with the increase in number occurring along the proximal region of the mural-rim.

Avicularia of one kind only; small, interzooecial. They are spatulate, with the aperture often slightly raised distally above the zoarial surface. The distal end of the aperture is prolonged into an elongate, narrow finger, that encroaches on to the gymnocyst of the distally adjacent zooecium, as far as its mural-rim. Variable development of proximal gymnocyst occurs (text-fig. 10). A small distal and one pair of distal-lateral dietellae are present.

Other heterozooecia: in conjunction with the gymnocystal pore, there is often developed a rim of calcareous tissue on the proximal gymnocyst of the autozooecium, which is very reminiscent of the base of an eroded heterozooecium.

Measurements. (For an explanation of the abbreviations, see text-fig. 1.)

	1	2		1	2
N	10	10	N	10	10
L_z	55-66/59/4	56-67/61/4	h_r	37-43/40/2	37-43/40/2
l_z	33-38/36/1	35-46/40/4	l_r	23-27/24/1	24-31/27/2
h_a	43-47/46/1	42-49/45/2	h_{ov}	15-19/17	17-19/18
l_a	28-32/30/1	29-36/32/3	l_{ov}	17-19/18	18-20/19

1 = B36283, the syntype of *D. suffragista* (Brydone); 2 = B36284, the lectotype of *D. suffragista* (Brydone).

Remarks. Brydone (1914, p. 346) established *Membranipora suffragista* as a species that 'might by its spines be ancestral to *M. tringhamensis*, but by its avicularia it is probably ancestral to *M. griffithi*'. Voigt (1930, p. 434) placed *M. suffragista* into his division that possessed 'a complete ring of spines around the area' and 'which belongs to *Callopora*' [translation]. He recorded specimens from the 'Granulatensenen' of Germany and the 'Mammillatensenen' of Sweden, but in neither of his figures can the diagnostic feature of this species, the spatulate nature of the avicularium, be recognized; moreover, the specimens have been destroyed, and so his identifications are only tentatively accepted.

The re-examination of the syntypes and all available specimens has shown that the spatulate nature of the interzooecial avicularium is very constant. The avicularium is quite distinct from that possessed by *D. tringhamensis* (Brydone) and *D. trifaria* (von Hagenow). The autozooecia of the types of *D. suffragista* and *D. simulacrum* (Brydone) are, however, very similar, apart from the greater spinosity of the former species. A gymnocystal pore and associated secondary calcareous tissue have also been found in many specimens. The pore and tissue are absent in specimens from the Zone of *M. coranguinum*, present in a few specimens from the Zone of *Marsupites*: subzone of *Unitacrinus*, whereas all of the specimens from the subzone of *Marsupites* have them; finally, of the two specimens coming from the Zone of *O. pilula*: subzone of *E. scutata* var. *depressula*, only one has the pore and tissue. From the material examined, it is not possible to say whether this structure is an eroded heterozooecium, such as is found in specimens of *Callopora bipunctata* (Goldfuss); but if so, then there is a transition between *Dionella* and *Callopora* Gray.

Tegella aculeata, established by Canu and Bassler, is regarded as being a probable

synonym of *D. suffragista*. The only difference is the occurrence of fewer spine-bases spinosity and this character probably does not warrant the continued separation of these two species. However, no specimens have so far been recorded from deposits between the Senonian Zone of *G. quadrata* for *D. suffragista* and the Eocene (Middle Jacksonian) for *T. aculeata*, but this is not considered to be sufficient reason for the continued separation of these two species.

Stratigraphical Distribution. Senonian, zones of *M. coranguinum* to *O. pilula*: subzone of *E. scutata* var. *depressula* in England, and the zones of *Marsupites* and *G. quadrata* in Europe. Eocene (Middle Jacksonian) of Carolina, U.S.A.

Specimens. B36284. Lectotype—see above. B36283. Syntype of *D. suffragista* (Brydone). Incomplete zoarium. Horizon and locality as for the lectotype. Other specimens. From numerous localities in east and south-east England, ranging from the Isle of Wight to Suffolk. Sedgwick Museum: (a) Zone of *O. pilula*: subzone of *E. scutata* var. *depressula*—B69949–50. (b) Zone of *M. testudinarius*: subzone of *M. testudinarius*—B69936–48, B85642–5; subzone of *U. socialis*—B69933–5, B85641. (c) Zone of *M. coranguinum*—B69890–907, B69909–32, B85633–40.

EVOLUTION

Evolution has little, if any, apparent direction in this genus, and the major factor affecting the zoarial development is the environment. The present revision has resulted in the merging of several species and the plexus of evolution within the genus is now shown to be much more complex. It seems as if there were two main evolutionary developments, the first being the initial early Senonian one, and the second one being late Senonian (Zone of *B. mucronata*).

D. trifaria is the earliest occurring species, being first recorded in the Zone of *M. cortestudinarium*, and has the longest range, being present throughout the Senonian and the Maastrichtian; it is also represented by a large number of specimens, particularly in the Zones of *Belemnitella mucronata* and *Belemnella lanceolata*. It is probably ancestral to *D. surculus*, which is introduced in the Zone of *B. mucronata*, and to *D. trigonopora*, first introduced in the Zone of *G. quadrata*. *D. surculus* differs from *D. trifaria* by its increased spinosity of the mural-rim, whilst *D. trigonopora* possesses a reduced but greatly enlarged spinosity and the distal portion of its ovicell is not flattened.

D. simulacrum is first found in beds of the Zone of *M. coranguinum* and differs from *D. trifaria* both in the structure of the autozoecia and of the ovicell. It is probable that these two species possessed a common ancestor rather than *D. simulacrum* being evolved from *D. trifaria*.

D. suffragista, also first found in the Zone of *M. coranguinum*, possibly evolved from an early member of the *D. simulacrum* lineage, by an alteration in the structural type of the distal interzoecial avicularium; by the Subzone of *U. socialis* it had also developed a gymnocystal pore, and a specimen of this type has been recorded from the Eocene of the U.S.A.

D. flacilla is confined to the Zone of *B. mucronata* and it may have evolved from *D. simulacrum* by a reduction in the autozoecial spinosity, together with the development of a pair of very large oral spines and a reduction in the size of the dietellae.

D. tringhamensis is confined to the beds of Maastrichtian age; its ancestry is uncertain for, although it may have evolved from *D. simulacrum* by an increase in spinosity

and proximal-lateral gymnocyst development, no specimens of either of these two species have been found from the Zone of *B. mucronata*. *D. flacilla* is not considered to be a possible intermediate form. However, *Tegella nicklesi* Canu and Bassler, which is probably synonymous with *D. simulacrum*, is an Eocene form, and so *D. simulacrum* may continue into the Tertiary. Hence, the possibility that *D. trimminghamensis* is derived from *D. simulacrum* is not excluded.

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DISPHYLLIDAE AND PHACELLOPHYLLIDAE FROM THE DEVONIAN GARRA FORMATION OF NEW SOUTH WALES

by D. L. STRUSZ

ABSTRACT. As part of a revision of the rugose coral fauna of the Garra Formation of New South Wales, the families Disphyllidae and Phacellophyllidae are studied, particular note being taken of Schouppé's (1958) revision of this group. The arrangement of trabeculae and the dissepimental structure of the two families are discussed.

New taxa described are: *Mansuyphyllum bellense* sp. nov., *M. parvulum* sp. nov., *M. catombalense* sp. nov., *Paradisphyllum haruudinetum* gen. et sp. nov., and *Hexagonaria approximans cribellum* subsp. nov., in the family Disphyllidae; *Peneckiella boreensis* sp. nov., in the family Phacellophyllidae.

Biostratigraphic subdivision of the Garra Formation, a folded and faulted complex of reef and detrital limestones, is not yet possible. It is deduced to be probably Emsian in age, possibly extending to early Couvian.

THE disphylloid species described in this paper form a significant part of the coral fauna of the Devonian Garra Formation of New South Wales. This formation is a succession of calcareous rocks which crop out in a sixty-mile wide meridional belt; to the north this disappears beneath the margin of the Great Artesian Basin, and southwards it ends near Orange, a city some 120 miles west-north-west from Sydney (see text-fig. 1). This belt of outcrops of the Garra Formation, up to five miles wide, is recognized as marking an area of relatively shallow water (the Molong Geanticline) throughout most of the early Palaeozoic history of the Lachlan Geosyncline, as Packham (1960) has called this part of the Tasman Geosyncline.

STRATIGRAPHY

Overlying the Garra Formation are sandstones of the Late Devonian Catombal Group, recently described by Conolly (1963). The junction between the two is in some places disconformable, in others gently unconformable. Beneath the formation is a succession of volcanic rocks and sediments, ranging in age down into the Silurian. This boundary, on the present available evidence, appears to be conformable over much, if not all, of the western side of the Molong Geanticline, but on its eastern side the situation is confused by strike faulting, and the relationship to the underlying beds is obscure, possibly unconformable.

Sedimentation apparently ceased after deposition of the Catombal Group, and the region was then folded about an echelon meridional axis, probably in the early Carboniferous.

Essentially, the Garra Formation consists of some 3,000 to 4,000 feet of deposits formed in and around an area of reef development. Consequently, these deposits show highly complex horizontal and vertical relationships. The two dominant lithologies are calcareous shale and detrital limestones. These are interspersed with reef-type deposits, which range from two or three rather large bioherms down to thin biostromes built by

laminar stromatoporoids. The detrital limestones include all types, but are predominantly fossiliferous calcarenites, which are frequently thinly interbedded with calcareous to non-calcareous shale. In some areas there are extensive outcrops of algal limestones and pellet or oolite calcarenites; these are generally only sparsely fossiliferous.

It has, unfortunately, not yet proved possible to subdivide the Garra Formation, and so no attempt can be made to assign the various species to precise stratigraphic levels. In a few cases only, it may be possible to state that a particular outcrop is near the top or bottom of the formation. This lack of subdivision follows from the interaction of a number of factors. Firstly, it was found that the rock types vary rapidly both laterally and vertically—a natural consequence of the environment of deposition. However, individual horizons could not be traced for any great distance along the strike, because of highly sporadic outcrop. In many areas the sporadic outcrops are confined to creeks and gullies, and the gaps in outcrop (often occupied by wheat-fields) may be as much as four miles. Further, it was found that there is considerable tectonic disturbance, consisting of strong folding, with close drag-folding in the less competent strata, and frequent strike faulting of variable and often uncertain extent.

The result is that correlation of outcrops is hazardous, even at times over distances (along the strike) of as little as a quarter of a mile. Certainly no detailed stratigraphic or faunal correlation can at present be attempted for the Garra Formation.

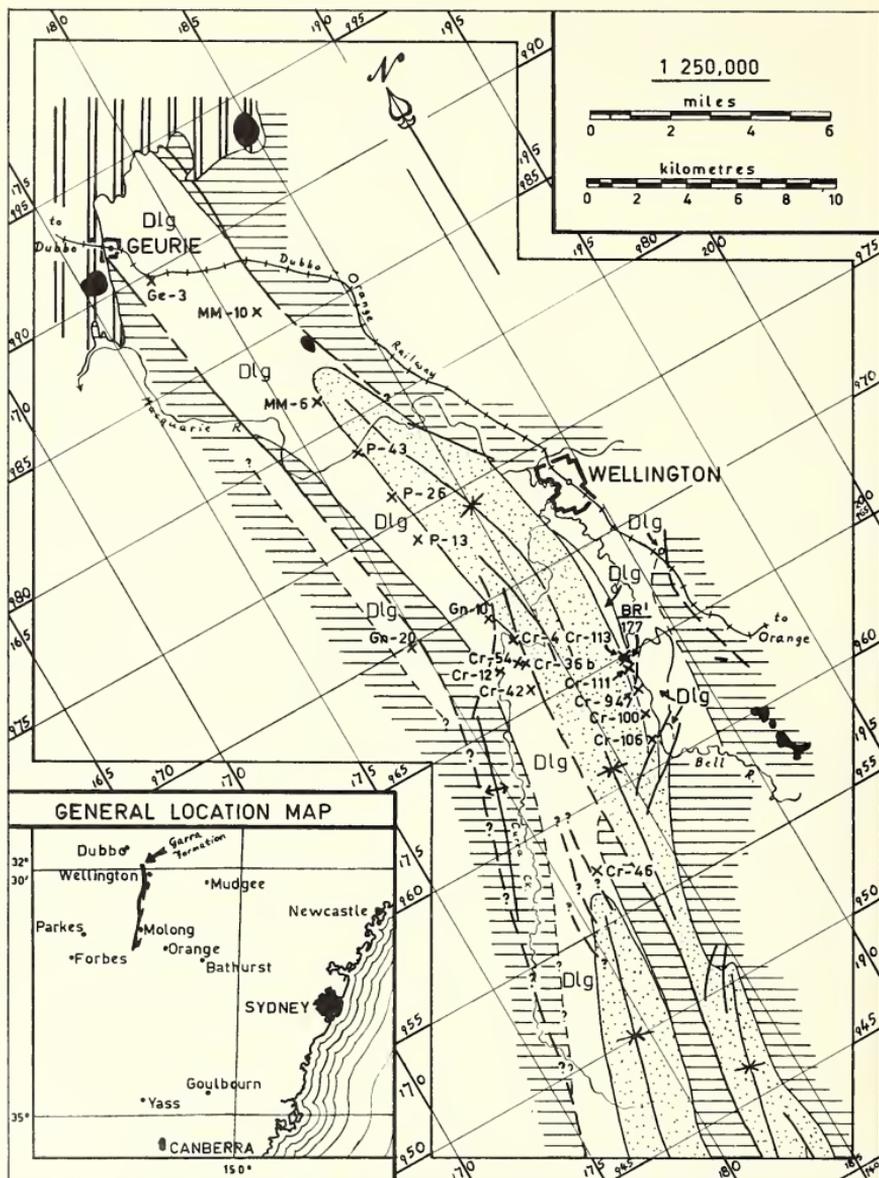
Further descriptions of the geology of the region may be found in: Joplin and Culey (1938), Basnett and Colditz (1946), Joplin and others (1952), Conolly (1963), and Strusz (1963, 1964, 1965).

AGE OF THE FAUNA

Hill (1942c) recognized two distinct coral faunas, one ('Garra') early Devonian and the other ('Murrumbidgee') early Middle Devonian in age. The much more extensive collections made during this study show that this simple division is probably not tenable, since all the species which characterize the 'Garra' fauna, with the possible exception of *Radiophyllum arborescens* (Hill and Jones 1940), appear to extend from the bottom to the top of the formation, and many of the 'Murrumbidgee' species either do likewise, or are confined to a large biostrome near the top of the formation as preserved in the Wellington district.

The eastern Australian coral fauna with which the Garra fauna (as now known) may be most readily compared is that from the Murrumbidgee River area of New South Wales (Hill 1940b). This has generally been regarded as equivalent to the Couvinian Stage, but Pedder (1964, p. 365) considers it '. . . more likely to be Siegenian'—without stating reasons for this suggestion. This Murrumbidgee fauna in turn is very similar to the Buchan Limestone fauna of Victoria; a third of the Murrumbidgee species is known from Buchan, and over 40 per cent. of the Buchan species occur in the Murrumbidgee limestones. On the basis of goniatites, Teichert (1948) placed the Buchan Limestone in the Lower Couvinian, but Erben supports a Lower Devonian age.

Garra species also known from overseas faunas are: *Pseudochonophyllum pseudo-heliantoides* (Sherzer)—Siegenian of Czechoslovakia; *Rhizophyllum enorme* Etheridge fil.—Coblentzian, Kuznetsk Basin (Bulvanker 1958); *Spongophyllum halysitoides* Eth. fil.—Lower Couvinian, Kuznetsk Basin; probably *Xystriphyllum dunstani* (Eth. fil.)—Couvinian, Kuznetsk Basin.



TEXT-FIG. 1a. Geological map of the Wellington region, showing positions of localities listed in the text. Inset: general location map, central and eastern N.S.W.

From the foregoing, I consider that the Garra Formation is probably equivalent in age to the Emsian; it may range up into the early Couvianian, or possibly down into the Siegenian.

PREVIOUS TAXONOMIC WORK

The first corals to be described from the Garra Formation were those of Etheridge Jr. (1895*b*, 1898, and 1903). His final contribution was in the 1907 monograph on Australian species of *Tryplasma*. More recent and extensive descriptions of Tabulata and Rugosa are in the series of papers by Hill (1942*c*), Hill and Jones (1940), Jones (1936, 1944), and Jones and Hill (1940). Finally, Packham (1954) described a *Hadrophyllum* from Curra Creek, near Wellington. All of these papers were based on rather limited collections, representing less than half the outcrop area of the Garra Formation. The extensive collections made in the course of this study (over 6,000 specimens) include many new forms, which will be described in this and subsequent papers.

The following species are described:

Family Disphyllidae Hill 1939: *Mansuyphyllum bellense* sp. nov., *M. parvulum* sp. nov., *M. catombalense* sp. nov., *M. catombalense* subsp. nov.?, *M.* sp. A, *M?* sp. B, *M.* sp. C, *Zelolasma gemmiforme* (Etheridge fil. 1902), *Disphyllum* sp. cf. *gregorii* (Etheridge fil. 1892), *Paradisphyllum harundinetum* gen. et sp. nov., *Hexagonaria approximans cribellum* subsp. nov., *Billingsastraea aperta* (Hill 1942), *B. speciosa* (Chapman 1914).

Family Phacellophyllidae Wedekind 1922: *Peneckiella mesa* (Hill 1942), *P. boreensis* sp. nov., *P.* sp. cf. *minor kunthi* (Dames), *sensu* Rózkowska 1960, *Phillipsastrea oculoides* Hill 1942.

Abbreviations. The following abbreviations are used in both the text and illustrations:

- Dc* Corallite diameter; for solitary and fasciculate corals, the mean diameter measured in a horizontal transverse section, or the minimum diameter measured in an oblique transverse section. For cerioid corals, the maximum diagonal measured in a horizontal transverse section.
- Dt* Tabularium diameter.
- R* Corallite radius—used when expressing the relative width of concentric structures such as the dissepimentarium, or the relative length of septa.
- Ts* Tabularial spacing: the distance between the axes of neighbouring tabularia in astraeoid, thamn-astraeoid or aphroid corals, where it is frequently not possible to measure *Dc*.
- n* Number of septa (of both orders); *n*/2 is the number of major septa.
- L*₁ Length of major septa.
- L*₂ Length of minor septa.

The repositories of type and other specimens are indicated by the following prefixes to their catalogue numbers:

- AM thin-section numbers, Australian Museum, Sydney, N.S.W.
- AM F fossil numbers, Australian Museum.
- GSQ Geological Survey of Queensland.
- GSV Geological Survey of Victoria.
- NM National Museum, Melbourne, Victoria.
- SU University of Sydney Palaeontological Collection; Sydney, N.S.W.
- UQF University of Queensland Palaeontological Collection; Brisbane, Queensland.

SYSTEMATIC PALAEOLOGY

Subdivision of the disphylloid rugose corals into family-group taxa is still very unstable. Classifications range from that of Lecompte (in Piveteau 1952, p. 470), with all the disphylloid genera placed in the one family Disphyllidae, to the classification of Soshkina (1952 et seq.), with families Thamnophyllidae, Peneckielidae, and Neocampophyllidae. The generally accepted grouping is into two (either families, or subfamilies of the one family) characterized essentially by the presence or absence of a vertical series of horseshoe-shaped dissepiments. This is the grouping found in the *Treatise on Invertebrate Paleontology* (Hill in Moore 1956); subfamilies Phacellophyllinae and Phillipsastraeinae respectively. Wang (1950) proposed a similar subdivision, but based on the arrangement of the septal trabeculae into 'fans'. The two classifications differ in the detailed grouping of genera, because the two closely related features of dissepimental and trabecular arrangement were not considered in close conjunction by Wang.

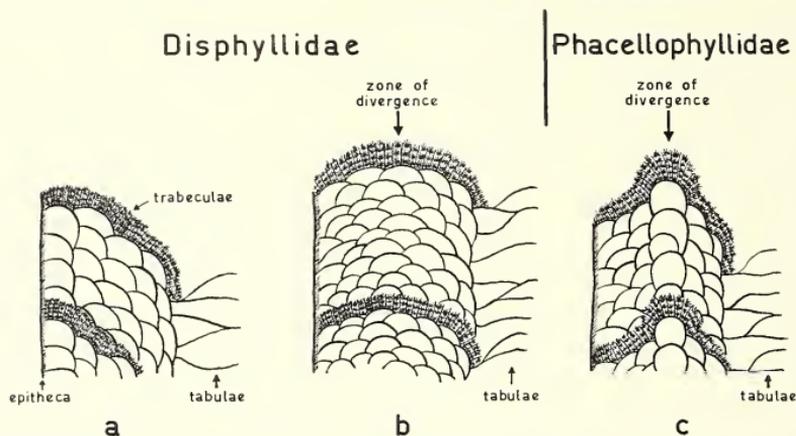
In this paper, the genera are grouped into the two families Disphyllidae Hill, and Phacellophyllidae Wedekind. Just how closely related these families are is still a matter for discussion. In both, the septa are composed of slender trabeculae, which in tangential sections through dilated portions are seen to diverge symmetrically from the median plane of the septum. The dissepimentarium is well developed, generally consisting of several series of globose interseptal vesicles. The structure of the tabularium is variable, and frequently complex. The principal distinction lies in the presence (Phacellophyllidae) or absence (Disphyllidae) of horseshoe dissepiments, and in the consequent arrangement of the trabeculae; for in all cases, the trabeculae grow at right angles to the surface formed by the dissepiments at any given stage of growth (see text-fig. 2).

In the Disphyllidae, the most common arrangement is that shown by many species of *Hexagonaria* Gürich. The dissepiments are small, numerous, and globose; peripherally they are horizontal or gently axially inclined, and this inclination increases steadily towards the tabularium. In some species, the dissepiments forming the inner margin of the dissepimentarium are vertical. Consequently, the septal trabeculae are vertical or only slightly axially directed near the epitheca, and towards the tabularium become increasingly axially directed, that is, they are inclined upwards and inwards towards the axis at an angle from the vertical which increases as the axis is approached. The resulting trabecular arrangement may be termed a 'half-fan'. See text-fig. 2a.

A less common alternative arrangement is met with particularly in massive colonial species, but has not as yet been used to distinguish genera. The dissepiments are essentially grouped into three merging concentric zones. In the middle zone they are horizontal, while in the other two zones they are inclined away from this middle zone, the inclination increasing with distance. The calix in these species therefore has a broadly reflexed rim surrounding the axial pit. The trabeculae, reflecting this arrangement, are vertical in the middle zone, and diverge from this zone at ever-increasing angles towards both periphery and axis, so forming full 'trabecular fans'. These fans may or may not be symmetrical about the zone of divergence. See text-fig. 2b.

'Trabecular fans' are also present in the Phacellophyllidae—indeed are characteristic of the family. However, in this case the zone of divergence of the fans corresponds exactly to a vertical series of horseshoe-shaped dissepiments (text-fig. 2c), and it is this

combination of features which distinguishes the family from those Disphyllidae with trabecular fans. A further result of this feature is that in those genera in which the horseshoe series is separated from the epitheca by one or more series of normal dissepiments, the calix has a strongly reflexed rim, frequently with a concentric ridge immediately outside the axial pit. This condition is extreme in *Macgeea*, in which the outer edges of the septa are not covered by epithecal deposits for a considerable distance below the distal extremity of the calice (e.g. *Macgeea proteus* Smith 1945, pl. 24, figs. 2, 3, 5).



TEXT-FIG. 2. Arrangement of the dissepiments and trabeculae in the Disphyllidae (a—'half-fans', b—'disphylloid fans') and the Phacellophyllidae (c—'phacellophylloid fans'); diagrammatic longitudinal sections, about $\times 2$.

To distinguish them, the two types of trabecular fan are herein termed 'disphylloid fans' (without horseshoe dissepiments), and 'phacellophylloid fans' (with horseshoes).

It should be noted that, contrary to various statements (e.g. Rózkowska 1953, p. 7), the trabecular fans are not always completely symmetrical about the horseshoe series. It is only in the immediate vicinity of this series that the trabeculae are symmetrically disposed. See for example *M. berdensis* Soshkina of Rózkowska (1953, pl. iv, fig. 10).

Apart from the problems of classification outlined above, there is also a difficult nomenclatural problem associated with this group of corals. The earliest family-group name used was Phillipsastracidae, by C. F. Römer (1883), with the nominal type-genus *Phillipsastrea* d'Orbigny 1849. The family concept attached to this name corresponds to the Disphyllidae as used herein. However, it has recently been shown (see Schouppé 1958) that the type species of *Phillipsastrea*, *P. hennahi* (Lonsdale 1840), possesses a series of horseshoe dissepiments surrounding the tabularium. Consequently this genus must be grouped with the Phacellophyllidae, and takes precedence as nominal type-genus for that group. This move would obviously cause some confusion of the generally accepted concepts attached to the resulting family-group names; this is therefore a case which should be submitted to the International Commission on Zoological Nomenclature for a decision.

Family DISPHYLLIDAE Hill 1939

Genus MANSUYPHYLLUM Fontaine 1961

Type species. *Cyathophyllum annamiticum* Mansuy, 1913, p. 9, pl. 1, fig. 11, pl. 2, fig. 12.

Diagnosis. 'Corallites solitary, ceratoid, with cup-shaped calix. Septa of two orders, often bearing weak carinae, continuous as far as the wall. The major septa extend almost to the axis. The minor septa are as long as, or slightly longer than, half the radius. The wide dissepimentarium consists of small globular vesicles; these, right at the periphery, are horizontal; towards the interior, convex and slightly inclined towards the axis, they decrease in size. The relatively narrow tabularium is divided into two series: an axial series where the tabulae are generally complete, horizontal; a periaxial series where they form large vesicles contrasting with the small vesicles of the dissepimentarium.' (Translated from Fontaine 1961, p. 100.)

Discussion. Fontaine erected this genus to contain solitary disphyllids with the internal structure of *Disphyllum*. He distinguished it from *Breviphyllum* Stumm 1949, by its biseriate tabularium and wide dissepimentarium. Moreover, *Breviphyllum* has amplexoid septa, and when these are dilated (which is rare) the dilatation occurs at the periphery, or is rhopaloid. In the type species of *Mansuyphyllum*, and in other species assigned to the genus, dilatation is spindlewise when present.

Mictrophyllum Lang and Smith 1935, differs in that the minor septa are absent or poorly developed; also the tabularium is generally composed of numerous tabellae which are not clearly arranged in two series.

Species placed in *Mansuyphyllum* by Fontaine are:

Cyathophyllum annamiticum Mansuy 1913: type species.

Campophyllum soeticum Schlüter, of Soshkina 1952, pl. 23, fig. 86.

Campophyllum boreale Soshkina 1951; Soshkina 1952, pl. 23, fig. 85. Soshkina (1952) stated that this species is colonial; it is therefore probably not *Mansuyphyllum*.

Campophyllum litvinovitchae Soshkina 1949; Soshkina 1952, pl. 23, fig. 87. As figured by Soshkina (1952), this species differs from *Mansuyphyllum annamiticum* in having a tabularium composed of sagging, generally complete tabulae, with no periaxial zone of tabellae; it seems to be closer to *Breviphyllum* Stumm.

Campophyllum crassoseptatum Yoh 1937, pl. 7, figs. 5-6.

Disphyllum (or *Macgeea*) *trochoides* Hill 1942a, pl. 8, figs. 5-10.

Disphyllum (or *Macgeea*) *excavatum* Hill 1942a, pl. 8, figs. 11-13.

Fontaine also considered that *Tabulophyllum cylindricum* Sun 1958, *T. curvatum* Sun, and *T. gigantum* Sun probably are species of *Mansuyphyllum*. Finally, he considered that two very poorly described species of *Sinodisphyllum* Sun, described as colonial but in the figures apparently solitary, may be *Mansuyphyllum*; in this case *Sinodisphyllum* would be the senior synonym. However, Fontaine considered that *Sinodisphyllum* at present is unusable because of the poor description. I have not seen the paper in question, so for the present accept Fontaine's conclusions.

I consider that the Australian species of *Mictrophyllum*, which differ from the Canadian species (particularly the type species) in having fairly well developed minor septa, are probably best placed in *Mansuyphyllum*. So also is *Mictrophyllum richardsoni* (Meek) of Smith (1945, pl. 5, figs. 10-12), from the Canadian Middle Devonian, which Smith only

tentatively assigned to *Mictophyllum*. The Australian species which are most like *Mansuiphyllum* are:

Mictophyllum trochoides Hill 1940*b*, pl. 11, figs. 7-10.

Mictophyllum cf. *cresswelli* (Chapman) of Hill 1942*b*, pl. 3, fig. 9.

Mictophyllum aff. *cresswelli* (Chapman) of Philip 1962, pl. 23, figs. 3, 4.

Hill (1954) has noted that *Mictophyllum cresswelli* appears to be weakly colonial, in which case it would not be *Mansuiphyllum* as strictly defined. *M. cresswelli* var. *cylindricum* Hill 1954, does not have a biseriate tabularium. All the Australian species of *Mictophyllum* require further study.

Mansuiphyllum bellense sp. nov.

Plate 72, figs. 1-3; text-fig. 7*e*

Holotype. SU 11295 (Pl. 72, fig. 1), loc. Be-10. Other material figured: SU 20099, 12110, both loc. Be-10.

Derivation of name. From the parish of Bell, in which is situated the type locality.

Diagnosis. Large *Mansuiphyllum* with fusiform septa, counter and cardinal longer than others; inner part of tabularium composed of small globose tabellae arranged in broad domes; peripheral dissepiments inclined outwards.

Description. The external characteristics are poorly known, as all available specimens are badly worn. The corallite is apparently trochoid, reaching a diameter of over 2.5 cm. The calix is apparently shallow, with a broad reflexed rim, and a broadly domed floor to the axial pit.

Dimensions in mm. (representative specimens):

	<i>Dc</i>	<i>Dt</i>	<i>Dt/Dc</i>	<i>n</i>
SU 11295	> 30.5	16.0	< 0.53	c. 70-80
SU 12109	> 26.0	13.5	< 0.52	64
SU 12110	> 23.0	11.0	< 0.48	64

All the specimens are worn, so the measured values of *Dc* are less than the true values, and calculated values of *Dt/Dc* are inflated accordingly. This is shown here and in subsequent tables by the use of the signs > and <.

There are over sixty septa. The long major septa leave an axial space only 3 mm. across, into which project the counter and cardinal septa. These generally intertwine at the axis, and frequently one or both extend nearly to the opposite side of the axial space. The remaining major septa frequently are pinnate about the counter-cardinal plane. The minor septa, about half as long as the major, terminate at the margin of the tabularium.

In the dissepimentarium both orders of septa are straight and fusiform, the major septa being more strongly dilated than the minor. Rare irregular carinae may occur outside the zone of dilatation. The ends of the counter and cardinal septa are generally slightly dilated.

The trabeculae are very slender, arranged in wide disphylloid fans. The zone of divergence of the fans is near the periphery; outside this zone, the trabeculae are moderately inclined outwards; inside the zone they are increasingly axially inclined, until

they are about 70–80° from the vertical at the margin of the tabularium. In the tabularium they curve upwards once more.

The biseriate tabularium consists of a very wide axial zone in which the tabular floors are domed, surrounded by a narrow trench-like periaxial zone. The axial zone is composed of numerous small, fairly globose tabellae, while the periaxial zone is made up of a series of flat or sagging tabellae, which tends to be vertically discontinuous. Consequently, the outermost axial tabellae often interleave with the innermost dissepiments, the only difference then being in the direction of inclination.

The dissepimentarium generally equals $\frac{1}{2} R$, and is composed of 9–14 series of small globose dissepiments. These diverge quite markedly from a zone near the periphery, so dividing the dissepimentarium into three zones. The outer zone is of 2–3 series of dissepiments which are moderately to strongly inclined outwards; the middle zone is of 1 or 2 series of globose horizontal plates; and the inner zone is of 6–9 series of strongly axially inclined plates.

Comparison. *M. bellense* is close to the type species in size and number of septa (50–60 in *M. annamiticum*), and also in having a wide dissepimentarium. The major differences are in the arrangement of the tabellae, and in the strongly fusiform septa in *M. bellense*. Another point of difference is in the marked elongation of the counter and cardinal septa—a character lacking in all described species assigned to *Mansuyphyllum*, but which is found in a number of Garra disphyllid species.

Known localities. Be–10 (common), Cr–4.

Mansuyphyllum parvulum sp. nov.

Plate 72, figs. 4–6; Plate 73, fig. 1; text-figs. 3, 7a, b

Holotype. SU 14224 (Pl. 72, fig. 6, Pl. 73, fig. 1), loc. Ct–40. Other material figured: SU 14223 (loc. Ct–40), 18151 (loc. CAT/255).

Derivation of name. Latin *parvulus*, very small.

Diagnosis. Diminutive *Mansuyphyllum* with numerous fusiform septa; calix deep, with everted rim.

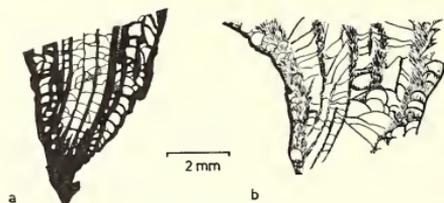
Description. Solitary turbinate to trochoid corallites, whose maximum diameter is about 10 mm. The epitheca is moderately rugate, and bears shallow, irregular septal grooves. There are also irregular lateral talons. The calix is wide and deep, with a flat or slightly domed floor, and a rather wide everted rim; the major septa project above the floor and walls of the calix.

Dimensions in mm.

<i>Specimen</i>	<i>Loc.</i>	<i>Dc</i>	<i>Dt</i>	<i>Dt/Dc</i>	<i>n</i>
SU 12296	Cr–36b	> 6.0	4.0	< 0.6	52
"	"	8.8	5.5?	0.6?	> 32*
SU 14223	Ct–40	5.2	3.0	0.58	38
SU 14224	"	8.8	c. 4.5	c. 0.5	48
"	"	10.1	> 38*
SU 18152	CAT/255	7.5	4.5	0.6	52

* Calical section.

Adult corallites have about 48–52 septa. Serial transverse peels of SU 18151 show that the septa are inserted quite rapidly: at $Dc = 5.9$ mm., $n = 46$; at 8 mm., $n = 50$, and at 9.5 mm. (the base of the calice) $n = 50$ still. The first section is from about half-way between the apex of the corallite and the base of the calix. The septa are strongly fusiform, with the major the more strongly dilated; they attenuate rapidly within the tabularium. The major septa are long, more than $\frac{2}{3} R$; one, probably the counter septum, extends into the axial space (which is 1.5–2 mm. across), and may reach its opposite side. The other septa may be slightly pinnate about the counter-cardinal plane. The minor septa equal $\frac{1}{3}-\frac{1}{2} R$, ending at the margin of the tabularium. Towards the periphery there are poorly developed irregular carinae, while in at least one transverse section there are short discontinuities in the septa about the margin of the tabularium.



TEXT-FIG. 3. *Mansuyphyllum parvulum* sp. nov. Longitudinal sections, $\times 5$. *a*, Holotype SU 14224 (loc. Ct-40), traced from photograph of celluloid 'peel' (Pl. 72, fig. 6). *b*, SU 18151 (loc. CAT/255), traced from photograph (Pl. 72, fig. 5).

The slender trabeculae are curved, arranged in disphylloid fans. Those at the periphery are directed only slightly outwards, while those at the margin of the tabularium are directed axially at about 30° from the vertical.

The tabularium is irregularly biseriate; the wide axial series consists of flatly domed complete and incomplete tabulae, while the narrow periaxial series consists of small, flat to inclined tabellae. The outer margins of the axial series are often supplemented by globose vesicular tabellae.

There are three to four series of dissepiments (more in the extensions of dissepimental tissue into the larger talons). These are irregular in size, generally strongly globose. The innermost series is moderately to strongly axially inclined, and the others are horizontal to slightly peripherally inclined. The inner one or two series are generally strongly invested with fibrous septal tissue.

Comparison. *M. parvulum* differs from all previously described species in its small size. It differs from the type species in having a slightly reflexed calical rim. Very similar in size and structure is *M. catombalense* sp. nov., described hereunder. For detailed comparison, see p. 530.

Remarks. This species at first seems close to *Kunthia* Schlüter 1885, with its deep calix and fusiform septa (see Stumm 1949, pl. 12, figs. 22–23). However, in that genus the calix reaches almost to the apex of the corallite, which is not the case in *M. parvulum*. As

the type, *K. crateriformis*, is poorly known, further comparison must await its re-examination.

Known localities. Cr-36b, Ct-40 (type), P-13, CAT/255.

Mansuiphyllum catombalense sp. nov.

Plate 73, figs. 2a-c; text-figs. 4, 7d

Holotype. SU 14155 (Pl. 73, figs. 2a-c); paratype. SU 14156, both from loc. Ct-18.

Derivation of name. From the parish of Catombal, in which occurs the type locality.

Diagnosis. Small *Mansuiphyllum* with narrow dissepimentarium; minor septa often discontinuous; counter septum extends across narrow axial space.

Description. This species is known only from thin sections, and so the external features are poorly known. Corallites are ceratoid, with marked growth irregularities, and talons are developed for lateral attachment. Adult corallites near the mode are 7 or 8 mm. in diameter; the maximum known is 10 mm. The calix has a narrow rounded rim, a steeply sloping wall, and a wide floor containing a broad, low, flat-topped axial boss.

Dimensions in mm.

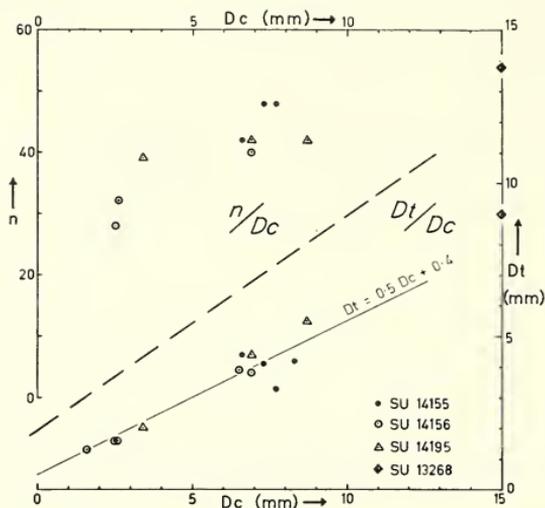
<i>Specimen</i>	<i>Dc</i>	<i>Dt</i>	<i>Dt/Dc</i>	<i>n</i>	<i>L</i> ₁	<i>L</i> ₂	<i>Axial space</i>
SU 14155	7.3	3.4	0.47	48	0.9 R	0.6 R	0.8
..	9.6	4.0	0.42	44	0.8 R	0.5 R	1.0
..	7.5	3.9	0.52	48	0.9 R	0.4 R	1.0
SU 14156	7.0	3.4	0.49	40	0.9 R	0.6 R	0.9

There are 40-48 septa in adults. The major are long (0.8-0.9 R), leaving an axial space about 1.0 mm. wide. The counter septum extends across this space, almost meeting the cardinal septum; it may be slightly dilated, or turned aside, but there is no definite columella. The counter-lateral septa are a little withdrawn, and the remaining septa are pinnately arranged about the counter-cardinal plane. The minor septa equal about $\frac{1}{2}$ R, and terminate just inside the tabularium. Septal dilatation is fusiform, and moderate to very strong. In a zone about 0.5 mm. wide around the tabularium the septa are frequently dilated so as to come into contact; outside this zone they may, rarely, retain this strong dilatation to the periphery, but are normally only moderately dilated. In the dissepimentarium the septa may be straight and smooth, or zigzag, or irregularly carinate. In the tabularium the septa are usually straight, and only rarely bear poorly developed carinae. The minor septa are generally discontinuous in the outer part of the dissepimentarium, and may be so throughout their length, at times to the extent of occurring as a series of detached trabeculae. In only one section are there peripherally discontinuous major septa, and these are in a portion of the corallite immediately below a sudden growth constriction.

The trabeculae are monacanthine and thick—up to 0.5 mm. in dilated portions of the septa; there is only one radial series in each septum. At the periphery they are vertical or slightly axially inclined; this inclination from the vertical increases steadily inwards, so that the individual trabeculae are curved. The inclination is about 60° from vertical at the margin of the tabularium. Within the tabularium the inclination appears to decrease, the trabeculae being generally directed sharply upwards.

The wide tabularium is biseriate. The axial series consists of wide, flat-topped domes. The periaxial series consists of peripherally inclined tabellae. The margins of the axial series are in places supplemented by small globose tabellae. A plot of Dt against Dc shows that this ratio remains constant during growth (text-fig. 4). The growth equation is: $Dt = 0.5 Dc + 0.4$.

The narrow dissepimentarium, about $\frac{1}{3} R$, is made up of one to five series of small globose dissepiments; these are horizontal at the periphery, increasing to steeply inclined or vertical at the tabularium.



TEXT-FIG. 4. Plots of n against Dc (above) and Dt against Dc (below) for *Mansuyphyllum catombalense* sp. nov. and subsp. nov.?

Comparison. A very similar species is *M. parvulum* sp. nov. Both are small, with fusiform septa and an elongate counter septum. They have similar biseriate tabularia, and not very dissimilar dissepimentaria. The differences are:

- (1) *Mansuyphyllum parvulum* is turbinata to trochoid; *Mansuyphyllum catombalense* is ceratoid.
- (2) *Mansuyphyllum parvulum* has an axial space of about 1.5–2.0 mm. In *Mansuyphyllum catombalense* it is 1.0 mm. or less.
- (3) The minor septa in *Mansuyphyllum parvulum* are very rarely discontinuous; in *Mansuyphyllum catombalense* they are generally so, as also at times are the major septa.
- (4) Unlike *Mansuyphyllum parvulum*, in *Mansuyphyllum catombalense* the septa may remain strongly dilated outwards from the zone of maximum dilatation.
- (5) In *Mansuyphyllum parvulum*, Dt/Dc is about 0.5–0.6, in *Mansuyphyllum catombalense* about 0.4–0.5.

It is nevertheless clear that the two species are quite closely related. *M. parvulum* is known from calcarenites or silty calcarenites, while *M. catombalense* is known only from two localities in a crinoid-coral biostrome. It is therefore highly likely that the two species have become differentiated by adaptation to the two distinct environments. See also p. 540.

Known localities. Ct-18 (type), Ct-28.

Mansuyphyllum catombalense subsp. nov?

Plate 72, figs. 8a, b; text-fig. 7f

Material. Transverse and longitudinal sections, SU 13268 from loc. Cr-100.

Description. The only known corallite is worn, but is apparently solitary and ceratoid. It is at least 15 mm. in diameter. Calix and epitheca are unknown.

There are fifty-four septa, showing a marked fusiform dilatation at the margin of the dissepimentarium; the major are considerably more dilated than the minor. The pinnate arrangement of the septa is more marked than in *M. catombalense* s.s., and both the counter and cardinal septa extend into the oval axial space, almost meeting at its centre. The trabeculae do not appear to be arranged in a disphylloid fan system. They are rather wavy, and axially directed at about 60° from the vertical. The tabularium is not well known, but appears to be biserial, with a periaxial series of globose tabellae supplementing an axial series of flat to domed tabulae. The dissepimentarium is wide, composed of at least nine series of small, globose, strongly inclined dissepiments.

Comparison. This specimen differs from *M. catombalense* s.s. essentially in its greater size and number of septa, and in having a relatively wider dissepimentarium with considerably more series of dissepiments. The fusiform dilatation of the septa around the tabularium is also more abrupt.

Remarks. The limited material does not warrant naming, but it seems likely that this is a subspecies of *M. catombalense* which has differentiated in response to a change of environment. The latter species has been found only in a crinoidal biostrome, while SU 13268 is from a large coral biostrome near Wellington, which appears to have been a rather quieter environment, associated with deposits of pellet calcarenites and algal limestones. See also text-fig. 7.

Mansuyphyllum sp. A

Plate 72, figs. 9a, b; text-fig. 7c

Material. SU 20101 (Pl. 72, figs. 9a, b), loc. Be-10; SU 12250, loc. Cr-4.

Description. As the only material consists of thin sections, the precise external features are unknown. There appear to be some transverse growth irregularities, but septal grooves are only intermittently developed. The calix is unknown. Adult corallites are about 9 mm. in diameter.

Dimensions in mm.

<i>Specimen</i>	<i>Dc</i>	<i>Dt</i>	<i>Dt/Dc</i>	<i>n</i>	<i>L</i> ₁	<i>L</i> ₂
SU 20101	8.6	4.7	0.55	50	<i>c. R</i>	$\frac{1}{2} R$
"	5.4	2.9	0.54	36	"	"
SU 12250	9.6	4.8	0.50	50	"	"

The epitheca is thin, and is lined internally by lamellar tissue no more than 0.2 mm. thick. In adults, $n = 40-50$. The major septa are long, leaving an axial space 1.0×0.6 mm.; their ends are pinnately arranged about the counter-cardinal plane. The counter-septum crosses the axial space to unite with the end of the cardinal septum. The counter-lateral septa are a little withdrawn, and in the smallest of the available transverse sections the minor septa between them and the counter septum are nearly as long as the major septa. The other minor septa are about $\frac{1}{2} R$, barely entering the tabularium. Septal dilatation is very strongly fusiform, and at the margin of the tabularium spreads over the innermost dissepimental surfaces in the very narrow interseptal loculi, to form a sterozone up to 1 mm. wide. In the dissepimentarium the thinner parts of the septa develop irregular carinae.

The trabeculae are arranged in typical disphylloid half-fans. Vertical or slightly inwardly directed at the periphery, their inclination increases axially until within the tabularium they are inclined inwards at about 60° from the vertical. The tabularium is a little over $\frac{1}{2} Dc$; only one fragmentary longitudinal section is available, and in this the tabulae are apparently incomplete, globose, and possibly arranged in two series, the axial ones being flatter than those near the dissepimentarium. The narrow dissepimentarium is composed of some four or five series of small, highly globose vesicles. These are horizontal at the periphery, becoming very steeply inclined at the margin of the tabularium. The dissepiments also decrease in size axially.

Comparison. These two specimens appear to be about half-way between *M. parvulum* and *M. catombalense*. For a detailed comparison see table, p. 541.

Mansuyphyllum ? sp. B

Plate 73, fig. 3

Material. SU 20102 (Pl. 73, fig. 3), loc. Cr-106; SU 17117, loc. Gn-10.

Description. The two known specimens are small, trochoid corallites; the epitheca is without septal grooves, but bears strong growth wrinkles. The calix is unknown.

EXPLANATION OF PLATE 72

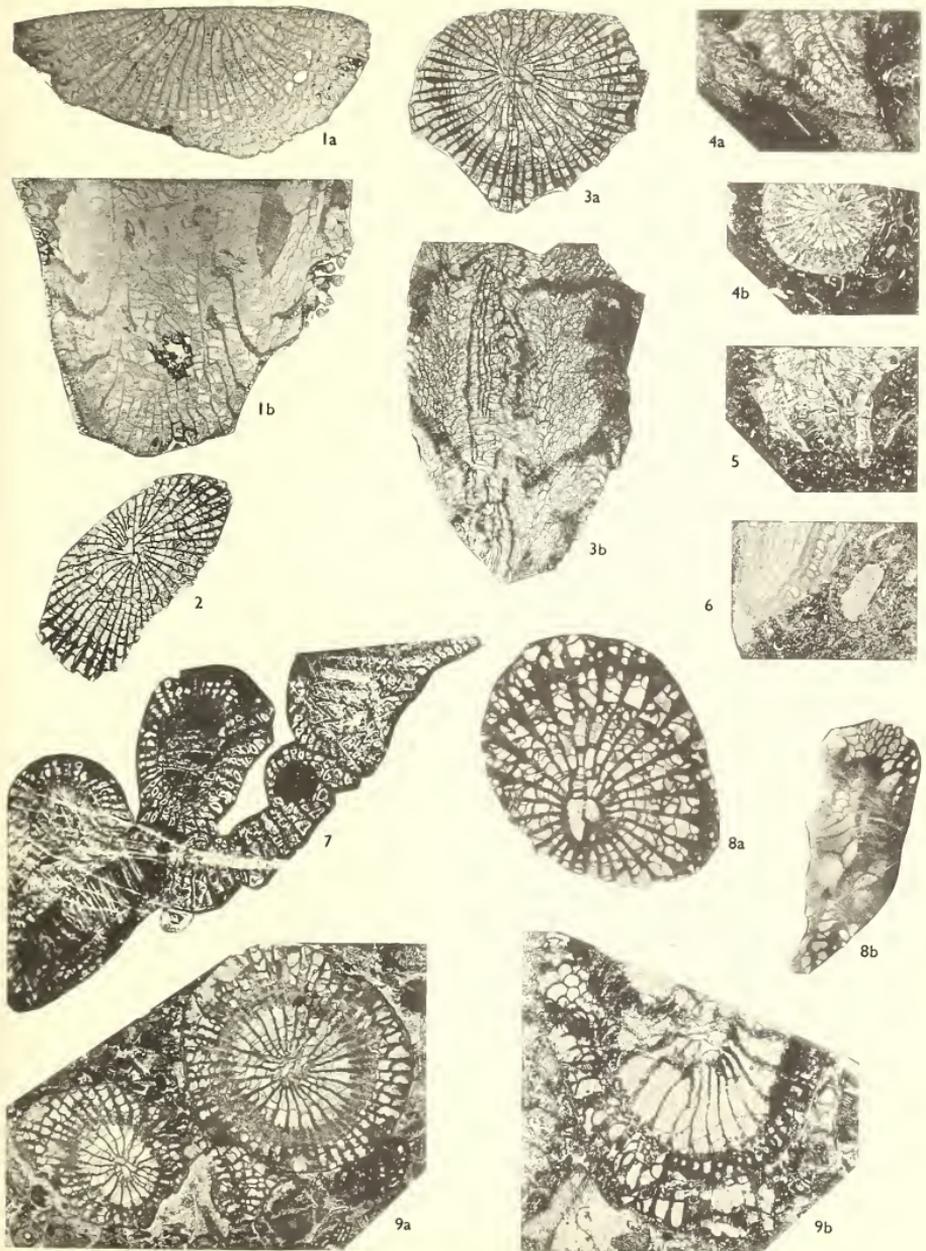
Figs. 1-3. *Mansuyphyllum bellense* sp. nov. 1 *a, b*, Holotype SU 11295; transverse (*a*) and longitudinal (*b*) sections; celluloid 'peels', $\times 2$. 2, Topotype SU 12110; transverse section, showing elongate cardinal and counter septa, $\times 2$. 3 *a, b*, Topotype SU 20099; transverse (*a*) and longitudinal (*b*) sections, $\times 2$ (see also text-fig. 7e). All from loc. Be-10.

Figs. 4-6. *Mansuyphyllum parvulum* sp. nov. 4 *a, b*, Topotype SU 14223, loc. Ct-40; longitudinal section (*a*) showing lateral talons, and transverse (*b*) section, $\times 4$ (see also text-fig. 7a). 5, SU 18151, loc. CAT/255; longitudinal section of fragmentary corallite, $\times 4$ (see also text-fig. 3b). 6, Holotype SU 14224, loc. Ct-40; longitudinal section—celluloid 'peel'— $\times 4$ (see also text-fig. 3a).

Fig. 7. *Zelolasma gemmiforme* (Etheridge fil.). SU 5278, loc. MM-10, figured Hill (1942c, pl. 6, fig. 6); transverse and longitudinal sections of corallites growing on the surface of a large solitary rugose coral (not shown); $\times 4$ (see also text-fig. 5). Photograph courtesy Prof. D. Hill.

Figs. 8 *a, b*. *Mansuyphyllum catombalense* subsp. nov? SU 13268, loc. Cr-100; transverse (*a*) and longitudinal (*b*) sections of fragmentary corallite, $\times 4$ (see also text-fig. 7f).

Figs. 9 *a, b*. *Mansuyphyllum* sp. A. SU 20101, loc. Be-10; transverse (*a*) and longitudinal (*b*) sections, $\times 4$ (see also text-fig. 7c).



Dimensions in mm.

Specimen	Dc	Dt	Dt/Dc	n	L ₁	L ₂
SU 20102	6.0	2.0	0.33	36	$\frac{2}{3} R$	$\frac{1}{3} R$
SU 17117	7.5	3.0	0.40	38	$\frac{3}{4} R$	$\frac{1}{4} R$

The septa are strongly fusiform, the major little longer than the minor, and extending axially about $\frac{2}{3}$ – $\frac{3}{4} R$. The minor septa end at the margin of the tabularium. In one specimen the septal dilatation is so strong that it forms a stereozone encompassing all but the outer 0.8 mm. of the dissepimentarium. In both specimens, there are numerous yardarm and zigzag carinae in the outer part of the dissepimentarium. The trabeculae are almost parallel, slightly axially directed, the inclination from the vertical being only a little greater at the tabularium than at the periphery. The tabularium is $\frac{1}{3}$ – $\frac{2}{3} Dc$ across; in the one available longitudinal section it is composed of irregular, distant, complete, flat to domed tabulae. In the same section, there are about four series of small, highly globose dissepiments, moderately inclined towards the axis.

Comparison. *Mansuyphyllum* sp. B differs from *M. parvulum* in the different trabecular structure of its fewer septa, and in having a uniseriate tabularium.

Remarks. This species is doubtfully included in *Mansuyphyllum*, because it does not have the biseriata tabularium characteristic of the type species. The carinate septa suggest *Tipheophyllum*, but that genus also has a biseriata tabularium, divided at the ends of the major septa. Further material is required before the precise affinities of this species are known, and until then it is best left un-named.

Mansuyphyllum sp. C

Plate 73, fig. 6

Material. SU 17117 (Pl. 73, fig. 6), 17118, loc. Gn–10.

Description. The external shape is unknown, both specimens being worn. The calix has a sharp rim, steep walls, and a wide flat floor. *Dc* is at least 3 cm.

Dimensions in mm.

Specimen	Dc	Dt	Dt/Dc	n
SU 17117	> 29	13.5	< 0.47	68
SU 17118	> 15	6.5	< 0.43	?

The major septa equal about $\frac{3}{4} R$; they are radial, and straight or slightly wavy. The minor septa, only about $\frac{1}{3} R$, terminate within the dissepimentarium. The septa are fusiform, moderately dilated, the major more than the minor; they are thin in the tabularium. The zone of maximum dilatation is about the middle of the dissepimentarium.

The trabeculae form disphylloid fans, with the zone of divergence in the middle of the dissepimentarium. Peripherally they are slightly outwardly directed, and towards the tabularium they are increasingly axially directed, so that at the margin of the tabularium they are inclined at 60° from the vertical.

The tabularium is wide—at least $\frac{1}{2} Dc$. It is biseriata. The wide axial series consists of complete and incomplete tabulae, forming flat-topped domes. The narrower periaxial series consists of numerous horizontal and slightly outwardly inclined globose to sagging tabellae. Many of the tabulae are quite thickly coated with fibrous sclerenchyme.

The dissepimentarium contains nine or ten series of dissepiments. The outermost two to four series are small, globose, and vary from slightly outwardly inclined at the periphery, to horizontal in the zone of maximum septal dilatation, where they are often coated by extensions of the septal tissue. Axially from here, the dissepiments are increasingly inwardly inclined and elongate, until at the margin of the tabularium they are nearly vertical.

Comparison. These specimens differ from the type species in their slightly greater size, in a wider tabularium, and in the more dilated septa. From *M. bellense* they differ in having a relatively wider tabularium. From other Australian species of the same size they differ in the form of the tabularium. Further material is required, but it may be possible that these specimens are closely related to *M. bellense*.

Genus ZELOLASMA Pedder 1964

1964 *Zelolasma* Pedder, p. 364.

Type Species: *Diphyphyllum gemmiformis* Etheridge fil. 1902, pp. 253–5, pl. 37, fig. 1; pl. 39, figs. 1, 2; pl. 40, fig. 1.

Diagnosis. Phaceloid to subcerioid disphyllid with frequent multiple peripheral budding. Septa subequal, generally thin, smooth peripherally, but wavy, slightly carinate, and sometimes slightly dilated, axially. Trabeculae in half-fans. Narrow dissepimentarium of a few series of small globose plates. Tabularium dominantly uniseriate, of gently sagging tabulae.

Remarks. Of the other phaceloid disphyllids so far described, *Disphyllum* has a biseriate tabularium (in the type species—see Hill 1939a, p. 225), *Cylindrophyllum* has well-developed yardarm carinae, and *Acinophyllum* McLaren has unequal septa, peripherally carinate, and prominent connecting processes. The new genus *Paradisphyllum*, described below, has a considerably more complex structure. See also p. 535.

Zelolasma gemmiforme (Etheridge fil. 1902)

Plate 72, fig. 7; text-fig. 5

For complete synonymy, see Pedder 1964, p. 365.

EXPLANATION OF PLATE 73

Figs. 1 *a, b.* *Mansuyphyllum parvulum* sp. nov. Holotype SU 14224, loc. Ct-40; (*a*) transverse section through calice (see also text-fig. 7*b*), (*b*) oblique longitudinal section; $\times 4$.

Figs. 2 *a-c.* *Mansuyphyllum catombalense* sp. nov. Holotype SU 14155, loc. Ct-18; (*a, b*) transverse sections of two corallites, (*c*) longitudinal section; note septal discontinuity in *b, c*; $\times 4$ (see also text-fig. 7*d*). 2 *a, b*, photographs by Mr. A. G. Smith, University of Queensland.

Figs. 3 *a, b.* *Mansuyphyllum?* sp. B. SU 20102, loc. Cr-106; transverse (*a*) and longitudinal (*b*) sections of corallite surrounded by a stromatoporoid; $\times 4$.

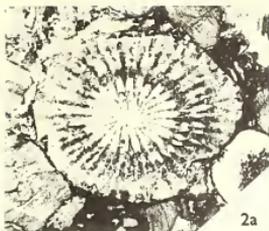
Figs. 4, 5. *Disphyllum* sp. cf. *gregorii* (Etheridge fil.). 4 *a, b*, SU 16143, loc. E-16; transverse (*a*) and longitudinal (*b*) sections, $\times 2$. 5, SU 16153, loc. E-21; transverse section through base of calix, $\times 2$.

Fig. 6. *Mansuyphyllum* sp. C. SU 17117, loc. Gn-10; oblique longitudinal section, $\times 2$.

Fig. 7. *Phillipsastrea oculoides* Hill. Holotype SU 5281, loc. MM-10; figured Hill (1942c, pl. 6, fig. 9); transverse section, $\times 2$. Photograph courtesy Prof. D. Hill.



1a



2a



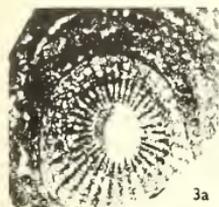
1b



2b



2c



3a



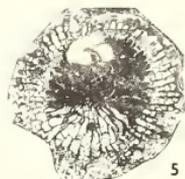
3b



4a



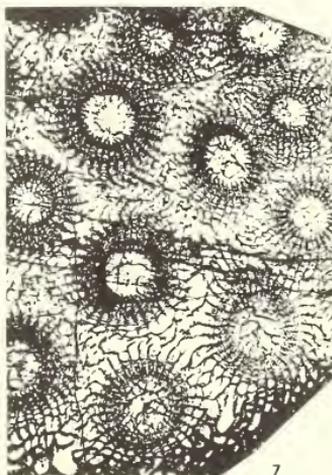
4b



5



6



7

Holotype. AM F 5171: Cavan Bluff Limestone, Taemas bridge, north bank of Murrumbidgee R., parish Warroo, near Yass, N.S.W. See also Pedder 1964, p. 365.

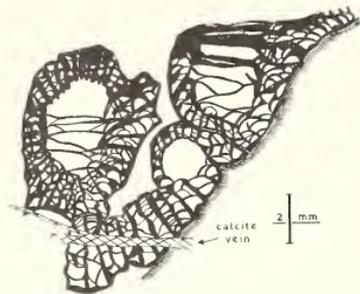
Material figured. SU 5278, loc. MM-10; figured Hill (1942c, pl. 6, fig. 6).

Diagnosis. As for the genus.

Remarks. Pedder has noted that the figures of maximum Dc and n given by both Etheridge Jr. and Hill are too low, and has given corrected values of $Dc = 13.0$ mm., and $n = 50$.

The specimen figured herein and by Hill (1942c) from the Garra Formation agrees very closely with the type material. Pedder, in his synonymy, queries inclusion of this specimen in the species, but I do not consider this doubt to be justified. As no further Garra material is available, no additions to existing descriptions are possible.

Known range. The species is so far known from the Couvinian? of the Murrumbidgee River area (Siegenian?), according to Pedder, p. 365), and from a locality (MM-10) in the Garra Formation probably towards the top, and most likely of early Couvinian or late Emsian age.



TEXT-FIG. 5. Portion of a small colony of *Zelolasma gemmiforme* (Etheridge fil.) adhering to the surface of another rugosan; traced from photograph (Pl. 72, fig. 7). SU 5278, figured Hill (1942c, pl. 6, fig. 6). $\times 4$.

Genus DISPHYLLUM de Fromentel 1861

- 1861 *Disphyllum* de Fromentel, p. 302 (*vide* Lang, Smith, and Thomas 1940, p. 53).
 1893 *Cannophyllum* E. J. Chapman, p. 45 (obj. syn., Stumm 1949, p. 33).
 1935 *Disphyllum* de Fromentel; Lang and Smith, p. 545 (*partim*). This paper contains a very full synonymy to 1935; however, the authors took a broad view of the genus, which has not been substantiated by recent workers.
 1956 *Disphyllum* de Fromentel; Hill, p. F280, in Moore. (See for further synonymy, post-1935.)

Type species: *Cyathophyllum caespitosum* Goldfuss 1826, p. 60 (*partim*) = *Disphyllum goldfussi* (Geinitz 1846); subsequent designation Lang and Smith 1934, p. 80.

Diagnosis. Fasciculate Disphyllidae with smooth septa, whose maximum dilatation is peripheral; tabularium biseriate, the periaxial tabellae axially inclined; several series of globose dissepiments; trabeculae parallel or in half-fans.

Discussion. As shown by Lang and Smith (1934, 1935), and also by Smith (1945, p. 21), the holotype of *D. goldfussi* has smooth septa which are moderately dilated in the dissepimentarium (particularly at the periphery) and thin in the tabularium. The tabularium is biseriate, and the dissepimentarium consists of several series of dissepiments. Other fasciculate disphyllids are *Cylindrophyllum* Simpson 1900, *Acinophyllum* McLaren 1959, *Zelolasma* Pedder 1964, and *Paradisphyllum* sp. nov. The first is characterized by strongly developed yardarm carinae in both dissepimentarium and tabularium, and by a fairly narrow dissepimentarium. *Acinophyllum* was erected to include those American disphyllid species previously placed in *Synaptophyllum* Simpson 1900, which McLaren has shown to be a stauriid. The type species is characterized by a narrow dissepimentarium.

a uniseriate tabularium, septa which are weakly dilated peripherally and zigzag carinate in the dissepimentarium, and numerous connecting processes. *Zelolasma* differs from *Acinophyllum* principally in lacking the connecting processes, and in having subequal septa which are only carinate (and sometimes slightly dilated) axially. All three genera have trabeculae either subparallel or arranged in half-fans. *Paradisphyllum* has a more complex structure, with strong disphylloid trabecular fans, a wide dissepimentarium, and a biseriate tabularium.

The simplicity of the tabularium in *Acinophyllum* is one of the diagnostic features stressed by McLaren. However, the taxonomic value of this feature is debatable. Thus *Sudetia* Rózkowska 1960, has as type a species in which both uniseriate and biseriate tabularia occur. Those specimens with a uniseriate tabularium resemble very strongly *Acinophyllum*. This raises the question of the validity of both genera. *Sudetia* was erected for a 'descendant form' of *Peneckiella minor kunthi* (vide Rózkowska 1960, p. 33), in which the horseshoe dissepiments have become obsolete. However, the dissepimental types figured for *Sudetia lateseptata*, the type, are not even 'peneckielloid' (see p. 556). Moreover, I find it difficult to see how *S. lateseptata* can be a descendant of *Peneckiella minor kunthi* (Dames), as the former species is known only from the one locality, where it is intergrown with its supposed predecessor. It is likely that *Sudetia* Rózkowska 1960, is a junior synonym of *Acinophyllum* McLaren 1959.

Disphyllum gregorii (Etheridge fil. 1892)

- 1892 *Campophyllum gregorii* Etheridge fil. in Jack and Etheridge Jr., p. 60, pl. 3, figs. 15-18. Locality—Reid Gap, N. Qld.; Givetian.
 1895a *Campophyllum gregorii* Etheridge fil. p. 522, pl. 40, fig. 2. Locality—the same.
 1942a *Disphyllum gregorii* (Etheridge); Hill, p. 247, pl. 8, figs. 1-4. Locality—the same, also Fanning R. and Burdekin Downs areas; Givetian.
 non 1912 *Campophyllum gregorii* Etheridge; Chapman, p. 219, pl. 34, figs. 3-5, which is *Breviphyllum recessum* (Hill 1940).

Lectotype. By subsequent designation Hill 1942a, p. 247. GSQ F 1655; figured Etheridge Jr., pl. 3, fig. 15, in Jack and Etheridge Jr. 1892.

Type locality. Regan's Limestone Quarry, probably portion 397v, parish Magenta; Reid Gap, near Townsville, N. Queensland. Reid River Limestone, Givetian (Hill 1942a).

Diagnosis. 'Disphyllum with ceratoid to cylindrical corallites with about 30 septa of each order; typically the major septa reach about half way to the axis, while the minor septa are less than half as long; there is typically one or two series of small, very globose dissepiments, and the septa are dilated so that they extend laterally over the upper surfaces of the dissepiments; typically the tabulae are complete and horizontal, supplemented at the margins by smaller plates; variability is great; the number of series of dissepiments may increase, the septa may become long, and sometimes curved about a small axial space, when the tabulae become incomplete on concave floors; the dilatation of the septa varies in amount and position.' (Hill 1942a, p. 248.)

Remarks. Points of difference of *D. gregorii* from *Breviphyllum recessum* not brought out in the descriptions of Hill (1940, 1942a) are: firstly, in *B. recessum* the septa are thin, relatively short, and in transverse section exhibit discontinuities within the tabularium.

In *D. gregorii* the septa are usually dilated at some point in their length, and are never discontinuous. The trabeculae in *D. gregorii* are thick monacanth, subparallel, and directed axially at a high angle from the vertical; trabeculae are not visible in the holotype of *B. recessum*. Finally, the epitheca of *B. recessum* is marked by deep, narrow septal grooves, separated by wide flat interseptal 'ridges'. The septal grooves in *D. gregorii*, when developed, are very shallow and wide, essentially the intersection of two neighbouring slightly rounded to flat interseptal ridges.

Disphyllum sp. cf. *gregorii* (Etheridge fil. 1892)

Plate 73, figs. 4, 5

Material. Several fragments from locs. Cr-12, E-16, and E-21.

Figured specimens. SU 16143 (loc. E-16), 16153 (loc. E-21).

Description. The available fragments vary somewhat in structure, some sections being very like some figured sections of *B. recessum* (Hill 1940*b*, e.g. pl. 9, fig. 7). However, the Garra specimens all have about sixty septa, with $Dc = 13-16$ mm., contrasting with $n = 44$ and $Dc = 10$ mm. for normal *B. recessum*. They also have the type of septal groove found in *D. gregorii*, and continuous septa.

Dimensions in mm.

<i>Specimen</i>	<i>Locality</i>	<i>Dc</i>	<i>Dt</i>	<i>Dt/Dc</i>	<i>n</i>	<i>L</i> ₁	<i>L</i> ₂
SU 16143	E-16	15	9.5	0.63	c. 70	c. $\frac{1}{3}$ R	c. $\frac{1}{3}$ R
SU 16145	"	> 11.5	9.5	< 0.83	64	$\frac{1}{2}$ R	$\frac{1}{4}$ R
SU 16153	E-21	c. 14	8.0	c. 0.57	66	c. R	c. $\frac{1}{3}$ R

The specimens agree most closely with Hill's description of specimens from the Reid Gap area, in that all have about five or six series of dissepiments, and highly variable septal length and dilatation. Generally the septa dilate at the margin of the tabularium, where the dilatation may spread over the dissepiments, and then they either remain at a constant moderate dilatation throughout the dissepimentarium, or show successive moderate wedge-wise dilatations over the surfaces of successive series of dissepiments. However, this may vary even in the one transverse section, with the septa on one side remaining attenuate throughout. Similarly the tabularium is variable; in some cases the tabulae are complete, flat with down-turned edges, supplemented by periaxial inclined tabellae; in others, the tabulae are incomplete and sagging, and the periaxial tabellae are both more numerous and less regular in size.

Unfortunately none of the sections is sufficiently well preserved to show clearly the trabecular structure. There is a suggestion that the trabeculae are thin, and axially directed at a large angle from the vertical (as in *D. gregorii*), but I have not seen the thick monacanth so characteristic of the Queensland species.

Genus PARADISPHYLLUM gen. nov.

Type species. *Paradisphyllum harundinetum* sp. nov.

Diagnosis. Fasciculate disphyllids with septal trabeculae arranged in disphylloid fans. Septa fusiform, carinate outside the zone of greatest dilatation; the counter septum

may be elongate. Minor septa, and sometimes major septa, discontinuous near periphery. Tabularium as in *Disphyllum*.

Remarks. *Paradisphyllum* differs from other fasciculate disphyllids essentially in the arrangement of the trabeculae in marked disphylloid fans (see p. 523), and so in having a calix with a strongly reflexed rim. The type species is further distinguished by having discontinuous septa.

I would tentatively include in *Paradisphyllum* the Victorian species *Disphyllum cognatum* Philip 1962 (p. 177, pl. 24, figs. 5, 10, text-fig. 4*b*), from the Gedinnian Cooper's Creek Formation. This species has a similar trabecular arrangement to that of *P. harundinetum*; the only essential differences are that apparently the major septa are of uniform length, and that the septa are continuous. I consider that the trabecular structure is of far greater significance than the septal discontinuities.

Another possible species is *D. [Synaptophyllum] densum* Smith 1945 (p. 22, pl. 12, figs. 3*a-c*). As described and figured by Smith, this species has all the diagnostic features of *Paradisphyllum*. However, McLaren (1959, p. 30) has noted that horseshoe dissepiments are present in one longitudinal section of Smith's type material. All the other longitudinal sections show trabecular fans, and so McLaren has tentatively assigned the species to *Phacellophyllum*. Further study is needed on this matter.

Range. *Paradisphyllum* is definitely known from the Emsian or early Couvian of the Garra Formation, and is probably also represented in the Gedinnian of Victoria. It may also be present in the Frasnian of Canada.

Paradisphyllum harundinetum gen. et sp. nov.

Plate 74, figs. 1, 3; text-figs. 6, 7*g, h*

Holotype. SU 13236 (Pl. 74, fig. 1), loc. Cr-100. *Paratype* SU 20100 (Pl. 74, fig. 3).

Derivation of name. Latin *harundinetum*, a thicket of reeds; refers to the appearance of the trabeculae in longitudinal section.

Diagnosis. Dendroid to subcerioid *Paradisphyllum* about 7 mm. in diameter, with both orders of septa frequently discontinuous peripherally; with very irregular dissepiments, and crowded tabulae.

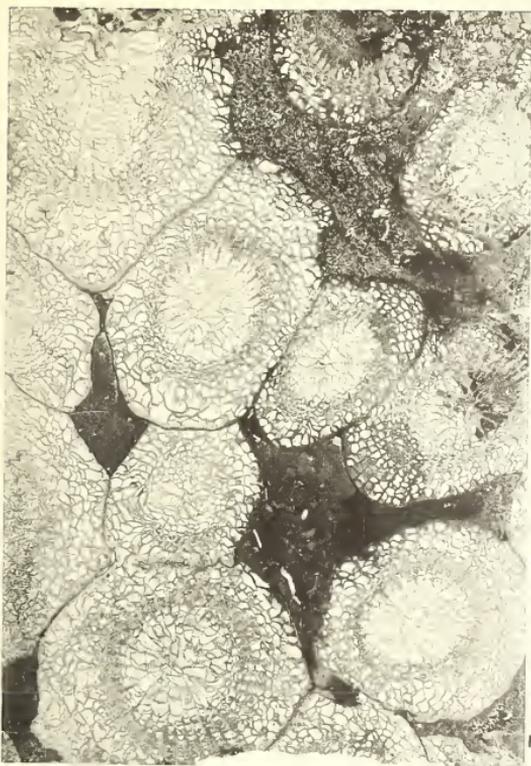
Description. The corallum is small, generally dendroid, and usually in the form of a low dome. In crowded, subcerioid parts, individual corallites are bounded by slightly curved to irregular walls; otherwise they may be separated by up to 1 cm., when they are ceratoid to cylindrical. The calix has a wide reflexed rim surrounding a shallow cup-shaped axial depression. Budding is lateral. *Dc* of adults = 5-11 mm., those near the mode being 6-7.5 mm.

EXPLANATION OF PLATE 74

Figs. 1, 3. *Paradisphyllum harundinetum* gen. et sp. nov. 1, Holotype SU 13236, loc. Cr-100; $\times 4$ (see also text-fig. 7*h*); specimen collected by Dr. J. R. Conolly. 3, Paratype SU 20100, loc. Cr-100; longitudinal section, $\times 4$ (see also text-fig. 7*g*).

Figs. 2*a, b*. *Hexagonaria approximans cribellum* subsp. nov. Holotype SU 13259, loc. Cr-100; transverse (*a*) and longitudinal (*b*) sections, $\times 2$; specimen collected by Dr. J. R. Conolly.

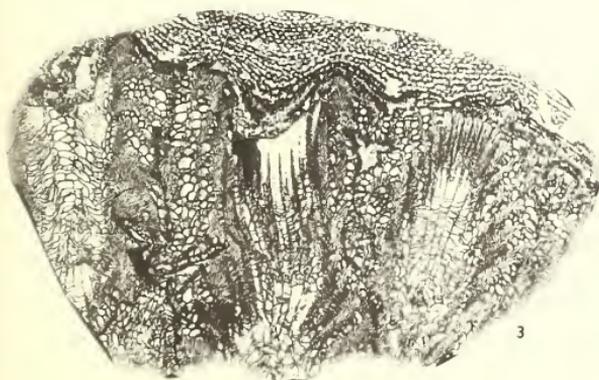
Fig. 4. *Billingsastraea aperta* (Hill). SU 13261, loc. Cr-100; transverse section of corallum with relatively strong septal dilatation, $\times 2$.



2a



2b



3



4

Dimensions in mm.	Specimen	<i>Dc</i>	<i>Dt</i>	<i>Dt/Dc</i>	<i>n</i>
SU 13236	max.	11.2	4.2	0.78	44
	mean	6.6	2.9	0.46	36
	min.	1.2	0.9	0.33	6
No. of readings		33	33	33	33
SU 20100	max.	8.0	3.6	0.51	34
	mean	6.3	2.8	0.45	..
	min.	4.4	1.9	0.39	32
No. of readings		6	6	6	2

The thin epitheca shows strong transverse growth irregularities, but no septal grooves; it is lined by a thin (0.2 mm.) fibrous stereozone, from which project the septa. For adults, *n* is generally 38–42. The major septa are long, straight in the wide dissepimentarium, and straight or slightly curved in the tabularium. They are unequally withdrawn from the axis, leaving a space 1–1.5 mm. across, into which the counter septum, and sometimes the cardinal septum, projects. The septa often show a moderate pinnate arrangement about the counter-cardinal plane, in which case the counter-lateral septa may be slightly withdrawn; however, the septa may be completely radial. L_2 is about $\frac{1}{3}$ to $\frac{2}{3}$ *R*; the minor septa end just inside the tabularium.

The septa are fusiform, and may be so strongly dilated as to form a stereozone up to 1 mm. wide near the inner margin of the dissepimentarium. However, the degree of dilatation is highly variable, even from one side of a corallite to the other, and in some juveniles it may be entirely absent. Towards the periphery the septa generally become attenuate, and bear irregular zigzag carinae. In this zone the minor septa are generally more or less discontinuous; less commonly the major septa also break up into discontinuous fragments.

The monacanthine trabeculae are arranged in broad disphylloid fans, closely resembling those which characterize the family Phacellophyllidae. The zone of divergence of the trabeculae corresponds exactly with the zone of maximum septal dilatation, at about the mid-radius, and about two-thirds of the way from the periphery to the tabularium.

The biseriata tabularium is about $\frac{2}{3}$ – $\frac{1}{2}$ *Dc* across, and consists of numerous closely crowded tabellae. The axial series is of globose plates, arranged in broad domes, and interfingering marginally with the periaxial tabellae, which are flat or gently sagging.

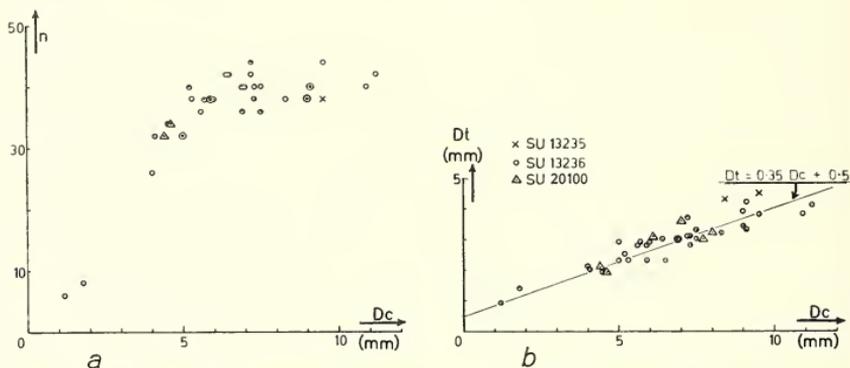
The dissepiments are small, globose, in five to eight series. Their inclination varies from vertical at the inner margin of the dissepimentarium, through horizontal in the zone of maximum septal dilatation, to moderately outwardly inclined outside this zone. In this outer zone the dissepiments may become lonsdaleoid.

Variation. As only one of the colonies so far found is relatively large and the total material is limited there are not enough data for a detailed study of intra-specific variation. No strong correlation between *n* and *Dc* could be found (text-fig. 6a), but a plot of *Dt* against *Dc* (text-fig. 6b) was clear enough to give a growth equation of $Dt = 0.35 Dc + 0.5$.

Comparison. *P. harundinetum* is apparently one of a group of closely similar disphyllid corals occurring in the Garra Formation, and is probably derived from one of these by acquisition of a colonial habit. The group is discussed below.

Known localities. This species is only known from the biostrome at loc. Cr-100.

Discussion of Phylogeny. During examination of sections of a large number of *Garra* disphyllids, it became apparent that many of them had several fairly distinctive features in common, suggesting that they may be in fact closely related. To check this, their salient features were compared in a chart (p. 531), and plots of available data for n/Dc and Dt/Dc were made. These show that the various species within this group of *Garra* disphyllids are indeed probably closely related, and a study of their stratigraphic distribution, in so far as it is known, further suggests a phylogenetic plexus, of which the progenitor is probably the small solitary coral *M. parvulum* (known from beds closer to the base of the formation than those containing the other species).



TEXT-FIG. 6. Plots of (a) n against Dc and (b) Dt against Dc , for three specimens of *Paradisphyllum harundinetum* gen. et sp. nov.

The features common to the species of this postulated plexus, and which distinguish them from other *Garra* disphyllids, are:

- (1) Strongly fusiform septa, peripherally weakly to strongly carinate.
- (2) Trabeculae arranged in half-fans or full disphylloid fans.
- (3) Long major septa, frequently pinnate about the counter-cardinal plane.
- (4) Counter septum elongate, generally reaching the axis, and in some extending completely across the axial space.

The differences between the various species are summarized in the table, p. 541. Note that for *M. catombalense* and *P. harundinetum*, the data for Dt/Dc , while rather limited, are sufficiently closely correlated to allow the determination of approximate growth equations (see also text-figs. 4, 6).

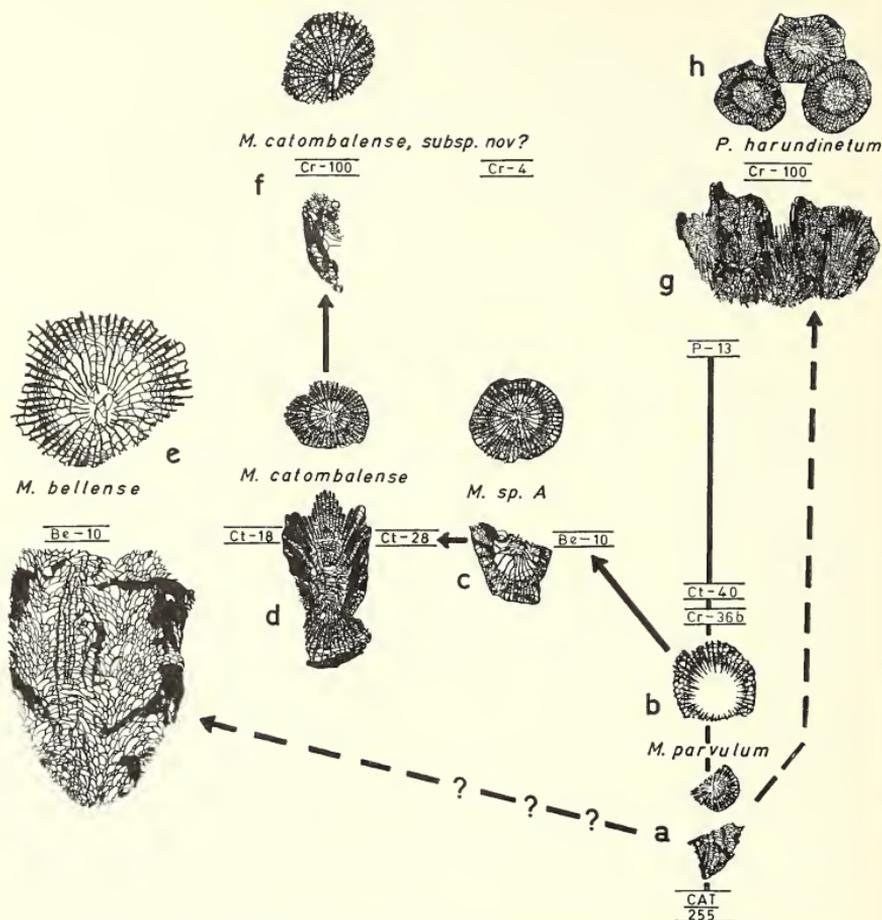
The inferred relationships of the species are shown in text-fig. 7. The most nearly certain is the lineage *M. parvulum*—*M. sp. A*—*M. catombalense*, while the least certain is *M. bellense*. The latter shares with the others most of the features distinctive of the group, but is considerably larger. As intermediate specimens have not been found, the relationship of *M. bellense* to the remaining species is as yet uncertain.

GENUS Species	Mansuyphyllum				Paradisphyllum harundinetum
	bellense	parvulum	sp. A	catambalense	
Corallum:	trochoid?	turbinate-trochoid	?	ceratoid	dendroid-subceratoid
Dc	20+ - 30.5+ mm	5.2 - 10.1 mm	5.4 - 9.6 mm	1.6 - 8.7 mm	12 - 11.2 mm
N° of readings:	6	10	3	3	41
(normal adults):	25 - 30 mm	9 - 10 mm	9 mm	7 - 8 mm	6 - 7.5 mm
Growth curve, Dt =	?	?	?	0.5 Dc + 0.4	0.35 Dc + 0.5
Diameter, axial space:	c. 3 mm	c. 2 mm	1.0 x 0.6 mm	c. 1 mm	1.0 - 1.5 mm
SEPTA:					
n	c. 50 - c. 76	32+ - 52	36 - 50	28 - 48	6 - 44
N° of readings:	≥ 60	6	10	3	1
(normal adults):		c. 50	c. 50?	c. 42	c. 40
L ₁	> 0.9 R	c. 0.7 R	← c. 0.9 R	← c. 0.9 R	0.8 - 0.9 R
L ₂	> 0.5 R	0.3 - 0.5 R	← c. 0.5 R	← c. 0.5 R	0.5 - 0.7 R
continuity	←	← continuous	← continuous	← continuous	← continuous
carinae in diss'arium:	←	← infrequent	← fairly common	← common	← numerous
Septal pattern:	← frequently	← sometimes, slightly	← always	← strongly	← frequently, moderately
pinnate?	←	←	← elongate	←	← variable length
K	←	←	← equal to metasepta	←	← may be slightly withdrawn
KL	←	←	← equal to metasepta	←	← sometimes elongate
C	←	←	← elongate	←	←
Series of dissepiments:	9 - 14	3 - 4	4 - 5	1 - 5	5 - 8
Width of diss'arium:	c. 0.5 R	← c. 0.2 R	←	← c. 0.3 R	←

Table comparing importance features of *Paradisphyllum harundinetum* gen. et sp. nov., and those species of *Mansuyphyllum* which are considered to be phylogenetically related.

GENUS species Characters	<i>Mansuyphyllum</i>					<i>Paradisphyllum</i>
	<i>bellense</i>	<i>parvulum</i>	<i>sp. A</i>	<i>catambalense</i>	<i>catambalense</i> <i>subsp. nov?</i>	<i>harundinetum</i>
Corallum:	trochoid?	turbinate-trochoid	?	ceratoid	ceratoid?	dendroid-subceroid
Dc { known range: N° of readings: normal adults:	20+ - 30.5+ mm	5.2 - 10.1 mm	5.4 - 9.6 mm	1.6 - 8.7 mm	15+ mm	1.2 - 11.2 mm
	25 - 30 mm	9 - 10 mm	9 mm	7 - 8 mm	?	6 - 7.5 mm
Growth curve, Dt =	?	?	?	0.5 Dc + 0.4	?	0.35 Dc + 0.5
Diameter, axial space:	c. 3 mm	c. 2 mm	1.0 x 0.6 mm	c. 1 mm	1.7 x 1.2 mm	1.0 - 1.5 mm
SEPTA:						
n { known range: N° of readings: normal adults:	c. 50 - c. 76	32+ - 52	36 - 50	28 - 48	?	6 - 44
	≥ 60	c. 50	c. 50?	c. 42	54?	c. 40
L ₁	> 0.9 R	c. 0.7 R	← c. 0.9 R →	← 0.8 R →	0.8 R	0.8 - 0.9 R
L ₂	> 0.5 R	0.3 - 0.5 R	← c. 0.5 R →	← c. 0.5 R →	> 0.3 R	0.5 - 0.7 R
continuity { major: minor:	← continuous →				continuous?	may be peripherally discontinuous
	← continuous →			← discontinuous →		
carinae in diss'arium:	← infrequent →		fairly common	common	common?	numerous
Septal pattern: pinnate?	frequently	sometimes, slightly	← always →	← strongly →	strongly	frequently, moderately
K	← elongate →					variable length
KL	← equal to metasepta →		← slightly withdrawn →	← withdrawn →		may be slightly withdrawn
C	elongate	← equal to metasepta →			elongate	sometimes elongate
Series of dissepiments:	9 - 14	3 - 4	4 - 5	1 - 5	≥ 9	5 - 8
Width of diss'arium:	c. 0.5 R	← c. 0.2 R →			← c. 0.3 R →	

Table comparing importance features of *Paradisphyllum harundinetum* gen. et sp. nov., and those species of *Mansuyphyllum* which are considered to be phylogenetically related.



TEXT-FIG. 7. Inferred phylogenetic relationships between species of *Mansuyphyllum*, and *Paradisphyllum harundinetum*; all $\times 1.5$, traced from photographs (see Pl. 72-74). Localities from which the various species are known are shown in their probable relative stratigraphic positions; where known with reasonable accuracy, these are in heavy lettering. *a*, Transverse and longitudinal sections, SU 14223 (loc. Ct-40). *b*, Transverse section through calyx, holotype SU 14224 (loc. Ct-40). *c*, Transverse and longitudinal sections, SU 20101. *d*, Transverse and longitudinal sections, holotype SU 14155. *e*, Transverse and longitudinal sections, paratype SU 20099. *f*, Transverse and longitudinal sections, SU 13268. *g*, Longitudinal section, paratype SU 20100. *h*, Transverse section, holotype SU 13236.

Genus HEXAGONARIA Gürich 1896

- 1896 *Hexagonaria* Gürich, p. 171 (*vide* Lang, Smith, and Thomas 1940, p. 69).
 1949 *Hexagonaria* Gürich, Stumm, p. 33. See for list of synonyms.
 1954 *Hexagonaria*, Moenke, p. 452. See for a full discussion of the genus (taxonomy and morphology).

Type species. By subsequent designation Lang, Smith, and Thomas 1940, p. 69, *Cyathophyllum hexagonum* Goldfuss 1826, p. 61, pl. 19, figs. 5*e, f*, pl. 20, figs. 1*a, b*; non pl. 19, figs. 5*a-d*.

Diagnosis. 'Cerioid corals with individual corallites separated by polygonal walls. Calices usually with an axial pit and a peripheral platform. Septa radially arranged, of two orders, major extend into tabularium while minor are confined to dissepimentarium. They are lightly or heavily carinate, rarely dilated. No modification of protosepta is visible. Dissepimentarium is wide and composed of many rows of horizontal or inclined dissepiments. Tabularium is relatively narrow and composed of closely set, complete or incomplete tabulae, that are horizontally disposed.' (Stumm 1949, p. 33.)

Discussion. A list of synonyms may be found in Stumm (1949). It should be noted also that in many cases Soshkina has included in her genus *Megaphyllum* species which are *Hexagonaria*, as well as some, including the type, which are considered by Stumm (1949) and others to be *Disphyllum*. In her discussion of *Megaphyllum* (1954, p. 37), Soshkina referred critically to Stumm's illustration of *H. hexagona* (1948, pl. 6, figs. 1, 2), stating that fig. 1 is of the holotype, and fig. 2 of a different species. Yet according to Stumm, both are sections of the same specimen, a hypotype. Still referring to this, Soshkina also stated: '. . . [Stumm] cannot distinguish the species of the genus *Phillipsastraea* from the massive colonies belonging to the group of species "*Cyathophyllum hexagonum* Goldf.", in other words belonging to genus *Megaphyllum* Soshk., . . .' This, with other statements on the same page, apparently indicates that Soshkina considered the type species of *Hexagonaria* to be a species of her genus *Megaphyllum*. At the same time, she placed *Prismatophyllum* Simpson 1900, in synonymy with *Megaphyllum*. In both cases, there is clear contravention of the rules of nomenclatural priority (Stoll *et al.* 1961: Art. 23). This apparent confusion of type species and of priority has unfortunately caused considerable divergence of usage in the work of authors from Europe, America, and Australia on the one hand, and from Russia on the other.

Megaphyllum bulvankerae Soshkina 1954 (p. 38) and *M. columellare* Soshkina 1954 (p. 40) are species of *Hexagonaria*.

Hexagonaria approximans (Chapman 1914)

- 1914 *Cyathophyllum approximans* Chapman, p. 304, pl. 47, figs. 5, 6. East Gippsland, Victoria: Early Devonian.
 1939*a* *Prismatophyllum approximans* (Chapman); Hill, p. 234.
 1954*b* *Hexagonaria approximans* (Chapman); Hill, p. 107, pl. 6, figs. 3*a, b*.
 1954*b* *Hexagonaria* aff. *approximans* (Chapman); Hill, p. 108, pl. 6, figs. 4*a, b*. Waratah Bay, Victoria: Bell Point Limestone, 'possibly Couvianian'.
 1962 *Hexagonaria approximans* (Chapman); Philip, p. 177, pl. 24, figs. 4, 8, 9. Tyers R., Gippsland, Victoria: Cooper's Creek Formation, early Gedinnian.

Holotype, NM 1247: specimen figured Chapman 1914, pl. 47, figs. 5, 6. Quoted and figured as holotype by Hill 1954*b*, p. 107, pl. 6, figs. 3*a, b*. Type locality given by Chapman as 'Cooper's Creek, behind

Chinaman's Garden'; probably from the early Gedinnian Cooper's Creek Formation of Philip 1962, p. 127. Chapman also listed specimen no. 746, but this is not quoted by either Hill or Philip.

Diagnosis. Large *Hexagonaria* with thirty-two to forty-two long, slightly fusiform septa, with carinae well developed near periphery; trabeculae arranged in half-fans or in broad disphylloid fans; tabularium narrow, biseriate.

Remarks. This species has been well described by Philip (1962) who, from the type material and a large collection from the Tyers River area, was able also to assess variation, which he found to be considerable. One point to note is that according to Philip the trabeculae are directed inwards at all times, whereas according to Hill (1945*b*, p. 107) '... there may be an area of divergence ... near the inner margin of the dissepimentarium'. This is not clear in her figures of the holotype, but is quite definite in her *H. aff. approximans* (pl. VI, fig. 4*b*), which Philip placed in synonymy with *H. approximans*.

Known range. The holotype comes from Cooper's Creek, probably from the same horizon as the Cooper's Creek Formation of Philip (1962), some miles to the south. Philip considered this horizon to be probably Gedinnian in age. The species is also known from the Bell Point Limestone of Waratah Bay, Victoria; Hill (1954*b*) considered this horizon to be '... possibly Couvianian'. Philip (1960*b*) placed it between the Cooper's Creek-Loyola faunas and the Buchan fauna, probably Siegenian.

Hexagonaria approximans cribellum subsp. nov.

Plate 74, figs. 2*a*, *b*; Plate 75, figs. 1*a*, *b*; text-figs. 8, 9

Holotype, SU 13259 (Pl. 74, figs. 2*a*, *b*), loc. Cr-100. Other material figured: SU 13260 (loc. Cr-100).

Derivation of name. Latin *cribellum*, a small sieve; in reference to the complex carinae.

Diagnosis. *H. approximans* with numerous strongly fusiform septa, and tabulae with upturned margins.

Description. All known coralla are small, and apparently in the shape of low domes. The calix has a narrow rim, either flat or slightly everted, and rather steep sides surrounding a relatively shallow axial pit whose floor is gently domed.

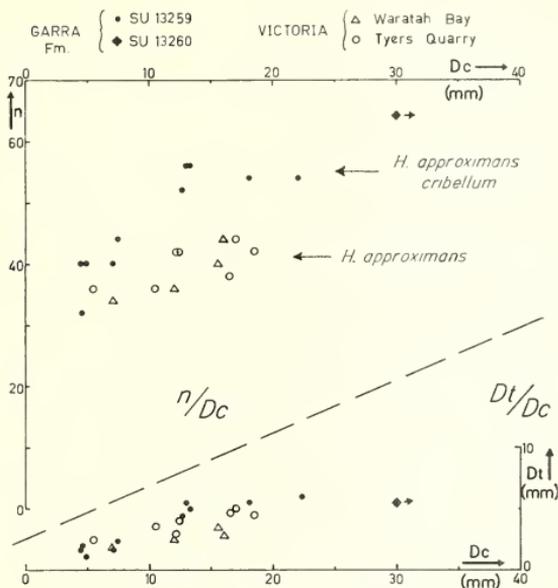
Dimensions in mm. (representative corallites).

<i>Specimen</i>	<i>Dc</i>	<i>Dt</i>	<i>Dt/Dc</i>	<i>n</i>	<i>L</i> ₁	<i>L</i> ₂
SU 13259	4.9	1.2	0.24	40	0.8 R	0.5-0.7 R
	12.7	4.4	0.35	52	0.7 R	0.6 R
	13.3	5.0	0.38	56	0.8 R	0.5 R
	22.1	6.0	0.27	54	0.8 R	0.7 R
SU 13260	> 30	5.5	< 0.18	64	c. 0.9 R	c. 0.8 R

In adult corallites, *Dc* is about 2 cm. Each corallite is bounded by a very thin epitheca, lined by a fibrous stereozone 0.2-0.5 mm. thick. For adults, *n* = 54-64. The major septa are long, leaving an axial space of 3-4 mm.; the minor septa are little shorter, and end at the margin of the tabularium. Attenuate in the tabularium, the septa are strongly fusiform in the dissepimentarium, with the zone of maximum dilatation being $\frac{1}{3}-\frac{1}{2} R$ in from the periphery. Peripherally the septa are generally thin, but bear prominent,

flanged zigzag carinae, and occasionally break up into naotic segments consisting of these complex carinae without the intervening lamellar portions of the septa.

The thin trabeculae are arranged in strongly asymmetrical disphylloid fans, the zone of divergence approximately corresponding to the zone of maximum septal dilatation. At the periphery the trabeculae are vertical, or more generally are inclined outwards



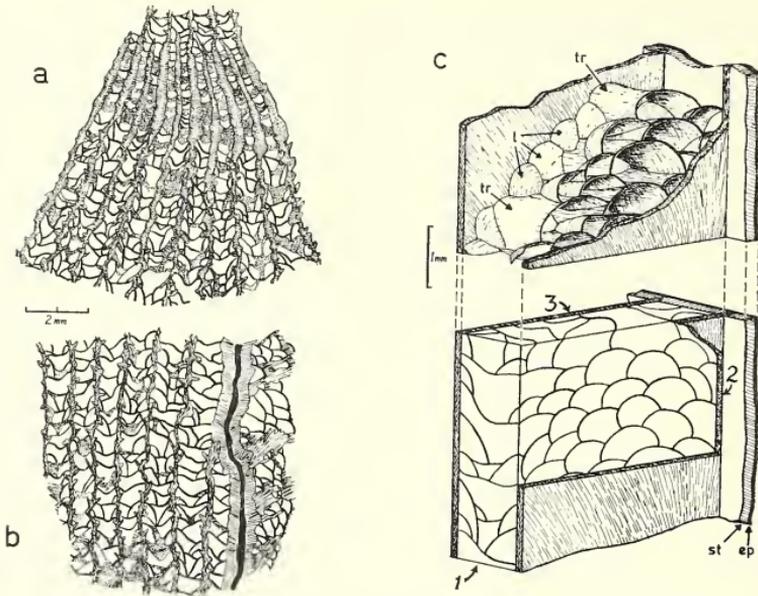
TEXT-FIG. 8. Plots of n (above) and D_t/D_c (below) against D_c for *Hexagonaria approximans* (Chapman) and *H. approximans cribellum* subsp. nov. Data for *H. approximans* s.s. obtained from published figures: Hill (1954b—Waratah Bay) and Philip (1962—Tyers Quarry).

at a small angle from the vertical. Inward from the zone of divergence they are increasingly curved, and at the margin of the tabularium they are generally inclined at a very high angle from the vertical, and may be horizontal. Within the tabularium their inclination becomes increasingly steep axially.

A plot of D_t against D_c shows a fairly strong correlation (text-fig. 8); for the holotype, the corresponding growth equation is approximately: $D_t = 0.33 D_c$. The tabular floors are flat or gently domed, with sharply upturned margins. The tabulae are crowded, complete or more usually incomplete, and slightly sagging to slightly domed. Those which abut against the dissepimentarium are moderately to sharply upturned marginally. Rarely, the tabulae are marginally supplemented by slightly globose tabellae, inclined towards the axis.

The wide dissepimentarium consists of up to eighteen series of small, highly globose

dissepiments, which are horizontal or outwardly inclined peripherally, horizontal until about the fourth series, then steeply and evenly inclined towards the tabularium until the last two to four series, which are vertical and elongate. Towards the periphery, the dissepiments in each interseptal loculus are frequently imperfectly arranged in three series: one series of transverse, cylindroidal plates, and two lateral series of convex,



TEXT-FIG. 9. Dissepimental structure, *Hexagonaria approximans cribellum* subsp. nov. *a*, Transverse section; *b*, tangential longitudinal section; SU 13260 (loc. Cr-100), $\times 5$ (cf. Pl. 75, figs. 1*a*, *b*). *c*, Schematic representation, $\times 10$; 1—tangential longitudinal section; 2—radial longitudinal section (part of septum removed to show dissepiments); 3—transverse section. *ep*—epitheca; *st*—peripheral stereozone; *tr*—transverse (cylindroidal) dissepiments; *l*—lateral dissepiments.

incomplete plates, resting partly on the sides of the septa, and partly on the cylindroidal plates or on each other (text-fig. 9).

Comparison. This subspecies differs from the original species principally in having considerably more septa—average about sixty as against about thirty-eight. This also shows up in plots of *n* against *Dc* for the two forms (text-fig. 8). In addition, the septa are in general more strongly dilated, and the trabeculae are arranged in more strongly developed fans. There seem to be more series of dissepiments, and the tabular floors tend to be sagging rather than domed. In other respects, including the high degree of variability (particularly in size), the new subspecies is quite close to *H. approximans* s.s.

Remarks. In view of the definite differences from the Victorian species, and in the interests

of stratigraphic precision, I feel it is desirable to separate the Garra form at the subspecies level. *H. approximans cribellum* is, however, quite probably a descendant of the Victorian species.

Known localities. Loc. Cr-100.

Genus BILLINGSASTRAEA Grabau 1917

1917 *Billingsastraea* Grabau, p. 957 (*vide* Lang, Smith, and Thomas 1940, p. 27).

1958 *Billingsastraea* Grabau; Schouppé, p. 253. Contains an exhaustive synonymy.

Type species. *Phillipsastrea verneuili* Milne-Edwards and Haime 1851, p. 447, pl. 10, fig. 5 (*vide* Lang, Smith, and Thomas 1940, p. 27).

Diagnosis. Massive Disphyllidae with walls between corallites absent, or represented by fibrous sclerenchyme, but no epitheca. Septa may be confluent, abutting, or peripherally discontinuous.

Discussion. In an extensive study of the '*Phillipsastrea*' group of Rugosa, Schouppé (1958) has shown that *Phillipsastrea* sensu stricto possesses a zone of horseshoe dissepiments, and so is a senior synonym of *Pachyphyllum* Milne-Edwards and Haime. Schouppé placed the species without horseshoe dissepiments in *Billingsastraea*. Until certain nomenclatural problems raised by this revision are resolved by the International Commission (see p. 524), I have accepted this re-assignment.

The following Australian species lack series of horseshoe dissepiments, and should, following Schouppé's revision, be placed in *Billingsastraea*: *Phillipsastraea aperta* Hill 1942*b*; *P. callosa* Hill 1942*b*; *P. carinata* Hill 1942; *P. delicatula* Hill 1936; *P. linearis* Hill 1942*b* (*P. walli* Etheridge of Chapman 1914, non Etheridge Jr. 1892); *P. maculosa* Hill 1942*b*; *P. speciosa* Chapman 1914.

P. curranii Etheridge fil. 1892, poses a problem which can only be solved by further study. Some specimens from the type locality (Limekilns, north of Bathurst, N.S.W.) lack horseshoes, while others have perfectly developed series of horseshoes. It is possible that two species are present. *P. oculoides* Hill 1942*c*, possesses definite small horseshoe dissepiments, and so remains in *Phillipsastrea* d'Orbigny 1849, sensu Schouppé 1958. *Phillipsastrea* sp. Hill 1954*a*, p. 14, pl. 3, fig. 2, is probably a *Billingsastraea*, but no longitudinal section is available.

Billingsastraea aperta (Hill 1942)

Plate 74, fig. 4; Plate 75, figs. 2, 3

1942*b* *Phillipsastraea aperta* Hill, p. 154 (non? pl. 2, figs. 7*a*, *b*).

1942*c* *Phillipsastraea aperta* Hill; Hill, p. 183, pl. 6, figs. 7*a*, *b*.

Holotype: SU 7289 (Pl. 75, figs. 3*a*, *b*), loc. Cr-113. Other material figured: SU 13261, 20104, both loc. Cr-100.

Diagnosis. Astraeoid *Billingsastraea* with widely spaced and only slightly dilated septa, with numerous small globose dissepiments, and with elongate tabellae arranged on slightly domed tabular floors. (After Hill 1942*b*, p. 154.)

Description. The description given by Hill (1942*b*) is very brief, and so the species is redescribed below.

The corallum is partly *astraeoid*, partly *thamnastraeoid*. The calicular pits are rather deep, with steep walls, gently domed floors, and rounded everted rims. The pits are about 6 mm. in diameter, while *Ts* (see p. 522) is about 13 mm.

Dimensions in mm.

	<i>Dt</i>	<i>n</i>	<i>n/Dt</i>	<i>Ts</i>
Mean	5.2	38*	7.3	13.7
Max.	6.0	46	7.9	17.9
Min.	3.8	30	5.3	10.1
No. of readings	9	8	8	24

* Mean *n* to the nearest even number. Data from 2 coralla, loc. Cr-100.

The major septa are long, leaving an axial space 1–2 mm. across, while the minor septa end just inside the tabularium. The axial space is elongate in the counter-cardinal plane; the cardinal septum projects a short distance into the space, but the counter septum extends right across it, its end either uniting with the cardinal septum, or turned abruptly aside. The remaining septa show a slight pinnate arrangement. The septa are fusiform; in a zone 2.5–3.5 mm. wide at the inner margin of the dissepimentarium they are usually as wide as the interseptal loculi. Away from this zone the dilatation decreases rapidly, the septa being attenuate peripherally and axially.

The slender trabeculae are arranged in well-developed asymmetrical disphylloid fans, whose zone of divergence corresponds exactly with the zone of maximum septal dilatation.

Dt = 3–5 mm.; the tabularia are composed of numerous flat or gently domed, complete and incomplete tabulae, arranged biserially. In the broad axial zone the tabulae are supplemented by moderately convex tabellae.

The dissepimentarium is composed of numerous small globose dissepiments, horizontal in the zone of maximum septal dilatation, steeply axially inclined inwards from this zone, and moderately peripherally inclined outside the zone. Midway between tabularia the dissepiments are again horizontal.

Comparison. *B. aperta* very closely resembles *Pseudoacervularia roemeri* (Verneuil and Haime 1850) of Rózkowska (1953), from the Frasnian of the Holy Cross Mts., Poland. This resemblance is most noticeable in the arrangement of the dissepiments, the trabecular fans, and the degree of variation of septal dilatation.

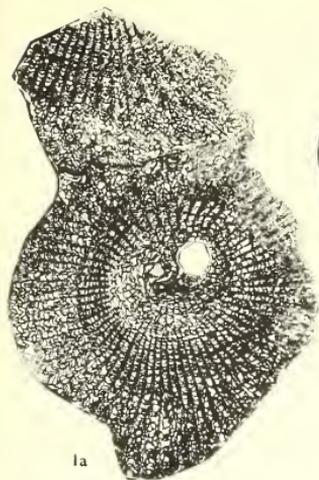
Remarks. SU 6199, from the Loomberah Limestone of Tamworth, N.S.W., placed in *B. aperta* by Hill (1942c, p. 154, pl. 2, figs. 7*a*, *b*), differs from the holotype, and from other specimens from the type horizon, in that its septa are slightly carinate in the

EXPLANATION OF PLATE 75

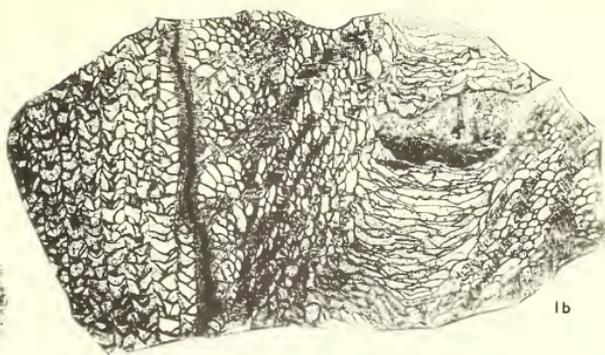
Figs. 1*a*, *b*. *Hexagonaria approximans cribellum* subsp. nov. Topotype SU 13260, loc. Cr-100; transverse (*a*) and longitudinal (*b*) sections, $\times 2$; note large diameter. (See also text-fig. 9*a*, *b*.)

Figs. 2, 3. *Billingsastraea aperta* (Hill). 2, SU 20104, loc. Cr-100; longitudinal section, $\times 2$. 3*a*, *b*. Holotype SU 7287, loc. Cr-113, figured Hill (1942c, pl. 6, figs. 7*a*, *b*); longitudinal (*a*) and transverse (*b*) sections, $\times 2$, photographs by courtesy of Prof. D. Hill.

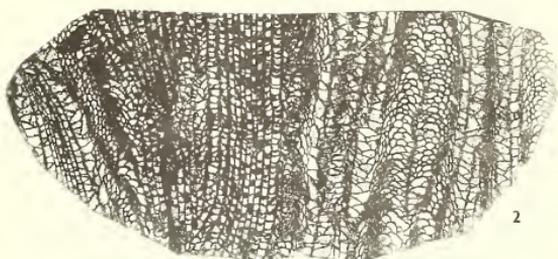
Fig. 4. *Peneckiella mesa* (Hill). Topotype SU 20103, loc. Gn-20; transverse section, $\times 4$. Specimen collected E. M. Bassett.



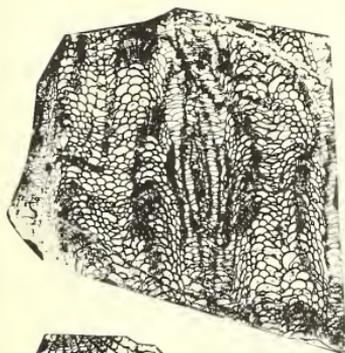
1a



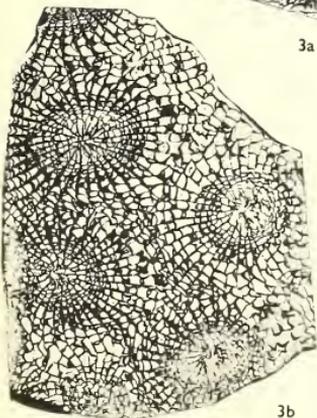
1b



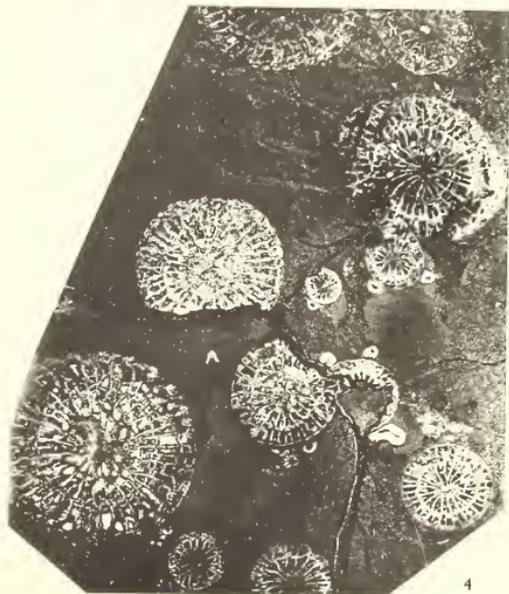
2



3a



3b



4

tabularium, and are less strongly dilated in the dissepimentarium. The Tamworth form may not be conspecific with the Wellington specimens.

Known localities. Cr-100, -113 (both in the same biostrome); P-43 (probably the same horizon as the above).

Billingsastraea speciosa (Chapman 1914)

Plate 76; text-figs. 10-14

- 1914 *Phillipsastraea speciosa* Chapman, p. 306, pl. 49, figs. 10, 11; pl. 50, figs. 12-14. Loyola, Victoria; Gedinnian.
 1939a *Phillipsastraea speciosa* Chapman; Hill, p. 237, pl. 16, figs. 1, 2 only.
 1942c *Phillipsastraea speciosa* Chapman; Hill, p. 183, pl. 6, figs. 8a, b. Wellington, N.S.W.; Garra Formation, Emsian?
 1942c *Phillipsastraea* sp. Hill, p. 186 (not figured). Wellington, N.S.W.; Garra Formation, Emsian?
 1962 *Phillipsastraea speciosa* Chapman; Philip, p. 176, pl. 24, fig. 6. Tyers R., Victoria; Cooper's Creek Formation, Gedinnian.

Holotype. GSV 2487 (Ferguson Colln.), and thin sections NM 1387, 1388 cut therefrom. Griffith's Quarry, Loyola, near Mansfield, Victoria. The locality was considered by Philip (1960a) to be an equivalent of the Cooper's Creek Formation of the Walhalla basin (south of Mansfield), and therefore early Gedinnian in age.

Diagnosis. Astraeoid and thamnsastraeoid, with moderately to strongly fusiform septa, of which the major may reach the axis, or may withdraw almost to the dissepimentarium; tabulae strongly concave.

Description. A large number of specimens have been collected from the Garra Formation; as the species is known from very few specimens at the several Victorian localities, I consider it worth while to describe fully the Garra material.

The coralla are either lamellar, growing on a flat surface of sand, &c., or are broad, low, mushroom-shaped expansions. The largest corallum collected is about 16 cm. across and 6 cm. deep. Only one specimen has an unworn upper surface exposed: on it, the calices are shallow, saucer-shaped, with only slight axial depressions. Adjacent corallites meet in sharp, slightly raised rims.

Thin sections show that individual coralla may be wholly thamnsastraeoid, wholly astraeoid, or more usually both. Within one corallum the septa of adjacent corallites may follow several patterns: (1) the septa may terminate within the dissepimentarium, leaving a small gap between their ends; (2) they may meet at a more or less abrupt angle, their ends being coincident or alternate; or (3) they may be completely confluent. Moreover, in a fair proportion of coralla, there may develop between some corallites an outer pseudotheca (Różkowska 1953, see particularly p. 52; this structure is essentially the trabecular wall of Flower 1961, p. 26), formed by the union of the bifurcating ends of septa. This simulates the wall between ceriod corallites (e.g. *Hexagonaria*), but may be clearly distinguished from that structure in lacking the median dark line (axial plate of Flower 1961) which indicates the presence of an epitheca around the individual corallites. The outer pseudotheca is in fact constructed of the same trabeculae as are the septa. When formed at all in *B. speciosa*, it is usually very incomplete; consequently in thin section it is generally not possible to measure *Dc*. A more objective measure is *Ts*,

the distance between the axes of corallites whose septa abut or are confluent. The data are summarized in the following table of dimensions, and in somewhat more detail under 'Variation'.

Dimensions in mm.

	<i>Dt</i>	<i>n</i>	<i>Ts</i>
Mean	1.76	23.9* 24†	5.12
Minimum	0.9	16	1.5
Maximum	2.8	32	13.8
Lowest mean‡	1.26	18.7* 18†	3.26
Highest mean‡	2.37	27.8* 28†	7.49
No. of readings	374	374	1,050

* Calculated mean; † mean to nearest even number; ‡ means for individual coralla. Readings taken from 12 coralla, from localities Cr-94, -100, -113, P-26, -43.

Most coralla show a fairly small range of *n*, but this range differs markedly from one corallum to another (see 'Variation'). Most septa are greatly dilated, forming a wide stereozone around the tabularium. Outside this stereozone the degree of dilatation varies greatly. Generally the septa are fusiform, but in some coralla they remain dilated throughout the dissepimentarium. This dilatation is often confined to more or less clearly differentiated horizontal layers, which are separated vertically by layers in which the septal dilatation is much reduced. In the dilated layers, the dissepiments may be almost completely suppressed. In the regions of reduced dilatation the septa vary from strongly fusiform, with the stereozone around the tabularium, to only weakly fusiform and almost attenuate, so that there is no stereozone.

In the dissepimentarium the septa may be smooth, but are more often irregularly carinate, the carinae being generally of the zigzag type. The carinae are usually only poorly developed, but on occasions may be very strong; the latter occurs mostly when the septa are fairly thin. Some septa split into two or three parallel thin strands in the dissepimentarium. Finally, there often occur septa which for a short distance become fragmented into discrete trabeculae.

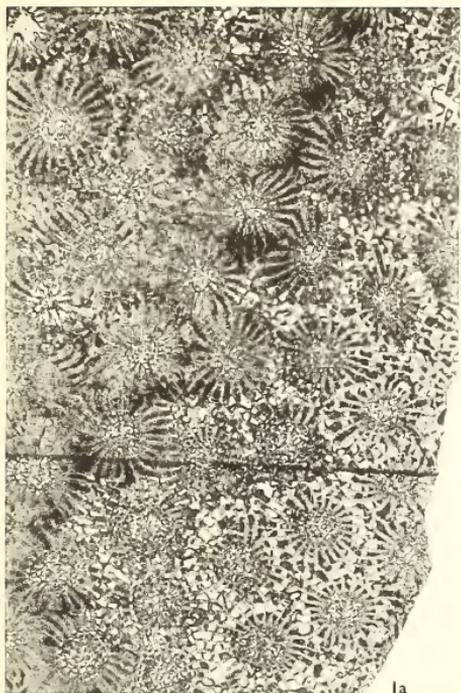
Minor septa barely enter the tabularium. The major septa are more variable; in some cases they extend unequally to the axis, either as continuous plates or as discrete trabeculae; in other cases they withdraw, sometimes to become equal in length to the minor septa. One septum, probably the counter septum, generally extends to the axis, where it is frequently enlarged, forming a rudimentary columella.

The slender trabeculae are arranged in strong asymmetrical disphyloid fans. The zone of divergence corresponds with the centre of the septal stereozone. In the tabularium the trabeculae are axially inclined at about 45° from the vertical.

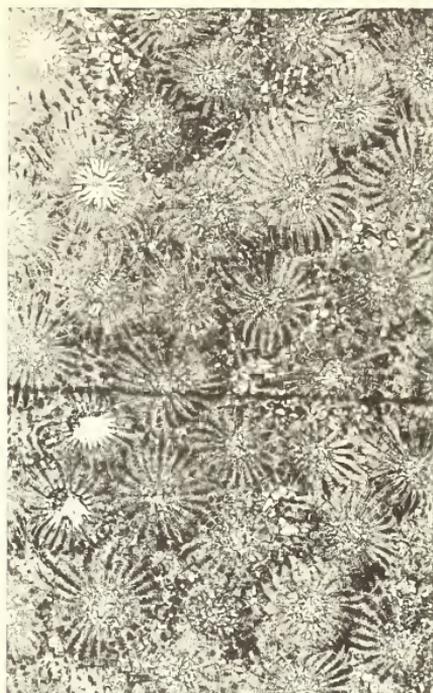
The tabularium is narrow. In the coralla measured, *Dt* varied from 0.9–2.8 mm., but a plot of all *Dt* showed two peaks at 1.4 mm. and 2.0 mm. (see 'Variation'), and most coralla correspond to one or other of these. The tabulae are moderately sagging, with

EXPLANATION OF PLATE 76

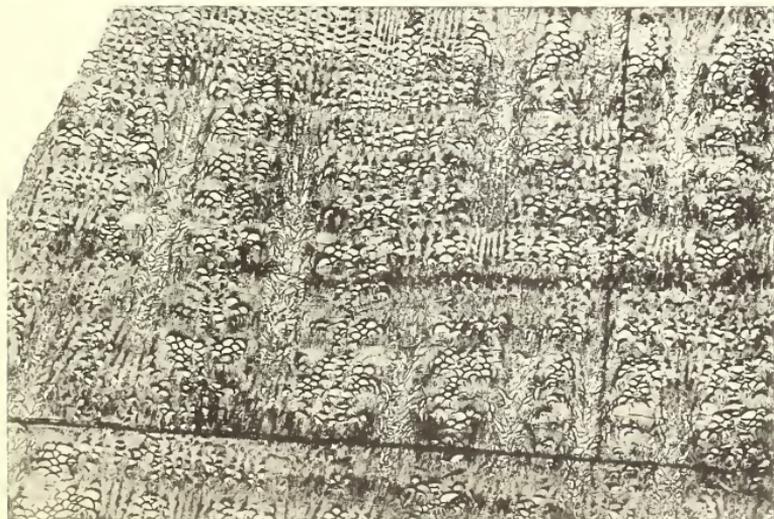
Figs. 1 a-c. *Billingsastraea speciosa* (Chapman). SU 13206, loc. Cr-100; (a) transverse section showing a region of reduced septal dilatation; (b) transverse section of a region of maximum septal dilatation, showing two corallites with shortened major septa; (c) longitudinal section; all $\times 4$. Specimen collected by Dr. J. R. Conolly.



1a



1b

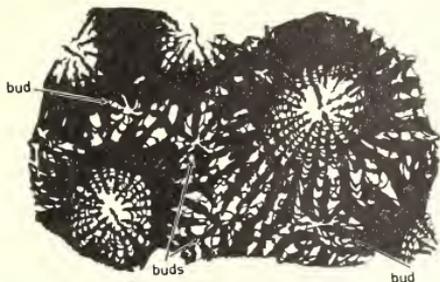


1c

rather strongly upturned margins which are supplemented by strongly inclined elongate tabellae.

The dissepimentarium is composed of small globose plates. In a narrow zone around each tabularium, there are two or three series which are very strongly inclined and rather elongate. Outside these, in the zone of maximum septal dilatation, there are one to three series of more or less horizontal dissepiments; beyond these the dissepiments are gently outwardly inclined until midway between tabularia when they are again horizontal.

Ontogeny. The earliest discernible stage in the formation of a corallite occurs generally at the point of intersection of three corallites. Careful inspection of the septa reveals a very small region in which there are six radially arranged plates; some of these may



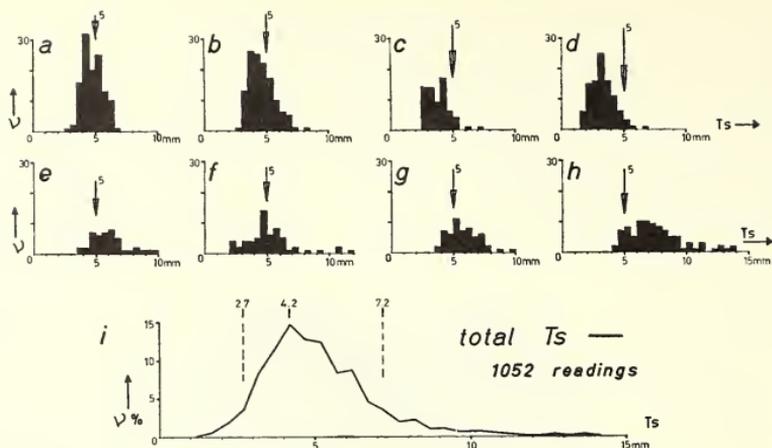
TEXT-FIG. 10. *Billingsastraea speciosa* (Chapman); transverse section $\times 5$, showing several buds. Traced from photograph of celluloid 'peel'.

be the 'peripheral' ends of septa, others may be carina-like offshoots of septa (text-fig. 10). The next observed stage is a corallite of about 1.2 mm. diameter, with some fourteen septa still not divisible into major and minor. At this stage, the tabularium is distinguishable, $Dt = 0.6$ mm. Beyond this point, offshoots are not distinguishable from adult corallites. Apparently, therefore, the growth of a bud and the rate of septal insertion are both very rapid. This type of increase is the exact equivalent of the extra-tentacular budding of scleractinians (see Wells, p. F 348, and fig. 250, in Moore 1956).

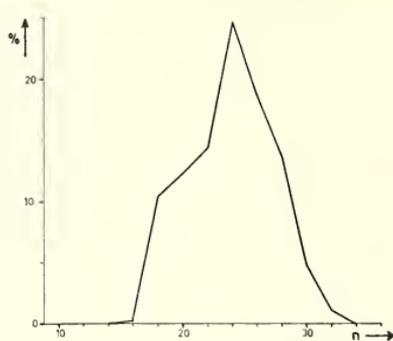
Variation. The three measurable variables in *B. speciosa* are Dt , n (measured at the margins of the tabularia), and Ts . Only for n and Dt can bivariate analysis be employed using individual readings; for comparison with Ts , mean values of coralla must be compared. It has been found that all three variables show considerable variation from one corallum to another, but relatively little within the one corallum.

Ts (text-fig. 11): this shows the widest range for data from one corallum. Frequency histograms show a broad spread more often than a sharp peak. This spread is even more pronounced in a plot of all data from twelve coralla: the range is from 1.5 mm. to 13.8 mm. overall. Using class intervals of 0.5 mm., the mode is 4.2 mm., and 68 per cent. of the data fall within the interval of classes 2.7-7.2 mm.

n (text-fig. 12): frequency histograms generally show a pronounced peak and a fairly small spread. However, the modes for the 12 coralla measured vary from 18 to 28,



TEXT-FIG. 11. *Billingsastraea speciosa* (Chapman); frequency histograms (*a-h*) and percentage frequency curve (*i*) for *Ts*. *a*, loc. Cr-94; *b-d*, loc. Cr-100; *e*, loc. Ge-3; *f-h*, loc. P-43. *i*, Total of *Ts* from twelve coralla, localities Cr-94, -100, P-26, -43, Ge-3.



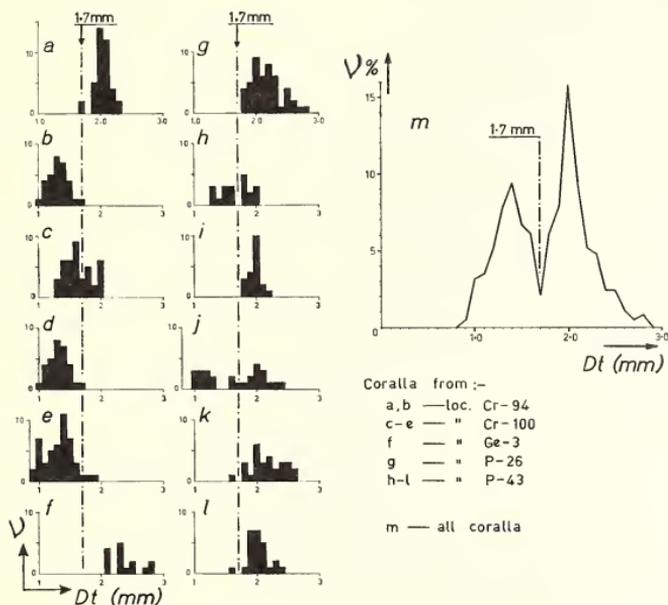
TEXT-FIG. 12. *Billingsastraea speciosa* (Chapman); percentage frequency curve for *n*: 374 readings from twelve coralla, as text-fig. 11.

with a complete range between. A frequency curve for total *n* is also a fairly tight curve, with a peak at *n* = 24, and overall range 16-32.

Dt (text-fig. 13): this provides the most interesting frequency distribution. Individual histograms vary considerably both in position and spread. However, a curve for total *Dt* is distinctly bimodal, modes 1.4 mm. and 2.0 mm., with a sharp low at 1.7 mm. Examination of the histograms in the light of this curve shows that only three of the twelve coralla have modes near 1.7 mm., and of these two also show a very wide spread

of data. Most coralla fall clearly to one or other side of 1.7 mm., and in no one of these coralla do more than 4 per cent. of the measurements fall on the other side of 1.7 mm. from the mode for that corallum.

The plot of n against Dt (text-fig. 14) for all data reflects this dichotomy in Dt , but individual plots give a very wide spread in all directions. The correlation, while not close,



TEXT-FIG. 13. *Billingsastraca speciosa* (Chapman); frequency histograms (a-l) and percentage frequency curve (m) for Dt .

is enough to suggest that correlation would be obtained for individual coralla by measuring a large number of corallites.

The dichotomy in Dt might suggest the possibility of dividing the species into two formae on this basis; unfortunately this is not possible, as several coralla cannot easily be placed on one side or the other of the dividing line.

Comparison. The Garra specimens, apart from the greater degree of variation shown by the much larger sample available, differ from the Victorian specimens principally in the high proportion of tabularia in which there is an elongate, columella-like counter (?) septum. The layered effect of the septal dilatation in the Garra coralla is visible to a lesser degree in the sections of the holotype. The relations of *B. speciosa* to other species have been noted by Hill (1939).

Known localities. Locs. Cr-94, -100, -111, -113; Ge-3; P-26, -43; BR¹ /177. All except

Genus PENECKIELLA Soshkina 1939

- 1939 *Peneckiella* Soshkina, p. 23.
1949 *Synaptophyllum* Simpson; Stumm p. 37, non Simpson, 1900. (Subj. synonym, McLaren 1959, pp. 16, 22 q.v. for further discussion on the confusion of these two genera).
1953 *Thamnophyllum* Penecke 1894 (*partim*); Rózkowska, p. 14.
1958 *Peneckiella* Soshkina; Schouppé, p. 299. Contains an extensive synonymy.
1959 *Peneckiella* Soshkina; McLaren, p. 22.
1960 *Peneckiella* Soshkina; Rózkowska, p. 29.
1961 *Peneckiella* Soshkina; Lenz, p. 505.

Type species. *Diphyphyllum minus* F. A. Römer 1855, p. 29, pl. 6, figs. 12*a-e*. Soshkina 1939, p. 23, incorrectly called the species *Peneckiella minima*. *Minus* is the neuter form of *minor* (m., f.), the comparative of *parvus*; *minimus* is the superlative of this word. The type species is therefore *Peneckiella minor* (Römer).

Diagnosis. Fasciculate or cerioid phacellophyllid with septa smooth or weakly carinate, dilated peripherally, or fusiform; with a peripheral series of horseshoe and peneckielloid dissepiments, supplemented by inner, and occasional outer, accessory dissepiments; tabulae generally complete.

Discussion. This genus has been fully discussed recently by Flügel (1956), Schouppé (1958), and McLaren (1959). Flügel described topotypic material, and examined the holotype of *Diphyphyllum minus* Römer. Unfortunately, he only figured a transverse section, and a diagrammatic longitudinal section. Schouppé described and figured topotypic material. His figures show distinct trabecular fans, a series of horseshoe dissepiments, and occasional dissepiments on either side of this series. These dissepiments are here termed inner and outer accessory dissepiments.

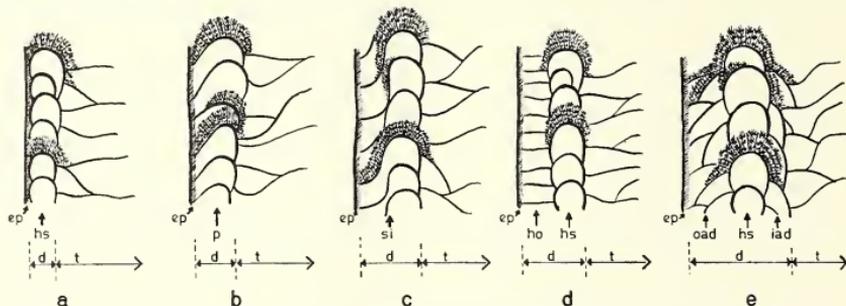
McLaren (1959) discussed the relationship of several American species to the type species of *Peneckiella*, and concluded that they differed from it in lacking horseshoe dissepiments. For the American species he erected the disphyllid genus *Acinophyllum*, which is characterized by carinate septa and only one or two series of normal dissepiments.

Rózkowska (1960) described a subspecies of the type species, from the Frasnian of Poland, and, after examining topotypic material from Grund, concluded that the dissepimental structure of *P. minor* (s.l.) is variable. She distinguished four types of dissepiment, which are also recognized herein (text-fig. 15): (i) horseshoe dissepiments *sensu stricto*; (ii) 'horizontal' dissepiments, usually occurring as what are here termed outer accessory dissepiments; (iii) 'peneckielloid' dissepiments; and (iv) a rare variant of (iii), 'sigmoidal' dissepiments. She found all four types in the one corallite, but more usually only one or two types occur, particularly (i) and (iii) together. The 'horizontal' dissepiments somewhat resemble those in *Thamnophyllum*, but are far less uniformly developed. The 'peneckielloid' dissepiments consist of an inner half the same as for horseshoe dissepiments, and an outer half which slopes fairly steeply, straight down to the periphery. The 'sigmoidal' type is a variant of this, closely resembling a combination of horseshoe and horizontal dissepiments, particularly when the sigmoidal outer part touches the surface of a preceding dissepiment before proceeding to the periphery.

As well as occurring in *P. minor kunthi* (Dames) of Rózkowska (1960, see figs. 22, 25, 27-29), this variability in dissepimental form can be seen in Schouppé's (1958) figures of *P. minor* (Römer), and also in the specimens of *P. mesa* (Hill) described below.

Peneckiella mesa (Hill 1942)

Plate 75, fig. 4; Plate 77, figs. 1, 3; Plate 78, fig. 1; text-figs. 16-21

1940a *Disphyllum praecox*? Hill p. 399 (in text). Wellington, N.S.W.: 'Devonian?'1942c *Disphyllum mesa* Hill p. 185, pl. 5, figs. 4, 5. Wellington; Garra Formation, Emsian??1954a *Peneckiella teichert* Hill p. 25, pl. 2, figs. 29a, b. West Kimberley Ra., W. Aust. (Fitzroy Basin); 'Atrypa beds', Frasnian.non 1961 *Peneckiella teichert* Hill?; Lenz p. 505, pl. 1, figs. 1, 2. Lower Mackenzie Valley, Canada; Ramparts Limestone, Givetian.*Holotype*. SU 5276 (Pl. 77, fig. 1), loc. Gn-20. Figured Hill 1942c, pl. 5, fig. 4. Other material figured: SU 17125, 20103, both loc. Gn-20.

TEXT-FIG. 15. Dissepimental types found in phacelophyllid species (all diagrammatic, about $\times 2$ to $\times 4$). a, Horseshoe dissepiments; b, peneckielloid dissepiments; c, sigmoidal dissepiments; d, horseshoe and horizontal dissepiments (as in *Thamnophyllum* Penecke); e, horseshoe and accessory dissepiments. ep—epitheca; hs—horseshoe series; p—peneckielloid series; si—sigmoidal series; ho—horizontal series; oad—outer accessory dissepiments; iad—inner accessory dissepiments; d—dissepimentarium; t—tabularium.

Diagnosis. Fasciculate *Peneckiella* with moderately carinate or smooth, thin or fusiform septa, high mesa-shaped tabulae, and dominantly peneckielloid dissepiments.

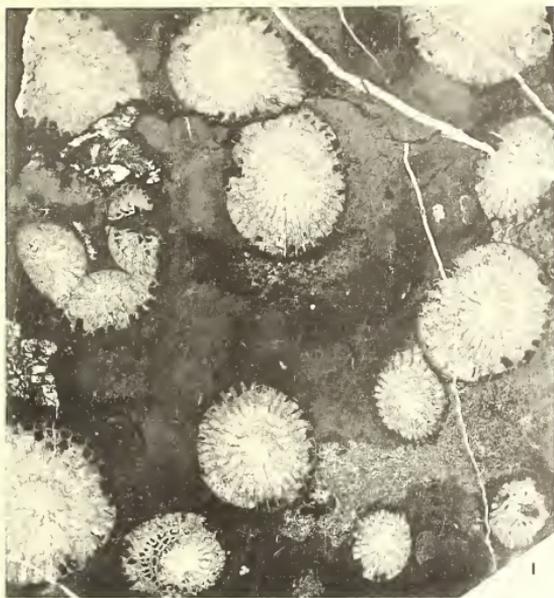
Description. Much additional material has been collected, and so the species is fully re-described.

The corallum is usually phaceloid. The corallites have a thin epitheca, with shallow septal grooves and only slight growth wrinkling. *Dc* is usually about 3–5 mm., but may be over 8 mm. The calix is deep, with vertical walls; the rim is narrow and slightly everted; the floor of the calix consists of a wide mesa-shaped axial boss, surrounded by a deep, narrow concentric trench. There are generally 30–40 septa (see table, p. 557);

EXPLANATION OF PLATE 77

Figs. 1, 3. *Peneckiella mesa* (Hill). 1, Holotype SU 5276, loc. Gn-20, figured Hill (1942c, pl. 5, fig. 4); transverse section, $\times 4$. 3, Topotype SU 17125, loc. Gn-20; oblique and longitudinal sections—note calix and dissepiments in lowermost corallite (see also text-fig. 16b); $\times 4$.

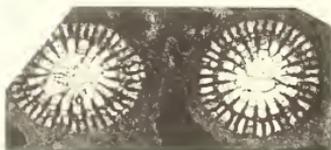
Figs. 2a–c. *Peneckiella teichert* Hill. Holotype, Univ. W. Aust. 33,515, figured Hill (1955a, pl. 2, fig. 29); Givetian or Frasnian, W. Kimberleys. a, longitudinal and b, c, transverse sections; $\times 4$, photographs by courtesy of Prof. D. Hill.



1



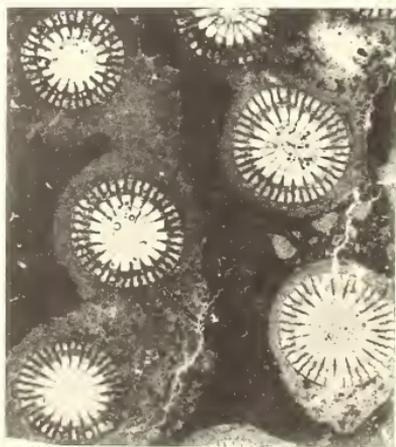
2a



2b



3



2c

the major are long, unequal, leaving an axial space of $c. \frac{1}{3} Dc$; L_2 is about $\frac{1}{2} L_1$, the minor septa normally extended a little way into the tabularium. The septa are weakly to strongly dilated, generally fusiform, with the zone of maximum dilatation a little outside the margin of the tabularium. This dilatation frequently spreads over the surfaces of the innermost dissepiments, and forms an inner stereozone. The septa may also dilate peripherally. Within the dissepimentarium, where the dilatation is slight or moderate, irregular zigzag carinae frequently develop. In the tabularium the septa are thin, and straight or wavy.

Specimen		SU 5276*	SU 17125†	SU 17126‡	SU 13145‡
<i>Dc</i> (mean)	(mm.)	4.1	3.1	3.0	4.0
<i>Dc</i> (max.)		6.4	5.6	4.7	8.4
<i>Dc</i> (min.)		2.4	1.4	1.8	1.9
No. measurements		20	47	25	70
<i>Dt</i> (mean)	(mm.)	2.5	1.9	1.8	2.3
<i>Dt</i> (max.)		3.9	3.3	2.8	3.2
<i>Dt</i> (min.)		1.5	1.0	1.2	1.3
No. measurements		20	47	25	58
<i>Dt/Dc</i>		0.61	0.61	0.59	0.56
<i>n</i> (mean)		32.5§	31.4	30.8	37.1
		32	32	30	38
<i>n</i> (max.)		40	37	38	46
<i>n</i> (min.)		23	22	26	28
No. measurements		20	33	18	58
<i>n/Dc</i> (mean)	(mm ⁻¹)	0.83	1.12	1.11	0.98
<i>n/Dc</i> (max.)		1.08	1.72	1.44	1.69
<i>n/Dc</i> (min.)		0.48	0.63	0.83	0.60
No. measurements		20	33	18	58
L_2 (mean)		..	0.39 <i>R</i>	0.38 <i>R</i>	0.46 <i>R</i>
L_2 (max.)		..	0.51 <i>R</i>	0.48 <i>R</i>	0.59 <i>R</i>
L_2 (min.)		..	0.21 <i>R</i>	0.24 <i>R</i>	0.25 <i>R</i>
No. measurements		..	35	25	70

* holotype, loc. Gn-20; † topotypes, loc. Gn-20; ‡ homeotype, loc. Cr-54; § calculated mean; || mean to nearest even number of septa.

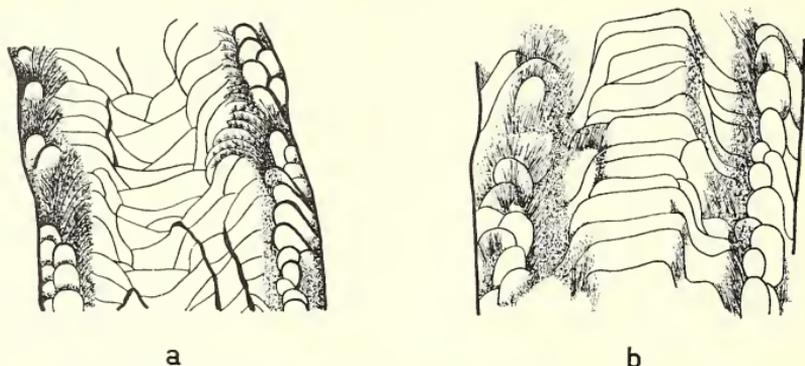
The septa consist of slender, straight, or slightly curved trabeculae. These are arranged in phacellophylloid fans symmetrical about the axis of the series of horseshoe and peneckielloid dissepiments. The zone of divergence of the fans corresponds to the zone of greatest septal dilatation.

The tabulae are generally complete, rarely incomplete. They are mesa-shaped: the axial parts are flat or gently sagging, while near the dissepimentarium they are turned abruptly down. The periaxial zone is narrow and deep; in it the tabulae, augmented by occasional concave tabellae, are gutter-shaped, with flat or concave floors, high vertical inner walls, and low, upward-slanting outer walls which abut onto the dissepiments. Rare incomplete axial tabulae rest, on all sides, on the edges of the preceding 'mesa'. *Dt* is $c. 0.6 Dc$, and the axial zone of the tabularium is about $\frac{1}{2} Dt$.

The narrow dissepimentarium consists mainly of a single series of peneckielloid dissepiments, augmented by small horseshoe dissepiments, which in some corallites are

the dominant element, and by inner and outer accessory dissepiments. Rarely, the peneckielloid and horseshoe dissepiments fail, and the dissepimentarium is composed of several series of globose dissepiments whose inclination diverges from the mid-radius of the dissepimentarium.

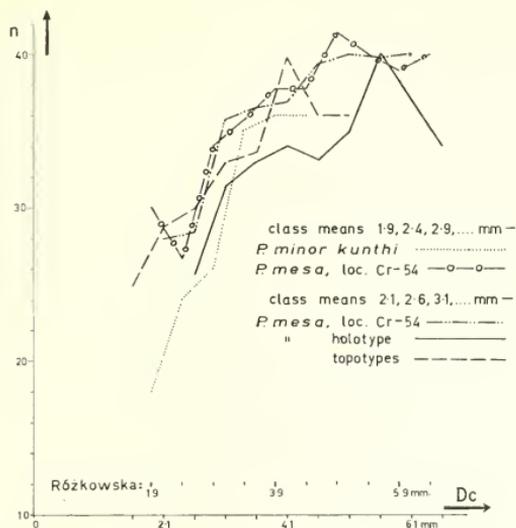
Ontogeny. Budding is parricidal. Two or three buds appear on top of the calical rim, and rapidly expand, sometimes to come into contact, while growth of the parent corallite ceases completely. Septa and dissepiments are added very rapidly, so that juvenile corallites soon assume the proportions of adults.



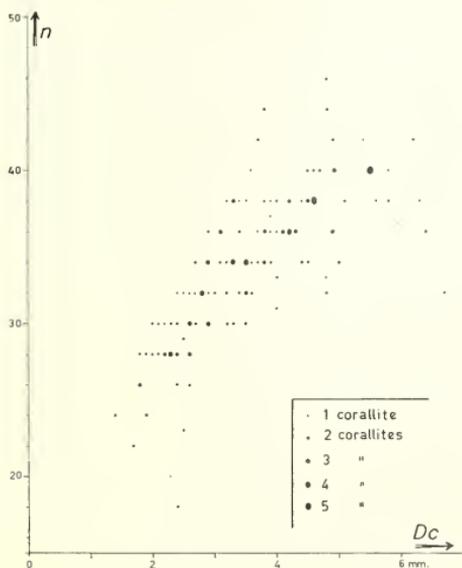
TEXT-FIG. 16. Longitudinal sections, $\times 10$, of: *a*, *Peneckiella minor kunthi* (Dames), after Rózkowska (1960, fig. 27); *b*, *P. mesa* (Hill), SU 17125, traced from photograph (Pl. 77, fig. 3).

Variation (text-figs. 17–21). In a series of papers on Devonian phacellophyllids, Rózkowska (1953, 1956, 1957, 1960) has made a detailed study of many species, and has distinguished them partly on a morphological basis, and partly statistically. Her statistical approach used the variation of n and Dt relative to Dc . To graph the data, she divided those for Dc into classes of 0.5 mm., and found the arithmetic mean of the data for n or Dt in each such class. For comparative purposes, similar data were obtained from a number of colonies collected from three localities in the Garra Formation, including the type. Scatter diagrams and mean curves for the individual colonies showed a greater spread than that of curves for separate species as figured by Rózkowska. As a further test, curves for $n:Dc$ were constructed for one corallum, using class sizes of 0.3 mm. and 0.5 mm., and in the latter case class limits coinciding with those of Rózkowska (1960) for *P. minor kunthi*, and removed from these limits by half a class interval. These curves showed that the choice of class size and position has a very strong effect on the form of the resulting curve. Consequently the data and curves provided by Rózkowska cannot safely be used for comparison with other species, and doubt is thrown on Rózkowska's application of these methods.

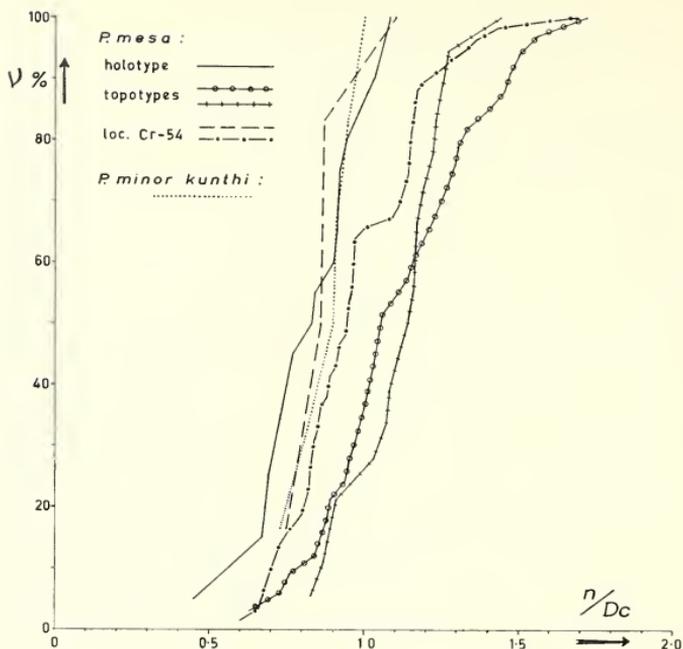
Variation of $n:Dc$ for *P. mesa* is wide; this is well shown in cumulative frequency curves of the ratio n/Dc , which vary strongly in both position and shape. However, scatter diagrams of $Dt:Dc$ for the coralla studied show fairly strong concentrations, to which closely similar isometric growth curves, of the approximate form $Dt = 0.6 Dc$,



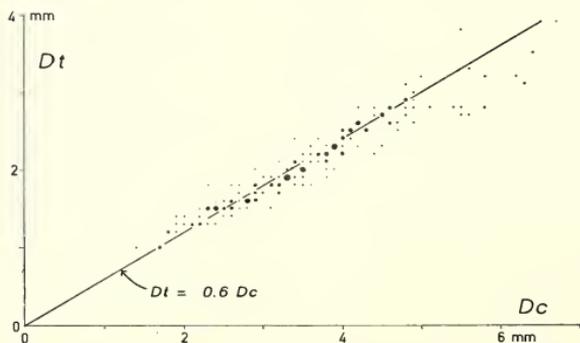
TEXT-FIG. 17. Mean curves for n against D_c , *Peneckiella mesa* and *P. minor kunthi* (from Różkowska 1960, fig. 26).



TEXT-FIG. 18. Scatter diagrams for n against D_c , *Peneckiella mesa*; 138 measurements from 5 coralla, locs. Cr-54, Gn-20.



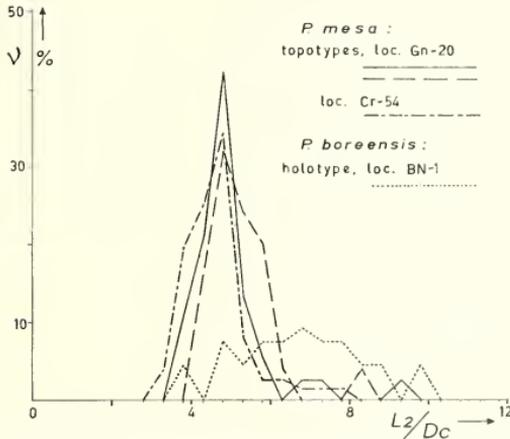
TEXT-FIG. 19. Cumulative frequency curves for n/Dc , *Peneckiella mesa* (five coralla) and *P. minor kunthi* (calculated from Rózkowska 1960).



TEXT-FIG. 20. Scatter diagram and estimated mean curve for Dt against Dc , *Peneckiella mesa*; 158 measurements from five coralla, locs. Cr-54, Gn-20.

may be fitted. It is possible that the ratio Dt/Dc may prove of greater diagnostic value for species of *Peneckiella* than the ratio n/Dc ; unfortunately data for the European species are lacking at present.

Frequency curves for the ratio L_2/Dc also show close correspondence between coralla. Plotted by classes 0.5 apart, curves for three coralla have a very strong mode at 4.8, and moderate right skew. This ratio also may prove a useful diagnostic parameter (compare *P. borensis*, p. 562).



TEXT-FIG. 21. Percentage frequency curves for L_2/Dc from three coralla of *Peneckiella mesa*, and the holotype of *P. borensis* sp. nov.

Comparison. The trabecular and dissepimental structure of this species, as shown very clearly by topotypic material, are those characteristic of *Peneckiella* Soshkina, as the genus is interpreted (from the type species) by recent workers who have examined the type material (Flügel 1956; Schouppé 1958; Rózkowska 1960).

P. mesa differs from *P. minor* (Römer) in greater size, more septa, and the possession of strongly mesa-shaped tabulae; the mode of budding also appears to be somewhat different (see Rózkowska 1960). *P. mesa* does not resemble any of the species described by Soshkina from the Russian Upper Devonian.

P. teichertii Hill 1954, from the middle Frasnian *Ladja saltica* zone of the Fitzroy Basin, is tentatively placed in synonymy with *P. mesa*: its full range of variation is unknown, there being but one specimen. The only difference that I can detect is in the accessory dissepiments. In *P. teichertii* there is one series of small, vertical inner accessory dissepiments, but an outer series is rarely developed (Pl. 77, figs. 2 a-c).

P. teichertii? of Lenz (1961) is cerioid or phacelo-cerioid, with flat or sagging tabulae, and so differs strongly from both *P. mesa* and *P. teichertii*. Its tabulae are closer to those of the type species, and to some of the Russian species. *P. borensis* sp. nov. differs from *P. mesa* in having very strongly dilated septa within the dissepimentarium; the minor

septa are shorter, and the tabulae are more variable, seldom forming the high 'mesas' of *P. mesa*.

Known localities. Gn-20 (type locality); BN-2; Cr-42, -46, -54; Ct-53, -64; MM-6; P-43.

Peneckiella boreensis sp. nov.

Plate 78, figs. 2*a-c*; text-fig. 21

Holotype. SU 12118, loc. BN-1.

Derivation of name. From the parish of Boree Nyrang, in which occurs the type locality.

Diagnosis. Phaceloid *Peneckiella* in which the septa are extremely dilated in the dissepimentarium, often forming a wide stereozone; with short minor septa.

Description. The corallum is apparently dendroid; the only known specimen is intergrown with a stromatoporoid. Maximum *Dc* is 10 mm., most being 6-8 mm. The calix is generally deep, with steep sides and a wide, flat base. There is usually a low, flat-topped axial boss. The epitheca is thin, and apparently does not extend distally as far as the calical edge, as in several sections of adult corallites the wall of the corallite is formed by the rounded outer edges of the septa, as in *Macgeea* and *Thamnophyllum*. Several sections also show sharp rejuvenescence rims. Budding occurs at the outer margin of the tabularium, and is parricidal, as in *P. mesa*. The number of buds formed is not known.

Dimensions in mm.

	<i>Dc</i>	<i>Dt</i>	<i>Dt/Dc</i>	<i>n</i>	<i>L</i> ₁	<i>L</i> ₂
Mean	4.5	2.8	0.65	32	0.76 <i>R</i>	0.25 <i>R</i>
Max.	10.1	6.5	0.78	56	0.94 <i>R</i>	0.41 <i>R</i>
Min.	0.9	0.7	0.51	6	0.47 <i>R</i>	0.0 <i>R</i>
No. of Readings	24	24	24	19	24	24

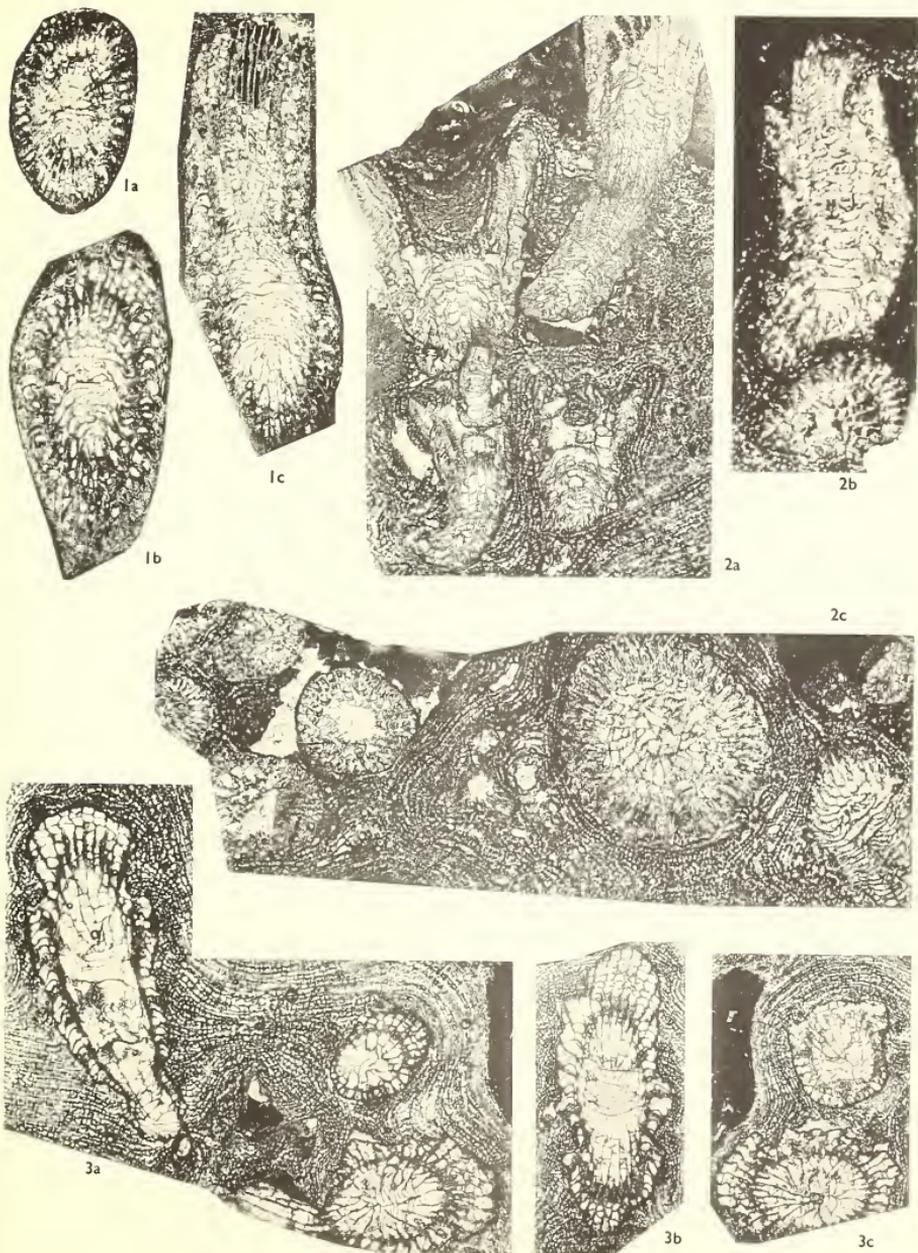
The long major septa extend unequally to the axis; the minor septa end at the margin of the tabularium. Septal dilatation is strong in the dissepimentarium, where the septa are generally considerably wider than the interseptal loculi, and are frequently in contact to form a wide stereozone; the dilatation is fusiform. In the tabularium the septa are attenuate and generally wavy. Carinae are lacking. The tabularium is wide; the tabular floors are gently domed to moderately mesa-shaped, often sagging axially. The tabulae are both complete and incomplete; at the margins of the 'mesas' there are frequent moderately domed tabellae. In juvenile corallites the tabulae are generally

EXPLANATION OF PLATE 78

Figs. 1*a-c*. *Peneckiella mesa* (Hill). Topotype SU 20103, loc. Gn-20. *a, b*, oblique transverse, and *c*, longitudinal sections; note the combination of horseshoe and peneckielloid dissepiments; $\times 4$. Specimen collected E. M. Basnett.

Figs. 2*a-c*. *Peneckiella boreensis* sp. nov. Holotype SU 12118, loc. BN-1. *a*, Longitudinal sections—note calix and horseshoe dissepiments in corallite at top left, horseshoe dissepiments in corallite at top right; *b*, longitudinal, and *c*, transverse sections; corallum invested by a stromatoporoid; $\times 4$.

Figs. 3*a-c*. *Peneckiella* sp. cf. *minor kunthi* (Dames) sensu Rózkowska, 1960. SU 11273, loc. BC-6; *a*, longitudinal and oblique transverse sections; *b*, longitudinal, and *c*, oblique transverse sections; $\times 4$. Compare text-fig. 16*a*. Corallum invested by a stromatoporoid.



complete, flat to sagging, and only rarely mesa-shaped. The narrow dissepimentarium consists of peneckielloid dissepiments, some horseshoe dissepiments, and occasional accessory dissepiments. The dissepiments are confined to narrow interseptal loculi, and are frequently immersed in the trabecular tissue of the zone of great septal dilatation.

Variation. There are insufficient corallites available for a detailed study of variation; however, the available data show that for the plots of *Dt:Dc* and *n:Dc*, *P. boreensis* cannot be separated from *P. mesa*, except in so far as *n* and *Dc* have higher maxima. The major difference between the two species lies in the ratio L_2/Dc . For *P. mesa*, frequency curves for this ratio have a strong peak at 4.8 mm., and are moderately right-skewed (see text-fig. 21). For *P. boreensis* the mode of 6.8 mm. is not marked, being the peak of a broadly symmetrical curve.

Comparison. *P. boreensis* differs from *P. mesa* principally in its considerably greater degree of septal dilatation in the dissepimentarium. The minor septa are shorter, being invariably confined to the dissepimentarium; the tabulae are more variable, and generally do not form the extreme 'mesas' characteristic of *P. mesa*. Finally, the maximum diameter is greater. Besides *P. mesa*, *P. boreensis* is most readily distinguished from all other described species of *Peneckiella* by the great dilatation of its septa.

Known localities: Loc. BN-1.

Peneckiella minor (F. A. Römer) *kunthi* (Dames 1868)

1868 *Cyathophyllum kunthi* Dames, p. 699 (*vide* Flügel 1956, p. 360, and Rózkowska 1960 p. 29).

1960 *Peneckiella minor* (Römer) *kunthi* (Dames); Rózkowska, p. 29, figs. 20-29. Contains a complete synonymy.

Diagnosis. 'Phaceloid colony; corallites straight, covered by thick epitheca, locally touching. Diameter 2.5 to 4.8 mm. Number of septa ranging from 12×2 to 16×2 , only exceptionally 18×2 . Major septa long with bent axial ends, thick and zigzagged, within the dissepimentarium frequently carinate. Minor septa short. Double row of diversely shaped dissepiments (horizontal, horseshoe, sigmoidal, peneckielloid). Tabulae usually complete, horizontal or concave. Trabecular fans, trabeculae thick (0.08-0.16 mm.). Budding latero-thamnophylloid.' (Rózkowska 1960, p. 29.)

Peneckiella sp. cf. *minor kunthi* (Dames) sensu Rózkowska 1960

Plate 78, figs. 3a-c

Material. SU 11273, loc. BC-6.

Description. The available material consists of corallites irregularly scattered through a stromatoporoid; the corallum is probably dendroid. The corallites are initially ceratoid, later cylindrical, and show strong growth irregularities. Adults are about 4.5-5 mm. in diameter. The deep calix apparently has a rather narrow everted rim, steeply inclined sides, and a flat floor. Budding is apparently peripheral, the initial stage being marked by slight withdrawal of two or three adjacent septa from the periphery.

There are 34–36 strongly fusiform septa in adults. The major, sometimes more dilated than the minor, extend very unequally to the axis: some are about $\frac{3}{8} R$, while one or two meet or pass at the axis. The septa are attenuate in the tabularium. The minor septa end at the margin of the tabularium, at about $\frac{1}{2} R$. The septa are slightly wavy in the tabularium, and irregular or zigzag in the dissepimentarium, particularly peripherally. The sides of the septa may be rough, particularly in dilated portions, but carinae are not developed. The septal dilatation spreads over the dissepimental surfaces just outside the tabularium, forming an inner wall as in *Thanunophyllum*.

The trabeculae are arranged in nearly symmetrical phacellophyllid fans, but are always vertical or nearly so.

The tabularium, a little over $\frac{1}{2} Dc$, is composed of thin, generally complete tabulae. These are flat or a little irregular, and are partly supplemented periaxially by an intermittent series of axially inclined tabellae.

The dissepimentarium consists predominantly of sigmoidal dissepiments (see p. 555), with some peneckielloid and horseshoe dissepiments. In addition, there are occasional outer accessory dissepiments, and an intermittent series of inner accessory dissepiments, which are generally small and vertical.

Comparison. This specimen closely resembles the Polish species in the structure of the septa, tabularium, and dissepimentarium, but is slightly larger, with correspondingly more septa. It differs from *P. mesa* principally in having flat tabulae, supplemented periaxially by strongly inclined tabellae. *P. borensis* is larger, with shorter minor septa, and also differs in the structure of the tabularium.

Remarks. The Polish species is discussed further in conjunction with *P. mesa*. See text-figs. 16, 17, 19.

Known localities. BC–6.

Genus PHILLIPSASTREA d'Orbigny 1849

- 1849 *Phillipsastrea* d'Orbigny, p. 12 (*vide* Lang, Smith, and Thomas 1940, p. 99).
 1850 *Pachyphyllum* Milne-Edwards and Haime, p. lxxviii (*vide* Lang, Smith, and Thomas 1940, p. 92).
 1958 *Phillipsastrea* d'Orbigny; Schouppé, p. 234. Contains an extensive synonymy.
 1961 *Pachyphyllum* Edwards and Haime; Semenoff-Tian-Chansky, Lafuste, and Delga, p. 304.

Type species. *Astraea hennahi* Lonsdale 1840, p. 697 (*partim*—pl. 58, figs. 3–3b only); subsequent designation Milne-Edwards and Haime 1850, p. lxxi (*vide* Lang, Smith, and Thomas 1940, p. 99).

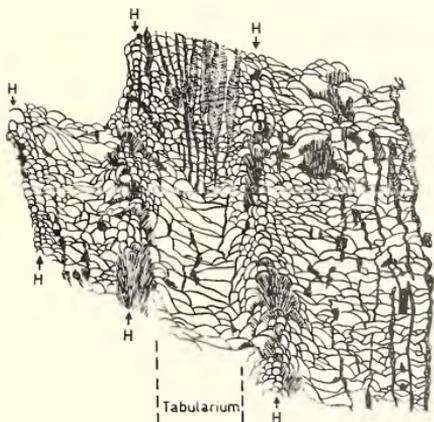
Diagnosis. Astracoid, thamnastracoid, or aphroid phacellophyllid.

Remarks. The lectotype of *P. hennahi* has recently been shown to possess a series of horseshoe dissepiments (Schouppé 1958, p. 234), and so *Phillipsastrea* becomes a senior synonym of *Pachyphyllum*.

As noted by Lang, Smith, and Thomas (1940, p. 99), much confusion has been caused by the invalid designation, by Milne-Edwards and Haime (1851, p. 173), of *Erismatolithus Madreporites radiatus* Martin 1809, as 'Exemple' of *Phillipsastrea*. That this confusion still exists is shown by the fact that this species is still quoted as 'type species' by Russian authors—e.g. Soshkina (1954, p. 46) and Bulvankar (1958, p. 118).

Phillipsastrea oculoides Hill 1942

Plate 73, fig. 7; text-fig. 22

1942c *Phillipsastraea oculoides* Hill, p. 186, pl. 6, fig. 9. Wellington, N.S.W.; Garra Fm., Emsian ?*Holotype*. SU 5281, loc. MM-10.*Diagnosis*. Partly aphroid *Phillipsastrea* with short major septa; septa strongly dilated around tabularium; tabulae complete and incomplete, gently concave.

TEXT-FIG. 22. Longitudinal section of *Phillipsastrea oculoides* Hill, $\times 4$. Traced from photograph of holotype, SU 5281.

Description. The type (and only) specimen is poorly preserved. Additional longitudinal sections have been made, and so the following comments may be added to Hill's description.

(1) There are one or two series of elongate, steeply axially inclined dissepiments inside the series of horseshoe dissepiments.

(2) The dissepiments between tabularia are very irregular in size, but those near the horseshoe dissepiments are frequently very small.

(3) The tabular floors are gently sagging, with somewhat upturned edges; the tabulae are both complete and incomplete, and vary from sagging to moderately domed.

(4) In transverse section, the septal dilatation around the tabularium may be in a single zone 3 mm. wide, or may divide into two narrow zones on either side of the series of horseshoe dissepiments.

Comparison. *P. oculoides* resembles *P. ibergense* (F. A. Römer) in its short major septa dilated around the tabularium, but differs in having more septa, and a partly aphroid corallum. In the latter character it resembles *P. ibergense* var. *progressa* Rózkowska 1953, which however is smaller. Both of these species are from the Frasnian of Poland (Rózkowska 1953).

Known localities. MM-10.

FOSSIL LOCALITIES CITED

The numbers given to localities are those used during field-work, and do not form part of any locality numbering system of the Department of Geology, University of Sydney; an extended list may be found in Strusz (1963). Numbers were allotted according to parishes, being consecutive within each parish, and included a letter prefix indicating the appropriate parish.

In the following list, the localities are listed alphabetically by parishes. In each case, the exact location is given: (a) by reference to portion numbers; (b) by reference to the Dubbo (SI 55-4) and Bathurst (SI 55-8) 1: 250,000 topographic sheets, with grid references to the nearest 100 yards; and (c) by nearby geographic features. In addition, the lithology from which the specimens were collected is given.

Parish Boree Cabonne, co. Ashburnham.

BC-6: portion 70 (north side, centre); grid reference 1796.8890 (Bathurst sheet); in Mousehole Ck., 1810 yds. along creek, east from Orange-Parkes road. 'Rubbly' limestone (thinly interbedded calcarenite and shale.)

Parish Bell, co. Ashburnham.

Be-10: portion 81 (north-west corner), 75 yds. east of portion 62, and near portion 82; grid ref. 1749.9103 (Bathurst); in gully. Coarse calcirudite.

Parish Boree Nyrang, co. Ashburnham.

BN-1: portion 222 (south-west sector), 170 yds. north of portion 201, and 380 yds. west of portion 111; grid ref. 1796.8956 (Bathurst); in Walkers Ck., east of road. Coarse calcirudite.

BN-2: junction of portions 4, 9, and 120; grid ref. 1803.8928 (Bathurst); west bank of Walkers Ck., just west of road bridge. Calcarenite (biostromal?).

Parish Curra, co. Gordon.

Cr-4: portion 171 (east side), extending into south-west corner of portion 153, parish Gundy, co. Gordon; grid ref. 1837.9680 (Dubbo); in bed, and on east bank, of Curra Ck. Fine calcarenite.

Cr-12: portion 90 (south-west corner); grid ref. 1823.9674 (Dubbo); Curra Ck. 'Rubbly' limestone.

Cr-36b: portion 173, just west of portion 112, and 150 yds. south of portion 172; grid ref. 1836.9672 (Dubbo); near gully, south of Wellington-Parkes road. Calcarenite.

Cr-42: boundary between portions 175 and 176, 160 yds. west of portion 89; grid ref. 1833.9661 (Dubbo); pile of 'floaters' collected from nearby area, beside fence, just south-west of bend in gully. All the floaters are calcarenite.

Cr-46: portion 59 (south-west sector), 110 yds. north of portion 83, and 280 yds. east of portion 74; grid ref. 1818.9575 (Dubbo). Calcarenite.

Cr-54: portion 172 (south-west sector), 208 yds. north-east of junction, portions 166, 167, 172, 173; grid ref. 1833.9673 (Dubbo); south bank of road cutting, Wellington-Parkes road. Hill's (1942c) 'Fingerpost' locality. 'Rubbly' limestone.

Cr-94: portion 39, just north of boundary with portion 1, and 570 yds. west of the Bell River; grid ref. 1868.9641 (Dubbo); hillside west of road. Biostromal limestone (coralline)—same horizon as locs. Cr-100, -111, -113, and BR¹/177, and probably as P-26, -43.

Cr-100: portion 80, 5 yds. west of portion 6, and 70 yds. north of boundary between portions 6 and 13; grid ref. 1864.9625 (Dubbo); hillside west of road. Coralline biostrome.

Cr-106: boundary between portions 10 and 80, 70 yds. west of junction with portion 9; grid ref. 1861.9614 (Dubbo); west of road, west bank of Bell R. Black foetid fossiliferous pellet calcarenite.

Cr-111: portion 111 (southern end), 70 yds. north of portion 39, and 180 yds. west of Bell R.; grid ref. 1870.9646 (Dubbo). Coralline biostrome.

Cr-113: portion 50 (southern end); grid ref. c. 1871.9651; west bank of Bell R. Coralline biostrome.

Parish Catombal, co. Gordon.

Ct-18: portion 45 (north-west sector), c. 100 yds. east of portion 38; grid ref. 1755.9444 (Dubbo); in gully, a tributary of Back Ck. Pink crinoidal/coralline biostrome.

- Ct-28: portion 40 (south-west corner), c. 30 yds. east of junction with portions 30, 45; grid ref. 1747.9437 (Dubbo); Yellow biostromal limestone; same horizon as loc. Ct-18.
- Ct-40: portion 125 (east side), 200 yds. due west from portion 48; grid ref. 1761.9417 (Dubbo); north bank of Sawpit Gully (tributary of Loombah Ck.), c. 1,000 yds. north-east of road crossing. 'Rubbly' limestone (biostromal?).
- Ct-53: portion 58 (north side, centre), midway between portions 77 and 79; grid ref. 1767.9391 (Dubbo); south bank of Loombah Ck., extending over the interval 75-200 yds. north of road. Coralline/brachiopodal biostrome.
- Ct-64: portion 65 (east centre), just west of boundary with portion 14, and 250 yds. south of portion 58; grid ref. 1771.9373 (Dubbo). Coralline biostrome.

Parish Eurimbula, co. Gordon.

- E-16: portion 123 (west side), extending for 70 yds. east of portion 70, and 90-280 yds. north of portions 13 and 52; grid ref. c. 1765.9240 (Dubbo). 'Rubbly' limestone.
- E-21: portion 57, 580 yds. south of portion 27; grid ref. c. 1787.9280 (Dubbo); in gully, 400 yds. east of road. 'Rubbly' limestone; same horizon as loc. E-16.

Parish Geurie, co. Lincoln.

- Ge-3: portion 210 (north-east corner); grid ref. 1777.9896 (Dubbo); south bank of road cutting, Mitchell Highway, on either side of mile-post 12 miles north-west of Wellington. Hill's (1942c, p. 183) locality 'Wellington-Dubbo Road near Geurie, 12 miles from Wellington'. Calcarenite and calcilitite.

Parish Gundy, co. Gordon.

- Gn-10: portion 132 (south-east sector), 60 yds. west of portion 115; grid ref. 1830.9644 (Dubbo); 600 yds. north of road. 'Rubbly' limestone.
- Gn-20: portion 30 (north-west corner); grid ref. c. 1795.9699 (Dubbo); south side of Wellington-Parkes road, c. 900 yds. east of Suntop Public School. Calcarenite (biostromal?).

Parish Micky Mulga, co. Gordon.

- MM-6: portion 35 (west), 35 yds. east of portion 36; grid ref. 1811.9812 (Dubbo); in gully, 100 yds. west of minor access track, and c. 1,100 yds. south of access road to 'The Holmes' homestead. Calcarenite.
- MM-10: boundary of portions 60 and 247, c. 500 yds. west of portion 208; grid ref. 1810.9863 (Dubbo); outcrop extends south from fence (portion 60), 200 yds. towards road. Hill's (1942c) locality 'Portion 247, north of road'. Calcarenite, in a succession of unfossiliferous calcilitites and pellet calcarenites.

Parish Ponto, co. Gordon.

- P-13: boundary of Water Reserve 33680 and portion 142, 590 yds. north of portion 131, parish Gundy; grid ref. 1821.9740 (Dubbo). Poorly fossiliferous silty calcarenite.
- P-26: portion 142 (centre), c. 530 yds. south of portion 104; grid ref. 1819.9761 (Dubbo); south of gully, and 570 yds. due east of road. Coralline biostrome.
- P-43: portion 103 (west side); grid ref. c. 1818.9786 (Dubbo); hillside east of 'Macquarie Park' homestead and outbuildings. Complex of thin coralline, bryozoan, and brachiopodal biostromes, calcarenites, lenticular pellet calcarenites, and quartzose arenites and lutites. Same horizon as loc. P-26, and probably as the Cr-100 biostrome.

Measured Sections

Disphylloid corals are herein described from two localities along measured sections, full details of which may be found in Strusz (1963). The two localities are:

- BR¹/177: 177 ft. west from start of section BR¹ (a marked tree c. 20 yds. west of the Bell R.); section measured along gully, southern edge of portion 50, parish Curra. This locality is just south of loc. Cr-113, and on the same horizon.
- CAT/255: 255 ft. east from start of section CAT (marked point on east side of base of a pair of wheat silos, 'Catombal' property, portion 29, parish Catombal); section measured east across fields. Olive-grey calcarenite.

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OERTLIANA, A NEW OSTRACOD GENUS FROM THE UPPER JURASSIC OF NORTH-WEST EUROPE

by T. I. KILENYI

ABSTRACT. A new genus of the family Cytherideidae is established under the name *Oertliana*; four species of the genus are described and their stratigraphical range in north-west Europe is examined.

IN 1955 G. Schmidt, describing the Upper Jurassic ostracods of north-west Germany, mentioned an ovoid-shaped ostracod with a rather simple hinge structure as Ostracod 102. In 1957 Oertli found a similar form in the Lower Kimmeridgian of the Paris Basin and recognized it as a hitherto unknown genus of the family Cytherideidae. The preservation of his specimens, however, made it impossible to establish a new genus as most of the internal features were unknown. The study of the ostracods of the Kimmeridge Clay type section in Dorset yielded specimens of this form in excellent preservation and the establishment of the genus became possible. So far four species of the genus *Oertliana* are known from the Upper Jurassic of north-west Europe; *O. kimmeridgensis* occurs in the Lower Kimmeridgian of Dorset and the Paris Basin, *Oertliana* sp. 1. was found in the Upper Kimmeridgian of Dorset. Of the remaining two species *O.* sp. 2 occurs in the Kimmeridgian of north-west Germany and *O.* sp. 3 in the Purbeck of southern Sweden.

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Abbreviations. In giving the dimensions of ostracod valves the following abbreviations are used throughout the text: *L*, length; *H*, height; *W*, width; *Hi*, hinge length; *M/a*, width of anterior margin. Dimensions are given in millimetres.

Repository. All the figured and described specimens are stored in the Geology Department of the University of Hull. The specimen numbers are indicated by the prefix HU.

SYSTEMATIC DESCRIPTIONS

Subclass OSTRACODA Latreille 1806

Order PODOCOPIDA Müller 1894

Suborder PODOCOPINA Sars 1866

Superfamily CYTHERACEA Baird 1850

Family CYTHERIDEIDAE Sars 1925

Subfamily unknown

Genus OERTLIANA gen. nov.

Type species. *Oertliana kimmeridgensis* sp. nov.

Diagnosis. Carapace almost elliptical in side view, anterior end slightly more rounded than posterior. Surface smooth or finely punctate. Hinge adont, consisting of a faint

curved ridge on the right valve and a corresponding groove on the left. Muscle scar pattern consists of a vertical row of four equally sized scars with one anterior scar that is larger than the other four. Stratigraphical range: Upper Jurassic, Kimmeridgian-Purbeckian.

Oertliana kimmeridgensis sp. nov.

Plate 79, figs. 1-12; text-fig. 1

1957 *Cytherideinarum?* sp. 1. Oertli, p. 661, pl. 3, figs. 86-91.

Holotype. A female left valve, HU 2.J.1.31. *Paratypes*. 100 valves and carapaces, HU 3.J.29.1-100.

Derivatio nominis. From typical horizon.

Stratum typicum. *Rasenia mutabilis* Zone, Lower Kimmeridgian.

Locus typicus. Black Head, Dorset.

Diagnosis. Carapace elliptical, anterior end rounded, posterior slightly pointed. Valves subequal, left being slightly larger. Surface of valves finely punctate. Radial pore canals relatively thick in the middle, narrowing suddenly near both ends. Sexual dimorphism strong.

<i>Measurements</i> .	<i>L</i>	<i>H</i>	<i>W</i>	<i>Hi</i>	<i>M/a</i>
Holotype	0.38	0.21	0.08	0.20	0.03
♀ Left valve	0.36-0.38	0.20-0.21	0.08	0.20	0.03
♀ Right valve	0.35-0.37	0.18-0.20	0.07	0.20	0.03
♂ Left valve	0.43-0.45	0.21-0.23	0.08	0.25	0.04
♂ Right valve	0.43-0.45	0.20-0.22	0.07	0.25	0.03

Description. Carapace elongate, elliptical. Left valve slightly larger than the right, with a slight overlap ventrally and dorsally. In dorsal view the carapace is lanceolate, the greatest width being at the middle in the females and somewhat nearer to the posterior end in the males. In side view the two valves are similar, although the right one is less high. The greatest height is at mid-point. The anterior end is rounded, the ventral and dorsal margins straight, running approximately parallel. The posterior end is slightly angular, more so in the right valve, where the postero-dorsal margin is straight and not rounded as in the left valve. Sexual dimorphism is pronounced, the males being much longer than the females. Their shape is essentially the same, but often the ventral margin of the male valve is slightly concave in the middle.

The surface of the valve is finely punctate. This ornamentation is strongest on the central part of the valve and disappears gradually towards the peripheral regions. It is connected with the finer structure of the shell, which in transmitted light seems to be perforated by irregularly spaced cavities. The size of these cavities decreases towards the periphery of the valve. The normal pore canals are few.

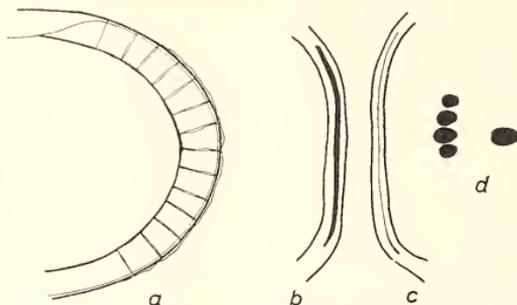
The duplicature is bilamellar. The inner lamella is moderately wide on the anterior, and narrow on the posterior part of the valve. Inner margin and line of concrescence coincide, the selvage is faint, but is better developed on the ventral parts, where it forms a fairly wide selvage lip. The radial pore canals are straight and simple. They are widest at their middle, narrowing suddenly at the ends. They number between ten and fifteen on the anterior margin.

The hinge is adont and rather weakly developed. It consists of a curved ridge on the right valve and a corresponding shallow groove on the opposite valve.

The muscle scar pattern consists of a slightly oblique row of four circular and equally sized scars. There seems to be only one anterior scar, which is larger than the others and lies in line with the second and third scars in the row.

Occurrence. *R. mutabilis* Zone, Lower Kimmeridgian, in Dorset and from the 'Lower Kimmeridgian' of the Paris Basin.

Remarks. The genus *Oertliana* does not seem to fit into any of the subfamilies of the family Cytherideidae, due to its primitive adont hinge. The muscle scars, however, are without doubt typical of the Cytherideidea.



TEXT-FIG. 1. *Oertliana kimmeridgensis* gen. et sp. nov. *a*, Anterior margin, male left valve, $\times 200$. *b*, Hinge margin, left valve, $\times 120$. *c*, Hinge margin, right valve, $\times 120$. *d*, Muscle scars, left valve, $\times 375$.

Oertliana sp. 1

Plate 79, figs. 13-16

Material. 39 valves, HU 2.J.34.1-39.

Measurements.

	<i>L</i>	<i>H</i>	<i>Hi</i>
Left valve	0.45	0.24	0.38
Right valve	0.44	0.23	0.38

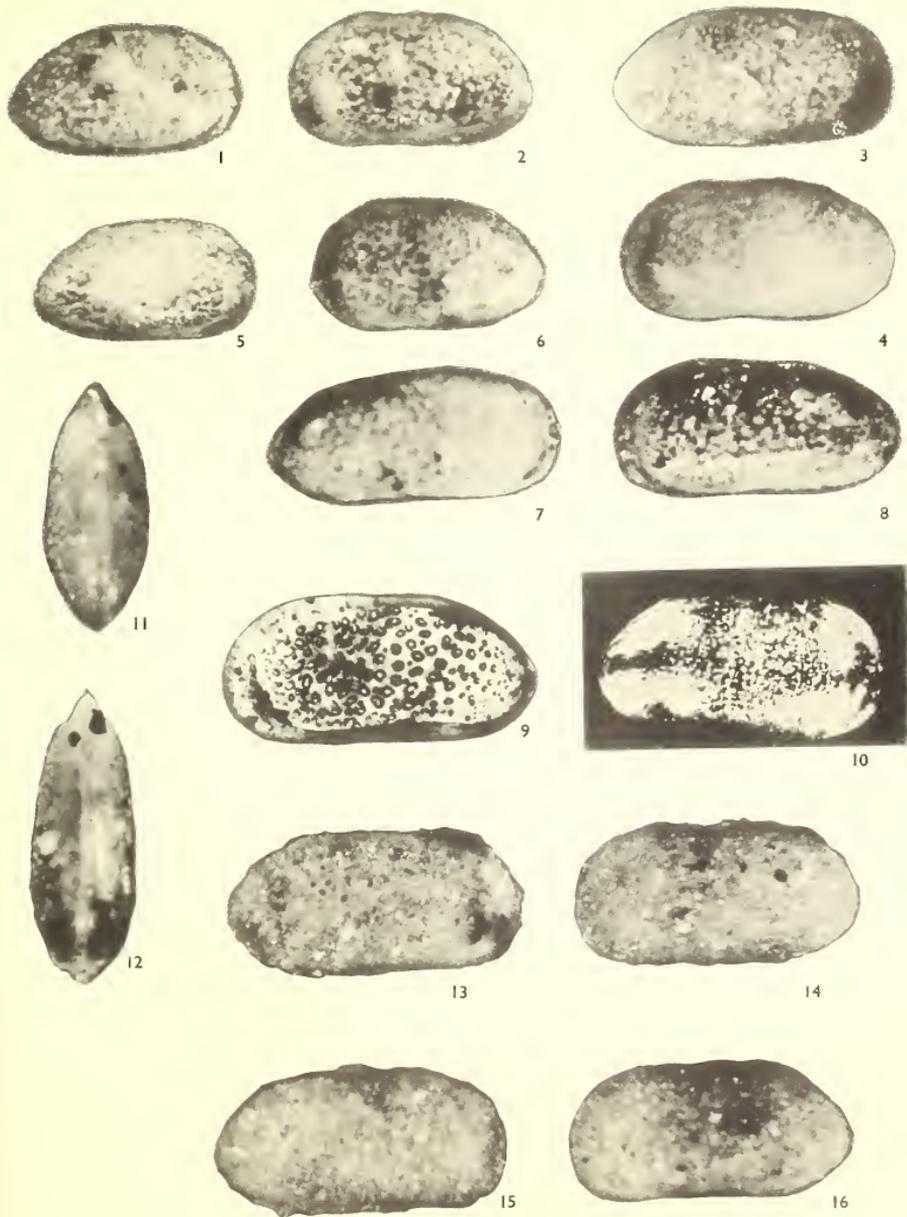
EXPLANATION OF PLATE 79

Figs. 1-12. *Oertliana kimmeridgensis* sp. nov., *Rasenia mutabilis* Zone, Lower Kimmeridgian.

- 1, Right valve, female, external view, HU 3.J.29.2, $\times 100$. 2, Left valve, female, external view, Holotype, HU 2.J.31.1, $\times 100$. 3, Right valve, male, external view, HU 3.J.29.6, $\times 100$. 4, Left valve, male, external view, HU 3.J.29.7, $\times 100$. 5, Right valve, female, external view, HU 3.J.29.3, $\times 100$. 6, Left valve, female, external view, HU 3.J.29.4, $\times 100$. 7, Right valve, male, external view, HU 3.J.29.17, $\times 100$. 8, Left valve, male, external view, HU 3.J.29.2, $\times 100$. 9, Right valve, male, transmitted light, HU 3.J.29.15, $\times 110$. 10, Left valve, male, polarized light, HU 3.J.29.16, $\times 110$. 11, Carapace, male, dorsal view, HU 3.J.29.9-10, $\times 100$. 12, Carapace, female, dorsal view, HU 3.J.29.11-12, $\times 100$.

Figs. 13-16. *Oertliana* sp. 1, *Pavlovia rotunda* Zone, Upper Kimmeridgian.

- 13, Right valve, female?, external view, HU 2.J.34.3, $\times 100$. 14, Left valve, female?, external view, HU 2.J.34.2, $\times 100$. 15, Right valve, male?, external view, HU 2.J.34.1, $\times 100$. 16, Left valve, male?, external view, HU 2.J.34.3, $\times 100$.



KILENYI, Upper Jurassic ostracod

Description. Carapace elongate, almost oblong shaped. The two valves are equal in size. Anterior end rounded, posterior slightly pointed. Dorsal margin straight and parallel to ventral margin, which is straight or gently concave. The surface of the valve is very finely punctate, almost smooth. There is no eye depression.

Little of the interior of the valve could be observed because of the bad state of preservation. The inner lamella seems to be rather broad, and the inner margin and line of

	OERTLIANA KIMMERIDGENSIS	OERTLIANA sp.1	OERTLIANA sp.2	OERTLIANA sp.3
PURBECK				?
PORTLAND				
UPPER KIMMERIDGE				
MIDDLE KIMMERIDGE				
LOWER KIMMERIDGE				

TEXT-FIG. 2. The stratigraphical distribution of species of *Oertliana* gen. nov. in north-west Europe.

concrecence probably coincide. The selvage lip is developed on both valves. The hinge is adont; a ridge on the right valve and a corresponding groove on the left. Sexual dimorphism is doubtful.

Occurrence. *Pavlovia rotunda* Zone, Upper Kimmeridgian, Chapmans Pool, Dorset.

Remarks. The muscle scars could not be observed owing to the rather bad preservation, but similarity in shape, hinge, and duplicature with *O. kimmeridgensis* makes it certain that this is a species of *Oertliana*.

Oertliana sp. 2

1955 Ostracod 102, Schmidt, p. 62, pl. 3a, figs. 39, 40.

Measurements. *L.*, 0.45; *H.*, 0.24.

Remarks. Ovoid carapace with very finely punctate surface. The left valve is larger than the right. Hinge adont.

Occurrence. *Oertliana* sp. 2 was described by Schmidt (1955) from boreholes in north-west Germany ranging from the 'Middle Kimmeridgian' to the top of the 'Gigas Schichten', almost the whole of the Kimmeridgian (in the English sense). It occurs both in marine and in brackish sediments. *Oertliana* sp. 2 closely resembles *O. kimmeridgensis* sp. nov., but in side view it appears much more rounded at the cardinal angles. Sexual dimorphism, which is strong in *O. kimmeridgensis*, seems to be absent.

Oertliana sp. 3

1961 *Cytherideinarum* sp. 2, Oertli, Brotzen, and Bartenstein, p. 13, pl. 1, figs. 3a, b.

Measurements. L, 0.45-0.47; H, 0.26-0.28.

Remarks. Bean-shaped carapace in side view, surface distinctly punctate, anterior and posterior end well rounded.

Occurrence. From a borehole at Landskrona (Hilleshog), southern Sweden. The horizon is given by Oertli, Brotzen, and Bartenstein (1961) as Wealden. According to their correlation this is the equivalent horizon to the middle Purbeck in English stratigraphy. The environment is marine-brackish. As the material is rather poorly preserved only the external characteristics are known. *Oertliana* sp. 3 differs from the other species of the genus in its much higher shell.

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PALAEONTOLOGY

VOLUME 8 · PART 3

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TRILOBITES FROM THE ALBANY DIVISION (ORDOVICIAN) OF THE GIRVAN DISTRICT, AYRSHIRE

by RONALD PEARSON TRIPP

ABSTRACT. Two new genera, and nine new species of trilobites from the Albany mudstones with nodular limestones, east of Doularg, near Girvan, are described. The fauna is most closely allied to that of the *superstes* Mudstones, Aldons, having twenty-two of twenty-five genera in common, and fourteen species closely related. Outside the district the closest resemblance is to the lower Edinburg Formation (Porterfield Stage) of the Appalachian Valley of the U.S.A.

THE trilobites are from the Albany mudstones with nodular limestones, exposed in a stream section, 950 yards east-north-east of Doularg Farm, Stinchar Valley, Girvan (Nat. Grid Ref. NX 269929). Correlation with the mixed shelly-graptolitic facies of the Lower Barr Series indicates that the fossiliferous member of the Albany mudstones is basal Caradoc (within the *Nemagraptus gracilis* zone): but the trilobite fauna *per se* is best compared with those typical of the Porterfield Stage of the standard Ordovician for NE. America. The exposure was discovered by Professor Alwyn Williams in the course of his field work in the district, and has been described by him (Williams 1962, pp. 45-47). I am greatly indebted to Professor Alwyn Williams for showing me the locality. Sincere thanks are also due to Dr. John Temple and Professor H. B. Whittington for help in the preparation of this paper.

The terminology is essentially that adopted in the Treatise on Invertebrate Paleontology, Part O. Almost all the specimens are preserved as internal and external moulds. All the specimens were collected by the author; the type and figured specimens have been presented to the Hunterian Museum, Glasgow University.

The following is a list of the species recorded in this paper:

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SYSTEMATIC DESCRIPTIONS

Family GERAGNOSTIDAE Howell 1935

Genus TRINODUS M'Coy 1846

Trinodus doulargensis sp. nov.

Plate 80, figs. 1-4

Diagnosis. Convexity moderately strong. Glabella two-thirds length of cephalon, parallel sided for most of its length; glabellar tubercle and furrows lacking. Posterior borders produced backwards into short spines. Surface smooth.

Holotype. A. 5830a, b (cephalon). Plate 80, figs. 1a, b.

Other material. One cephalon, one thoracic segment, three pygidia.

Dimensions of holotype (in mm.).

Length of cephalon	2.2
Maximum width of cephalon (est.)	2.1
Length of glabella	1.5
Maximum width of glabella	0.9

Description. Cephalon narrowly rounded, as wide as long. Glabella parallel sided for most of its length, two-thirds length of cephalon, moderately convex; glabellar tubercle and furrows lacking. Basal lobes small, triangular, not touching mesially. Axial and preglabellar furrows deep and broad. Cheeks convex, uniformly narrow. Border moderately wide and convex, narrowing out towards back. Border furrow well defined. Posterior borders swollen, produced backwards into short triangular genal spines. Surface smooth.

Thoracic segment with axis occupying three-quarters total width. Median lobe twice as wide posteriorly as anteriorly. Oval lateral lobes approximately one-third width of axis, their long axes inclined inwards and forwards, strongly demarcated. Axial furrows deep and broad. Pleurae narrow (tr.), longitudinally truncate, weakly swollen; anterior and posterior lobes scarcely developed.

Pygidium subquadrate. Articulating half-ring and pleural facets well developed. Axis slightly less than half length of pygidium. First ring short, with small, oval lateral lobes. Second ring long; elongate median lobe rising steeply towards back to form a rounded node. Terminal piece about one-third length of axis. Axial furrows deep and broad. Pleural lobes convex, narrowing towards front. Border weakly convex, extremely wide posteriorly particularly opposite the pair of small lateral spines. Border furrow well defined. Surface smooth.

Remarks. *T. doulargensis* bears a close resemblance to *T. elspethi* (Raymond) (see Cooper 1953, pp. 7-8, pl. 1, figs. 1-12) from the Edinburg Formation, in all parts. The glabella is more parallel sided and lacks the median tubercle, the pygidium has a broader axis and border, and the dorsal exoskeleton is smooth, not granular.

Trinodus sp.

Plate 80, figs. 5-7

Material. Two cephalata, two pygidia.

Description. Glabella moderately long, narrowing slowly forwards; glabellar tubercle and furrows lacking. Basal lobes small, sloping steeply backwards. Axial and preglabellar furrows moderately deep. Border narrows out towards back. Posterior borders strongly swollen, widening (exs.) laterally, not produced backwards as spines. Surface smooth.

Axis slightly less than half length of pygidium, strongly swollen. Two rings, subequal in length, occupy slightly more than half length of axis. First ring with large, well-defined lateral lobes. Elongate median tubercle on second ring rises towards back. Axial furrows moderately deep. Pleural lobes of uniform width. Border wide posteriorly. A pair of oblique ridges cross border at postero-lateral angles, produced into short, broad-based spines. Surface smooth.

Remarks. The cranium figured lacks glabellar tubercles and furrows and appears to be referable to *Trinodus*; it differs from the foregoing species in the shape of the glabella and absence of fixigenal spines. The long axis of the pygidium suggests reference to *Geragnostus* rather than *Trinodus*. However, it may be closely compared with *Trinodus* sp. from the Ashgillian of Poland (Kielan 1959, p. 62, pl. 1, fig. 5, text-fig. 14).

Family KOMASPIDIDAE Kobayashi 1935

Genus CARRICKIA gen. nov.

Diagnosis. Glabella subquadrate, weakly convex; lateral glabellar furrows absent. Preglabellar field short. Anterior border wide (tr.). Palpebral lobes narrow, depressed, two-thirds length of glabella, reaching almost to back of cheeks.

Type species. *Carrickia pelagia* sp. nov.

Remarks. So far as is known the genus is monotypic. The genus is referred to the Family Komaspidae on account of the long palpebral lobes, wide fixed cheeks, and short preglabellar field. Both cranium and pygidium bear a general resemblance to *Gonio-phrys prima* Ross (1951, pp. 81-82, pl. 18, figs. 9, 15, 17-20, 22, 27) from the Garden City Formation, but the new form differs conspicuously in the broader, less convex, glabella, and transversely wider anterior border. In the aforementioned features, *Carrickia* bears a resemblance to the dimeropygid *Chomatopyge* Whittington and Evitt (1954, pp. 49-53)

from the Lincolnshire and Edinburg Limestones, but the length of the palpebral lobes, short preglabellar field, absence of median preglabellar pit, and the conspicuously distinctive pygidium preclude affiliation with this genus.

Carrickia pelagia gen. et sp. nov.

Plate 81, figs. 17-21

Diagnosis. As for genus.

Holotype. A. 5878 (cranium). Plate 81, figs. 17a-c.

Paratype. A. 5882 (pygidium).

Other material. Fourteen cranidia, nine pygidia.

Material from other horizons. Cranidia from the platy upper Stinchar Limestone, and from the *superstes* Mudstones, Aldons.

<i>Dimensions</i> (in mm.).	<i>Holotype</i>	<i>A. 5880</i>
Length of cranium (sag.)	3.4	2.3
Length of glabella	2.4	1.7
Width of glabella	3.2	2.0

EXPLANATION OF PLATE 80

All the figured specimens are from the Albany mudstones with nodular limestones, 950 yards east-north-east of Doularg Farm, Stinchar Valley, Girvan; they have been deposited in the Hunterian Museum, Glasgow. The photographs are of internal moulds unless otherwise stated; the specimens were coated with ammonium chloride before being photographed.

Figs. 1-4. *Trinodus doulargensis* sp. nov. 1a, b, Cephalon (holotype A. 5830b). Latex cast from external mould. Dorsal and oblique lateral views, $\times 10$. 2, Thoracic segment (A. 5831). Latex cast from external mould, $\times 10$. 3, Pygidium (A. 5832). Latex cast from external mould, $\times 8$. 4, Pygidium (A. 5833b). External mould, $\times 8$.

Figs. 5-7. *Trinodus* sp. 5, Cranium (A. 5834b). External mould, $\times 8$. 6, Pygidium (A. 5835a), $\times 10$. 7, Pygidium (A. 5836b). External mould, $\times 10$.

Figs. 8, 9, 17. *Remopleurides* sp. A. 8, Left free cheek (A. 5837). Lateral view showing doublure, $\times 4$. 9, Right free cheek (A. 5838a), showing vincular ledge and ridge on doublure, $\times 4$. 17, Hypostome (A. 5839b). External mould, $\times 8$.

Figs. 10, 11. *Remopleurides* sp. B. 10, Left free cheek (A. 5840) $\times 5$. 11, Right free cheek (A. 5841). External mould showing raised lines, $\times 10$.

Figs. 12-15. *Remopleurides* sp. C. 12, Small cranium (A. 5842), $\times 8$. 13, Right free cheek (A. 5843), $\times 6$. 14, Hypostome (A. 5844), $\times 8$. 15, Pygidium (A. 5845), $\times 8$.

Fig. 16. *Hypodiceranotus* sp. Left free cheek (A. 5846b). Latex cast from external mould, $\times 8$.

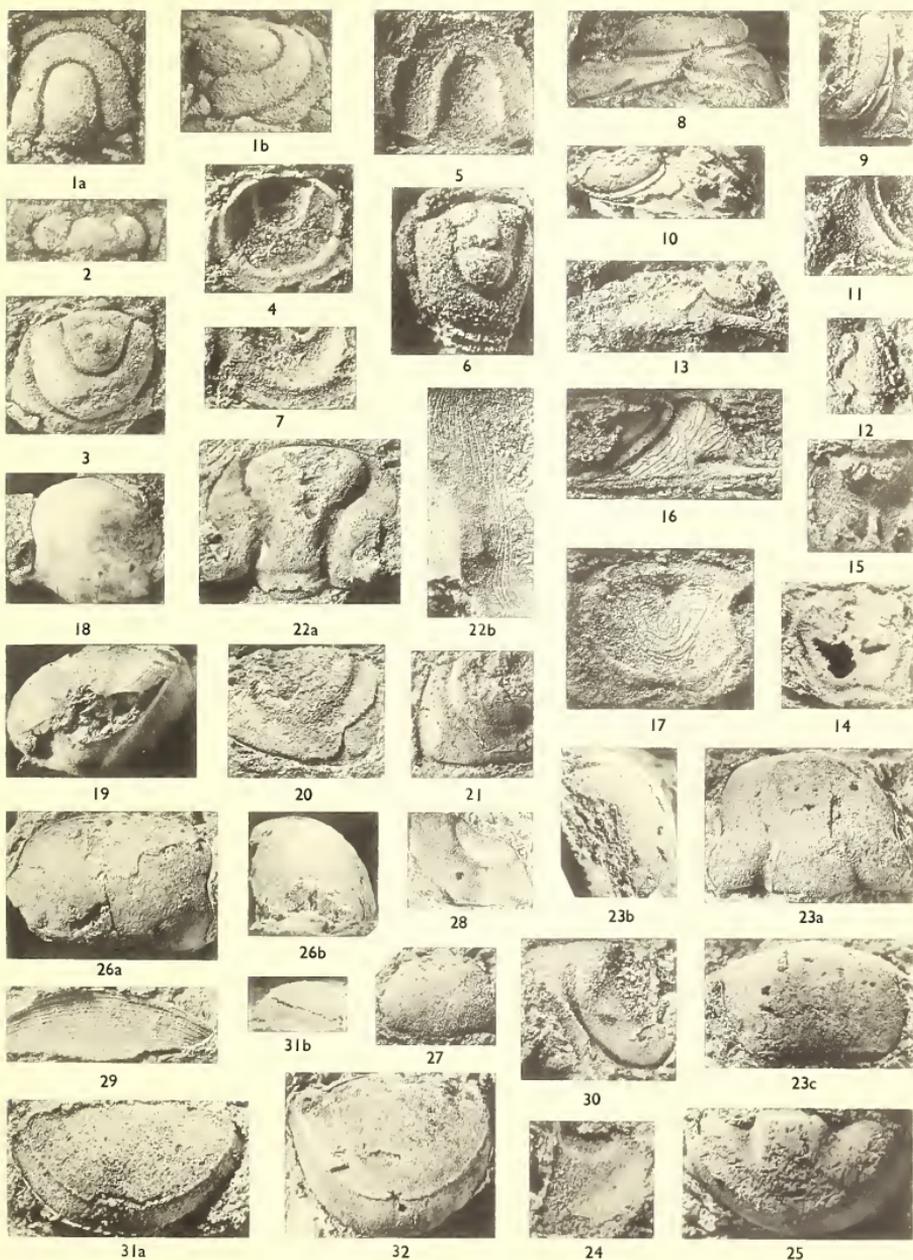
Figs. 18, 19. *Isotelus* sp. 18, Cranium (A. 5847). Oblique lateral view, showing elevated palpebral lobe, $\times 1$. 19, Pygidium (A. 5848), with doublure exposed, $\times 1$.

Figs. 20, 21. *Nileus* sp. 20, Left free cheek (A. 5849), $\times 5$. 21, Left free cheek (5850a) belonging to an individual with a shorter cephalon, $\times 5$.

Figs. 22a, b. *Raymondaspis* sp. 22a, Cranium (A. 5851a), $\times 4$. 22b, The same, external mould (A. 5851b), showing raised lines on glabella, and right basal lateral furrows, $\times 8$.

Figs. 23-25. *Illaeus* sp. 23a-c, Cranium (A. 5852a). Dorsal, lateral, and frontal views, $\times 4$. 24, Left free cheek (A. 5853). External mould, $\times 10$. 25, Pygidium (A. 5854a), $\times 5$.

Figs. 26-32. *Bumastoides scoticus* sp. nov. 26a, b, Cranium (A. 5855a). Dorsal and lateral views, $\times 3$. 27, Small cranium (A. 5856), $\times 6$. 28, Right free cheek (A. 5857), $\times 6$. 29, Rostral plate (A. 5858b). External mould, $\times 5$. 30, Hypostome (A. 5859), probably belonging to this species. External mould. Oblique lateral view showing left anterior wing with longitudinal raised lines, $\times 10$. 31a, Pygidium (holotype, A. 5860a). Dorsal view, $\times 7$. 31b, The same. Lateral view, $\times 5$. 32, Elongate pygidium (A. 5861a), $\times 4$.



Description. Cranium broadly rounded anteriorly, moderately convex in both directions. Glabella subquadrate, broadly rounded anteriorly, moderately convex. Lateral glabellar lobes and furrows absent. Occipital ring little longer mesially than laterally. Occipital furrow transverse but sinuous, deep, narrower than axial furrows. Preglabellar and axial furrows continuous, moderately deep and narrow. Preglabellar field short laterally, usually narrowing out mesially, weakly convex, continuous with fixed cheeks. Anterior border much wider (tr.) than glabella, of uniform length, rolled. Anterior border furrow broad. Fixed cheeks gentle convex, widening steadily towards back, sloping away from glabella. Palpebral lobes narrow, depressed, weakly rounded in outline, two-thirds length of glabella, reaching almost to back of fixed cheeks, posterior extremities much further apart than anterior extremities. Palpebral furrows broad, with outer wall lower than inner. Posterior borders convex, expanding little laterally. Posterior border furrows deep and broad, widening laterally. Anterior branches of facial sutures curve forwards and slightly inwards; posterior branches short, directed backwards and outwards. Surface smooth; glabella, occipital ring, and inner areas of fixed cheeks shallowly pitted.

Pygidium elliptical in outline, strongly convex in both directions. Axis occupies more than half anterior width, transverse curvature slightly greater than that of pygidium, broad and undefined posteriorly; articulating half ring and two rings well defined, bowed backwards, terminal piece with strong independent convexity. Axial furrows sharp, bowed outwards alongside rings and terminal piece, flaring posteriorly and dying out before reaching margin. Two pairs of pleurae; interpleural furrows sharp, extending to margin; pleural furrows oblique, deep. Surface finely granular.

Remarks. The diagnostic characters of the genus clearly distinguish this form. The pygidia described are attributed to this species mainly on the grounds of comparable frequency, but they are appropriate to the family.

Family REMOPLEURIDIDAE Hawle and Corda 1847

Genus REMOPLEURIDES Portlock 1843

Remopleurides sp. A

Plate 80, figs. 8, 9, 17

Material. Eight free cheeks, three hypostomes.

Remarks. These free cheeks and hypostomes closely resemble a form which occurs in the *confinis* Flags (Tripp 1962, pp. 4-5, pl. 1, figs. 10-14), the Stinchar Limestone, and the *superstes* Mudstones. The free cheeks differ in lacking the posterior border furrow, in their non-striate surface, and in the presence of an oblique ridge on the doublure, tangential to the vincular ledge which is situated further back (Pl. 80, fig. 9). The hypostome is narrower posteriorly, and the anterior boss is more prominent.

Remopleurides sp. B.

Plate 80, figs. 10, 11

Material. Two free cheeks, one pygidium.

Description. Free cheek moderately wide posteriorly; librigenal spine straight, slender,

moderately long; subgenal notch extends half-way across border. Surface with moderately spaced raised lines.

Pygidium elongate, with axis defined only by independent convexity. Pleurae fused except for two pairs of free points on posterior margin, outer pair extending slightly further backwards than inner pair.

Remarks. An allied species occurs in the *superstes* Mudstones, Aldons. The affinities of these two forms are with *R. caelatus* Whittington (1959, pp. 401-11, pls. 1-3; pl. 4, figs. 1-25; text-figs. 4, 5) from the Edinburg Formation, and with *R. plaesiourus* Whittington (1959, pp. 412-14, pl. 4, figs. 26-30; pl. 5; pl. 6, figs. 1-15) from the Lower Martinsburg shale, both from northern Virginia.

Remopleurides sp. C

Plate 80, figs. 12-15

Material. One cranium, two free cheeks, two hypostomes, one pygidium.

Description. One small, incomplete cranium; glabella abruptly expanded, weakly convex; anterior tongue long, moderately wide, almost horizontally extended. Occipital ring long and narrow. Palpebral lobes broad (tr.). Surface apparently smooth.

Eye short, broad, and strongly convex transversely, weakly rounded in outline. External rim of eye lobe broad and weakly rounded, depressed anteriorly where marked off by broad furrows, dying out posteriorly. Border convex anteriorly, with a steep, salient anterior extension. Border widens and merges with eye rim posteriorly, produced into a strong, straight, broad based, librigenal spine.

Hypostome elongatedly trapeziform in outline, almost as long as wide. Middle body convex, well defined. Anterior boss not prominent. Lateral and posterior borders narrow; postero-lateral forks absent.

Pygidium subquadrate. Axis swollen, composed of two segments. Anterior pleurae narrowly pointed, extending backward as far as second pair. Space between inner pair of pleurae long and narrow. Doublure broad, curling upwards along inner margin.

Remarks. The short eye is a commanding feature in both cranium and free cheek. All the parts described may not belong to one species.

Genus HYPODICRANOTUS Whittington 1952

Hypodicranotus sp.

Plate 80, fig. 16

Material. One free cheek.

Description. Free cheek narrow anteriorly, lateral outline almost straight. External rim of eye lobe marked off by sharp furrows. Cheek weakly convex. Lateral and posterior border furrows lacking. Genal angle acute. Subgenal spine narrow, directed almost straight backwards, extending a short way beyond posterior margin. Subgenal notch narrow, tapering slowly, more than half length of subgenal spine. Surface of posterior area and subgenal spine with faint, anastomosing, subconcentric terrace lines, widely spaced.

Remarks. The discovery of a *Hypodicranotus* type of hypostome in the upper platy Stinchard Limestone, Auchensoul Hill, establishes the occurrence of the genus in the Girvan District at a considerably earlier date than any of the North American records. The single free cheek from the Albany Mudstones differs from both *H. striatulus* (Walcott) (see Whittington 1952, pl. 1, figs. 1-6, 8, 10) and from *H. missouriensis* (Foerste) (see Bradley 1930, p. 30, figs. 6-8) mainly in the shorter (exs.) subgenal notch, more slender subgenal spines, and the presence of terrace lines on the posterior area.

Family ASAPHIDAE Burmeister 1843

Genus ISOTELUS DeKay 1824

Isotelus sp.

Plate 80, figs. 18, 19

Material. Two cranidia, two free cheeks, three pygidia.

Description. Cranidium narrow, gently convex in both directions. Glabella ill defined, weakly expanded anteriorly. Palpebral lobes placed far back, strongly elevated, with cheeks drawn up at base. Axial furrows faint.

[Free cheek with elevated eye. Vincular notches weakly developed. Surface pitted.]

[Pygidium subtriangular, gently convex in both directions, unsegmented. Axis broad at front, faintly defined by broad depressions anteriorly. Anterior half pleurae swollen, marked off by broad depressions; articulating facets strong. Doublure broad; inner area broad and gently concave at apex, narrowing and becoming convexly upturned anterolaterally. Terrace lines well marked.]

Remarks. The elevated eye lobes are a peculiar feature of this species.

Family NILEIDAE Angelin 1854

Genus NILEUS Dalman 1827

Nileus sp.

Plate 80, figs. 20, 21

Material. One cranidium, five free cheeks.

Material from other horizons. All parts from the *superstes* Mudstones, Aldons.

Remarks. The genus *Nileus* has not been previously recorded from the Girvan District. The long eyes are one of the diagnostic characters of this species which will be fully described on material from Aldons in a subsequent paper.

Family SCUTELLUIDAE Richter and Richter 1955

Genus RAYMONDASPIS Příbyl 1949

Raymondaspis sp.

Plate 80, figs. 22a, b

1931 *Bronteopsis* cf. *nitens* (Wiman) Reed, pp. 26-27.

Material. One cranidium, one hypostome.

Material from other horizons. All parts common in the *superstes* Mudstones, Aldons.

Remarks. The well-marked basal lateral glabellar furrows and the raised lines on the cranium occur also in *R. brumleyi* (Cooper 1953, p. 25, pl. 9, figs. 8–10) but are lacking in *R. nitens* (Wiman) (see Skjeseth 1955, p. 22, pl. 4, figs. 1, 3); the closer affinity appears to be with the former species.

Family ILLAENIDAE Hawle and Corda 1847

Genus ILLAENUS Dalman 1824

Illaeus sp.

Plate 80, figs. 23–25

Material. Five cranidia, one free cheek, four pygidia.

Description. Cranidia strongly convex longitudinally. Glabella wide, short. Axial furrows shallow, bowed strongly inwards. Cheeks with slight independent convexity. Palpebral lobes long, placed far back, weakly rounded in outline. Surface smooth except for a median tubercle near base of glabella.

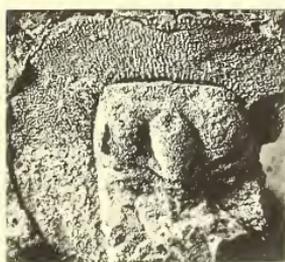
Free cheek wide, gently convex. Lateral margin rounded, basal angle acute, but not produced into a spine.

Pygidium moderately convex in both directions, broadly rounded in outline. Axis short, gently swollen, more than one-third anterior width, projecting anteriorly, defined by broad, shallow furrows. Doublure short, monocuspid.

Remarks. There is a similarity between this species and *I. devexus* Tripp (1962, p. 12, pl. 2, figs. 10a, b) in convexity, and in the proportions of the glabella, but the cranium is shorter in the Doularg form, and the glabella does not widen anterior to the eyes.

EXPLANATION OF PLATE 81

- Figs. 1–3. *Hibbertia whittingtoni* sp. nov. 1a–c, Cephalon without upper lamella (holotype, A. 5862a). Dorsal, frontal, and lateral views, $\times 6$. 2, Cephalon (A. 5863a), $\times 4.5$. 3, Fragmentary cephalon (A. 5864). External mould, showing pits on glabella, $\times 15$.
- Figs. 4–10. *Dimeropyge hystrix* sp. nov. 4a, Cranium (holotype, A. 5865a). Dorsal view, $\times 6$. 4b, c, The same. Anterior and lateral views, $\times 8$. 5, Cranium (A. 5866), with uniformly tuberculate occipital ring, $\times 6$. 6, Cranium (A. 5867a), with a pair of exceptionally large swellings at inner extremities of posterior borders, $\times 8$. 7, Cranium (A. 5868b). Latex cast from external mould, showing three aciculate tubercles at back of occipital ring, a pair of prominent tubercles on preglabellar field, and aciculate tubercle at left anterior margin of anterior border, $\times 10$. 8, Left free cheek (A. 5869). External mould, showing aciculate tubercles on margin, $\times 8$. 9, Right free cheek (A. 5870), showing vincular swelling on doublure, $\times 6$. 10, Pygidium (A. 5871a). Oblique posterior view, $\times 10$.
- Figs. 11a, b. *Toernquistia* sp. A. Cranium (A. 5872). Dorsal and frontal views, $\times 14$.
- Fig. 12. *Toernquistia* sp. B. Cranium (A. 5873a), $\times 8$.
- Figs. 13, 14. *Mesotaphraspis* sp. 13a, b, Cranium (A. 5874). Dorsal and lateral views, $\times 12$. 14, Right free cheek (A. 5875a), possibly belonging to this form, $\times 12$.
- Fig. 15. Unassigned free cheek (A. 5876), $\times 6$.
- Fig. 16. Unassigned hypostome (A. 5877a), $\times 8$.
- Figs. 17–21. *Carrickia pelagia* gen. et sp. nov. 17a–c, Cranium (holotype, A. 5878). Dorsal, frontal, and lateral views, $\times 8$. 18, Cranium (A. 5879b). External mould, showing pits on glabella and inner part of fixed cheek, $\times 12$. 19, Cranium (A. 5880), $\times 7$. 20, Small cranium (A. 5881b), with narrow glabella. External mould showing smooth surface, $\times 12$. 21a, b, Pygidium (A. 5882). Dorsal and posterior views, $\times 18$.
- Figs. 22, 23. *Ampyx* sp. 22, Cranium (A. 5883). Oblique lateral view, $\times 3$. 23, Pygidium (A. 5884a) attributed to this species, $\times 4$.



1a



2



4a



4b



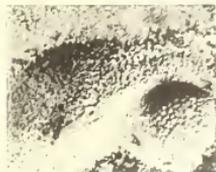
5



4c



1b



3



7



6



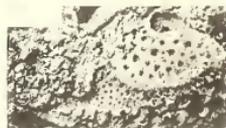
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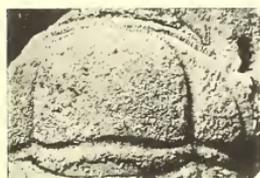
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9



8



17a



18



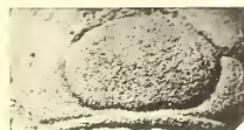
14



10



13b



17b



19



11b



13a



16



17c



20



11a



22



21a



21b



12



23

Genus BUMASTOIDES Whittington 1954

Bumastoides scoticus sp. nov.

Plate 80, figs. 26-32

Diagnosis. Cranidium subquadrate, strongly convex longitudinally, weakly so transversely. Palpebral lobes weakly rounded, forwardly placed. Anterior margin of pygidium almost transverse; doublure short, with a minute median cusp.

Holotype. A. 5860a, b (pygidium) Plate 80, figs. 31a, b.

Paratypes. A. 5855a, b (cranidium); A. 5857 (free cheek).

Other material. Twelve cranidia, seven free cheeks, two rostral plates, one hypostome, thirty-seven pygidia.

Dimensions (in mm.).

	<i>Holotype</i>	<i>A. 5861a, b</i>
Length of pygidium . . .	3.1	6.7
Width of pygidium . . .	5.3	8.3

Description. Cranidium subquadrate, strongly convex longitudinally particularly near back, weakly so transversely. Lunate muscle impressions shallow, situated near back of cranidium and four-sevenths of cranidial width apart. Shallow apodemes on posterior margin, slightly wider apart. Palpebral lobes weakly rounded, forwardly placed. Anterior branches of facial sutures run almost straight forwards at first, bending inwards anteriorly; posterior branches run backwards and slightly outwards. Surface smooth; one or two terrace lines run parallel to anterior margin and curve round parallel to facial sutures.

Free cheek weakly convex. Eye large, seven-tenths of its own length from posterior margin, situated at about the same distance from lateral as from posterior margin; lens surface convex, marked off by a shallow depression. Posterior and lateral margins almost straight; genal angle broadly rounded. Doublure lies close to dorsal surface posteriorly, increasingly convex anteriorly.

Rostral plate broadly rounded anteriorly, bowed backwards posteriorly, weakly convex longitudinally. Terrace lines about sixteen in number, most of which are continuous from side to side.

Hypostome rounded in posterior outline. Middle body evenly convex; crescentic posterior lobe slightly depressed, with small maculae laterally. Anterior wings large, broadly pointed, sloping dorsally upwards; continuous with narrow, swollen posterior border. Surface smooth, except for anterior wings which bear longitudinal terrace lines, widely spaced.

Pygidium gently convex proximal to doublure, sloping steeply downwards laterally. Anterior margin almost transverse. Axis indistinguishable except for slight forward convexity and depressions at positions of axial furrows, half width of pygidium, or more, apart. Doublure two-sevenths length of pygidium, weakly convex, with a faint longitudinal median depression; anterior margin simple except for a minute median cusp, distinguishable only on well-preserved specimens. Surface smooth; terrace lines on doublure closely spaced, faint.

Remarks. The pygidium of *B. scoticus* differs from the type species, *B. milleri* (Billings) (see Whittington 1954, pp. 138-9, pl. 62, figs. 16-18, 20, 25, 26, 29), in the almost

transverse anterior outline and in the monocuspid, not bicuspid, anterior margin of the doublure. The doublure is monocuspid also in *B. billingsi* (Raymond and Narraway) (see Bradley 1930, pl. 28, fig. 2), but the doublure is longer in that species.

Family HARPIDAE Hawle and Corda 1847
Genus HIBBERTIA Jones and Woodward 1898

Hibbertia whittingtoni sp. nov.

Plate 81, figs. 1-3

Diagnosis. Eye tubercles forwardly placed. Brim widest antero-laterally, forepart flexed upwards. Pits fine, radially arranged on cheek roll. Short genal caeca proximally on brim.

Holotype. A. 5862a, b (cephalon). Plate 81, figs. 1a-c.

Other material. Four cephalons and fragments of brim.

Dimensions of holotype (in mm.).

Length of cephalon (sag.)	5.0
Length of cephalon (exs.)	7.7
Width of cephalon . . .	8.9
Width of cheek roll . . .	4.4
Length of glabella . . .	1.9

Description. Width of cephalon approximately equal to length, but variable; glabella moderately long, narrowing forwards, swollen. Basal lateral lobes well developed. Occipital ring short; occipital furrow shallow. Alae small, depressed. Eye tubercles large, forwardly placed, strongly raised. Eye ridges indistinct. Preglabellar field extends less than half distance to brim. Cheek roll convex, strongly rounded in outline antero-laterally. Posterior borders raised, weakly defined. Border strong, extending to tip of brim. Brim widest antero-laterally, gently concave except for prolongations; forepart of brim anterior to cheek roll flexed upwards. Brim prolongation shorter than median length of cephalon, narrowing steadily, upwardly inclined. Cheek roll prolongation narrows slowly at first, extending to tip of brim prolongation. Outer rim moderately developed on both lamellae.

Glabella punctate medianly. Alae smooth. Pits on cheek roll and brim small, radially arranged on cheek roll; short genal caeca proximally on brim, either one or two pits between caeca. Outer rim smooth.

Remarks. This species is referred to *Hibbertia* rather than *Selenoharpes* because the girder extends to the tip of the cheek prolongation; shape and pitting of the glabella, and flexure of brim are other features of resemblance. The occurrence of genal caeca on the inner part of the brim, and the fineness of the pitting of the brim are characters of *Selenoharpes*, which serve to distinguish this from other species of *Hibbertia*.

Family OTARIONIDAE Richter and Richter 1926
Genus OTARION Zenker 1833

Otarion sp.

Material. One incomplete cranium.

Remarks. The distinctive feature of this specimen is the weak convexity of the glabella and of the large basal lobes.

Family DIMEROPYGIDAE Hupé 1953

Genus DIMEROPYGE Őpik 1937

Dimeropyge hystrix sp. nov.

Plate 81, figs. 4-10

Diagnosis. Glabella strongly swollen; margin of anterior border angled mesially; palpebral lobes situated anterior to mid-length of glabella; posterior borders with a pair of swellings proximally and several small tubercles laterally.

Holotype. A. 5865a, b (cranium). Plate 81, figs. 4a-c.

Paratypes. A. 5869 (free cheek); A. 5871a, b (pygidium).

Other material. Seventeen cranidia, six free cheeks, two pygidia.

Dimensions (in mm.).

	<i>Holotype</i> A. 5867a, b	
Length of cranium	3.0	3.0
Length of glabella	2.0	1.9
Width of glabella (maximum)	1.6	1.7

Description. Glabella narrowly ovate, strongly convex in both directions, standing well above cheeks, sloping forwards and downwards. Muscle areas absent. Preglabellar and axial furrows continuous and deep; axial furrows wide at back. Occipital ring convex longitudinally, moderately arched transversely. Occipital furrow broad and shallow. Preglabellar field moderately long, continuous with cheeks, steeply inclined, convex, with a shallow longitudinal median depression. Fixed cheeks broad, convex, highest near back. Palpebral lobes small, elevated, situated anterior to mid-length of glabella and twice their own length from posterior border; one- and two-thirds maximum width of glabella apart. Palpebral furrows well defined. Margin of anterior border angled mesially, convex, almost as long as preglabellar field. Anterior border furrow broad and shallow. Posterior borders short (exs.) proximally, increasing in length and inflation laterally. Anterior branches of facial sutures converge slightly forwards; posterior branches run obliquely outwards and backwards to posterior border furrows, thence curving more strongly outwards and cutting posterior margin immediately inside librigenal spines. Cranium set with aciculate tubercles directed upwards on glabella, backwards on occipital ring, and forwards on preglabellar field and on forefront of anterior border. Occipital ring more finely tuberculate than glabella, sometimes with three large tubercles placed towards back of ring. Fixed cheeks slightly more coarsely tuberculate than glabella; usually a single tubercle on median depression, with a pair of tubercles on either side, hind ones prominent. Posterior part of anterior border granular. Posterior borders with a pair of swellings proximally surmounted by one or more diminutive tubercles; lateral parts swollen, with several small tubercles; parts between low and smooth.

Eye small, strongly convex. Inner area of cheek broad, weakly convex. Lateral border set at an angle to inner area, narrow anteriorly, widest opposite posterior border furrow. Lateral border furrow moderately deep, curving inwards posteriorly to join posterior

border furrow. Librigenal spine moderately long, tapering steadily, curving strongly inwards near tip. Doublure narrow and produced anteriorly, as wide as free cheek opposite posterior border where a (concave) vincular swelling is developed, flattened under spines. Inner area of cheek coarsely tuberculate; border granular, with a marginal row of long slender tubercles; librigenal spine granular.

Pygidium short, flattened, with a deep, almost vertical, border. Axis broad anteriorly, narrowing strongly, composed of three segments. First ring well formed, moderately arched; second ring with transversely oval lateral areas more swollen than median part; third ring represented only by a pair of small, transversely oval swellings. Ring furrows shallow but continuous. Axial furrows shallow. Three pairs of narrow, slightly swollen pleurae; pleural furrows oblique, shallow. A pair of tubercles behind axis is the only indication of a fourth segment. Border deep, sloping steeply and uniformly downwards. Pygidium granular; a low tubercle placed proximally on each pleuron, a pair of aciculate tubercles, posterior much the larger, at extremities.

Remarks. In cephalic characters *D. hystrix* bears a close resemblance to *D. spinifera* Whittington and Evitt (1954, pp. 42-46, pl. 22; pl. 23; text-figs. 9, 10) from the Lincolnshire Limestone; the main points of similarity are the strongly swollen glabella, the shallow median depression crossing the preglabellar field, the incurved tips of the free cheeks, the aciculate tuberculation, and the arrangement of tubercles on the posterior borders. In pygidial characters the resemblance is less close.

D. minuta Öpik (1937, pp. 32-33, pl. 3, figs. 1, 2; pl. 4, fig. 5; pl. 12, figs. 1, 2; pl. 19, fig. 1) from the Kukruse Shales possesses even larger swellings than *D. hystrix* proximally on the posterior borders, but is quite distinct in other respects.

Genus TOERNQUISTIA Reed 1896

Toernquistia sp. A

Plate 81, figs. 11a, b

Material. Two cranidia.

Description. Glabella broadly rounded in outline anteriorly, convex; lateral glabellar furrows absent. Preglabellar and axial furrows continuous, deep and broad; median preglabellar pit large, indenting preglabellar field. Preglabellar field almost half length of glabella, convex, sloping steeply downwards. Anterior border moderately long, sloping forwards, border furrow well defined. Fixed cheeks moderately wide, gently convex. Shallow depressions run outwards and forwards from antero-lateral angles of glabella. Palpebral lobes large. Posterior borders widen (exs.) steadily laterally. Surface finely tuberculate.

Remarks. The cranidium figured bears some resemblance to the type species, *T. nicholsoni* (Reed 1896, pp. 433-5, pl. 21, figs. 3, 3a) but the glabella is much less swollen, and the divergent antero-lateral furrows are shallower.

Toernquistia sp. B

Plate 81, fig. 12

Material. One cranidium.

Remarks. This cranidium differs from the foregoing species in its shorter, more swollen glabella, and longer anterior border.

Genus MESOTAPHRASPIS Whittington and Evitt 1954

Mesotaphraspis sp.

Plate 81, figs. 13, 14

Material. One cranidium [two free cheeks].

Description. Cranidium weakly convex in both directions. Glabella lanceolate in outline, weakly convex. Lateral lobes and furrows lacking. Preglabellar and axial furrows continuous, lightly impressed; shallow median furrow extends a short way across preglabellar field. Occipital ring moderately long; occipital furrow shallow, transverse. Preglabellar field approximately three-eighths length of glabella, weakly inclined, continuous with fixed cheeks. Palpebral lobes moderately long, weakly defined. Anterior border of uniform width.

[Free cheek narrow, weakly rounded in outline. Eye large; lens surface convex. Anterior branches of facial sutures diverge slightly forwards; posterior branches run outwards and then curve strongly backwards to cut posterior margin just inside genal angle. Inner area gently convex, at narrowest part slightly wider than border. Lateral border of uniform width, well defined. Librigenal spine continuous with lateral border in curvature, tapering strongly. Surface smooth.]

Remarks. This species resembles *M. inornata* Whittington and Evitt (1954, pp. 48–49, pl. 24, figs. 1–39) from the Lincolnshire Limestone more closely than it does *M. parva* Whittington and Evitt (1954, pp. 46–48, pl. 3, figs. 31–36; pl. 4, fig. 11) from the Edinburgh Limestone. The following are the main differences from *M. inornata*: (1) The glabella is narrower and more pointed anteriorly; (2) the lateral lobes and furrows are lacking; (3) the preglabellar furrow is much more shallow and the median pit is lacking. The free cheeks described agree better with *Mesotaphraspis* than with *Toernquistia* (see Warburg 1925, pl. 5, fig. 41).

Family RAPHIOPHORIDAE Angelin 1854

Genus AMPYX Dalman 1827

Ampyx sp.

Plate 81, figs. 22, 23

Material. One cranidium, one pygidium.

Description. Cranidium convex in both directions, but distorted. Glabella swollen, widening steadily forwards; anterior part narrowing rapidly and projecting beyond cephalic margin. Anterior spine broken off at base, rounded in cross-section. First pair of lateral muscle areas faintly defined. Lateral glabellar areas not developed. Preglabellar and axial furrows shallow. Occipital ring convex, curved weakly backwards in outline, continuous with posterior borders, which slope steeply forwards laterally. Fixed cheeks wide (tr.) and sloping steeply downwards anteriorly, connected in front of glabella; anterior border flexed forwards.

Pygidium elliptical in outline, weakly convex. Axis about one-quarter anterior width, narrowing rapidly at first, then slowly, weakly defined. Inner parts of pleural lobes flattened; border slopes gently outwards, narrow (exs.), slightly embayed mesially.

One pair of faint pleural furrows, concave forwards; area anterior to furrows depressed. Surface smooth, except for shallow terrace lines closely spaced on border.

Remarks. The cranium resembles the type species *A. nasutus* Dalman (see Whittington 1950, pp. 554-6, pl. 74, figs. 3-9; text-figs. 6a, b) and also *A. camurus* Raymond (see Cooper 1953, p. 16, pl. 5, figs. 1-2, 6-7) in shape of glabella and absence of lateral glabellar areas. The pygidium is much shorter than in either of these species.

Genus LONCHODOMAS Angelin 1854

Lonchodomas pernix sp. nov.

Plate 82, figs. 1-7

Diagnosis. Glabella narrow, tapering slowly anteriorly, carina absent. Posterior borders curve slightly forwards; posterior border furrows sharp. Basal part of glabella pitted.

Holotype. A. 5885a, b (cranium). Plate 82, figs. 1a-d.

Paratypes. A. 5887 (free cheek); A. 5890 (pygidium).

Other material. Sixteen cranidia, two free cheeks, one hypostome, fourteen pygidia.

Dimensions of holotype (in mm.).

Length of cranium to base of spine	. 8.9
Width of cranium	. . . 9.3
Maximum width of glabella	. . . 3.7
Basal width of glabella	. . . 2.0

Description. Length of cranium great compared with width, but variable. Glabella narrow, tapering slowly anteriorly, moderately convex longitudinally, strongly arched particularly at back. Hindmost part of glabella swollen to form a transverse ridge. Frontal spine square in cross-section, straight, horizontally extended; upper pair of angular ridges converge for a short distance on glabella but do not meet; carina absent. Axial furrows broad and shallow, not crossing occipital segment; elongate fossulae just posterior to greatest width of glabella. Occipital ring bowed gently backwards, sloping forwards and downwards, continuous with posterior borders. Posterior borders become narrower laterally, and curve slightly forwards. Posterior border furrows sharp; lateral pits near extremities. Fixed cheeks narrow, convex, sloping forwards. Courses of facial sutures gently sinuous. Faint, longitudinal raised lines on antero-lateral slopes of glabella near base of frontal spine. Cranium shallowly but irregularly pitted. Basal part of glabella strongly pitted; smooth, triangular, basal muscle areas strongly developed, other muscle areas indistinct.

Free cheek narrow, sloping steeply outwards; inner area convex. Librigenal spine long and slender, rectangular in cross-section, horizontally extended, curving gently inwards. Doublure of cheeks continuous beneath glabella, longest (sag.) mesially, where doublure gently convex, narrowing laterally. Distal band flattened. Proximal band abruptly depressed, becoming wider and increasingly convex towards median line; outline of inner margin rounded, with a slight median embayment. Surface of cheek and doublure smooth.

Hypostome trapeziform in outline, weakly convex longitudinally, strongly arched transversely. Middle body broadly rounded in posterior outline. Posterior lobe and

maculae not developed. Border narrow, convex, thickened and bent down at posterior wings. Posterior border furrow shallow.

Thorax with axis three-eighths total width, weakly arched. Articulating half ring faint; articulating furrow deep and broad. Axial furrows shallow. Inner parts of pleurae wide (tr.), directed straight outwards, and horizontally extended. Pleural furrows transverse, placed at two-thirds length from front, widening laterally. Outer parts of pleurae bent vertically downwards, incomplete.

Pygidium subtriangular. Axis broad, ill defined, arched transversely, extending a short distance onto border. Axial furrows indistinct. Inner parts of pleural lobes weakly convex; border gently convex, sloping steeply downwards, wide (exs.) laterally, embayed mesially. One pair of pleural furrows, concave forwards, sharply defined laterally; area anterior to furrows depressed. Terrace lines closely spaced on border. Remainder of surface smooth.

Remarks. Professor H. B. Whittington has pointed out that the name *L. tumidum* (Tripp 1962, p. 15) is a secondary homonym of *A. tumidus* Forbes (1849, pl. 10, p. 4). I hereby propose *minuntionensis* as a substitute name. *L. pernix* differs from *L. minuntionensis* in its weaker longitudinal convexity and in the shape of the glabella. It is distinguished from most other species by the absence of carina and by the slowly tapering anterior part of the glabella.

Family CHEIRURIDAE Salter 1864
Genus CERAURINELLA Cooper 1953

Ceraurinella sp.

Plate 82, fig. 8

Material. One cranidium.

Material from other horizons. Cranidia from the *superstes* Mudstones, Aldons.

Remarks. The affinities of this cranidium are with *Ceraurinella* from which it differs in the weak definition and sinuous course of the axial furrows, and the absence of tuberculation on both glabella and cheeks.

Genus SPHAEREXOCHUS Beyrich 1845

Sphaerexochus sp.

Plate 82, figs. 10-17

Material. Twelve cranidia, two free cheeks, five pygidia.

Material from other horizons. All parts from the *superstes* Mudstones, Aldons.

Description. Glabella variable in proportions, frequently much wider than long, sloping steeply downwards with strong convexity. Basal lateral glabellar furrows deepest near anterior inner angles, proximal parts almost longitudinal, shallow. Palpebral lobes placed opposite basal lateral furrows. Fixed cheeks with genal angles bluntly pointed in large specimens (Pl. 82, fig. 12), produced into short spines in smaller specimens (Pl. 82, fig. 11b); lateral and posterior margins sigmoidal in outline.

Inner area of free cheek and lateral border narrow; vincular notch strongly developed, lateral border furrow shallow and narrow compared with other species.

Pygidium twice as wide as long. Axis narrow. Third ring fused with terminal piece and with third pleurae. Axial furrows shallow anteriorly, moderately deep and very broad alongside terminal piece, interrupted opposite third ring. Three pairs of short, narrow, swollen pleurae, extending successively further backwards. Free points long, narrow, bluntly pointed, or rounded, with broad, rounded notches between.

Dorsal surface and doublure granular, pygidium more densely so than remainder of exoskeleton.

Remarks. This species differs from *S. euryis* Tripp (1962, pp. 19–20, pl. 3, figs. 1–7) in that successive pygidial pleurae extend further backwards. Cranidia are extremely variable and hard to distinguish reliably.

Genus SPHAEROCORYPHE Angelin 1854

Sphaerocoryphe sp.

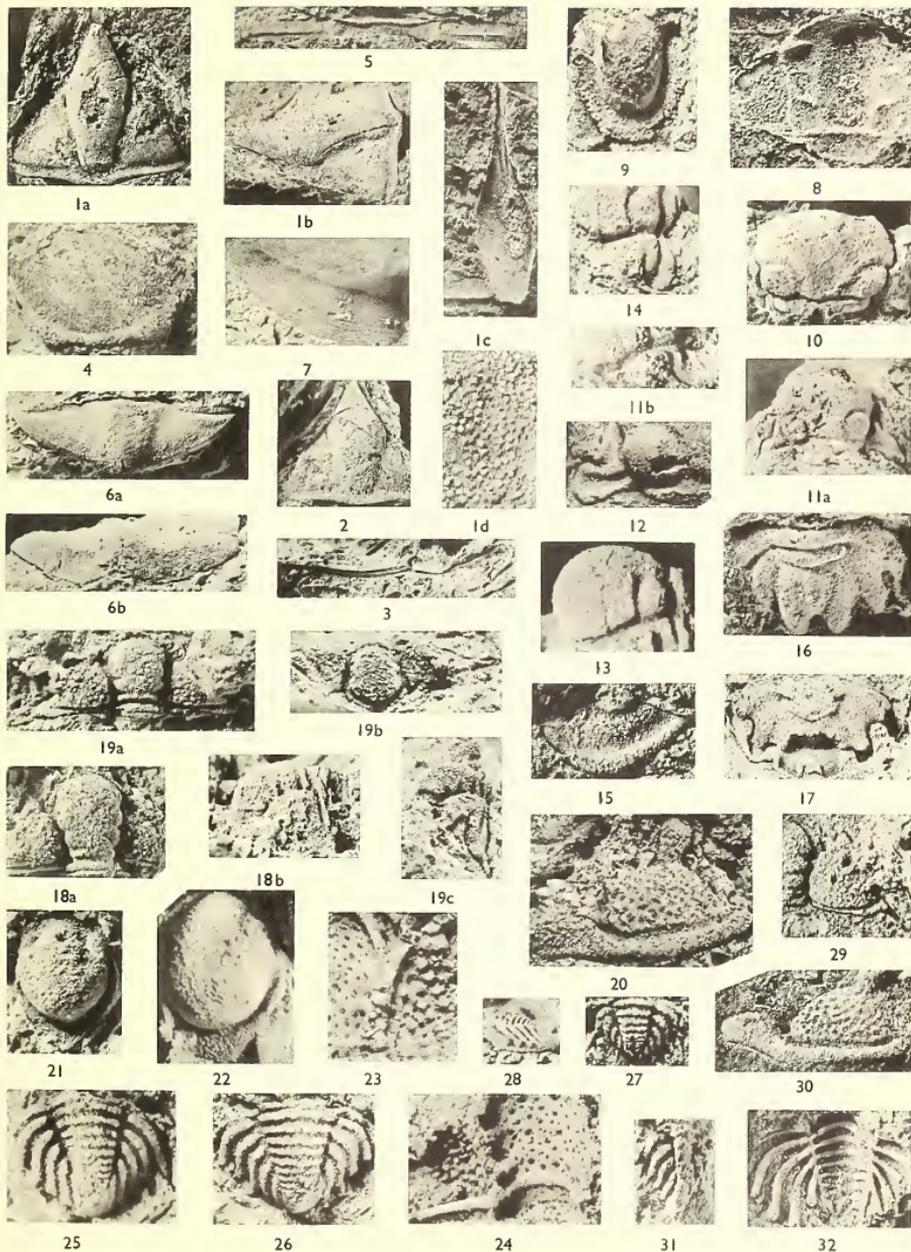
Plate 82, fig. 9

Material. One cranium, one hypostome, one fragmentary pygidium.

Remarks. Cranium small (1.6 mm. in length) with elongate bulbous glabellar lobe. Hypostome subrectangular, with elongate middle body. The anterior pair of pygidial pleurae end in comparatively long, outwardly directed free points. The species is too inadequately known for close comparison.

EXPLANATION OF PLATE 82

- Figs. 1–7. *Lonchodomas pernix* sp. nov. 1a, b, Cranium (holotype, A. 5885a). Dorsal and oblique lateral views, $\times 3$. 1c, The same, external mould (A. 5885b), $\times 3$. 1d, Enlargement of external mould of basal part of glabella to show pitted surface with smooth areas, $\times 12$. 2, Short cranium (A. 5886), $\times 3$. 3, Right free cheek (A. 5887), showing doublure and dorsal surface at base of librigenal spine, $\times 6$. 4, Posterior part of hypostome (A. 5888), $\times 10$. 5, Thoracic segment (A. 5889b), external mould, $\times 4$. 6a, b, Pygidium (A. 5890). Dorsal and posterior views, $\times 5$. 7, Pygidium (A. 5891). External mould showing anastomosing terrace lines on border, $\times 8$.
- Fig. 8. *Ceraurinella* sp. Cranium (A. 5892). External mould, $\times 6$.
- Fig. 9. *Sphaerocoryphe* sp. Hypostome (A. 5893), $\times 8$.
- Figs. 10–17. *Sphaerexochus* sp. 10, Cranium with broad glabella (A. 5894a), $\times 4$. 11a, Small cranium with narrow glabella (A. 5895a). Dorsal view, $\times 6$. 11b, The same. Lateral view, showing short fixigenal spine, $\times 8$. 12, Large cranium (A. 5896) devoid of fixigenal spines, $\times 4$. 13, Cranium (A. 5897a). Lateral view, $\times 12$. 14, Cranium (A. 5898a). Lateral view showing diminutive fixigenal spine, $\times 5$. 15, Right free cheek (A. 5899a), $\times 6$. 16, Pygidium (A. 5900b). Latex mould from external cast, $\times 5$. 17, Pygidium (A. 5901). Specimen with rounded pleurae and notches, $\times 4$.
- Figs. 18–28. *Encrinuroides obesus* sp. nov. 18a, b, Cranium (holotype, A. 5902a). Dorsal and lateral views, $\times 4$. 19a–c, Small cranium (A. 5903a). Dorsal, frontal, and lateral views. Note tall palpebral lobe in lateral view, $\times 8$. 20, Left free cheek (A. 5904a), $\times 8$. 21, Hypostome (A. 5905), $\times 8$. 22, Hypostome (A. 5906). Latex mould from external mould showing granulation of surface and pits on anterior part of middle body, $\times 10$. 23, Cranium (A. 5907). External mould, showing unpitted eye ridges, bordered by large pits, $\times 12$. 24, Cranium (A. 5908b). External mould, showing three pairs of sizable tubercles on glabella, $\times 12$. 25, Pygidium (A. 5909a), $\times 10$. 26, Pygidium (A. 5910a). Comparatively broad axis emphasized by slightly anterior view, $\times 8$. 27, Small pygidium (A. 5911a), $\times 12$. 28, Pygidium (A. 5912a). Lateral view showing steep doublure, $\times 6$.
- Figs. 29–31. *Encrinuroides* sp. 29, Cranium (A. 5913). Left fixed cheek is closely associated, $\times 6$. 30, Left free cheek (A. 5914), $\times 6$. 31, Pygidium (A. 5915a), laterally compressed, $\times 5$.
- Fig. 32. *Encrinuridae* indet. Pygidium (A. 5916b). External mould, $\times 6$.



Family ENCRINURIDAE Angelin 1854

Genus ENCRINUROIDES Reed 1931

Encrinuroides obesus sp. nov.

Plate 82, figs. 18-28

Diagnosis. Glabella slightly wider anteriorly than posteriorly, inflated; frontal lobe strongly rounded in outline. Eyes backwardly placed. Fixiginal spines slender. Tuberculation weak. Pygidium short, with broad axis, and six pairs of short pleural ribs.

Holotype. A. 5902a, b (cranidium). Plate 82, figs. 18a, b.

Paratypes. A. 5904a, b (free cheek); A. 5905 (hypostome); A. 5909a, b (pygidium).

Other material. Twenty-two cranidia, eighteen free cheeks, five hypostomes, ten pygidia.

Dimensions of holotype (in mm.).

Length of cranidium	4.4
Width of cranidium (estimated)	9.6
Length of glabella	3.5
Width of glabella across frontal lobe	2.9
Width of glabella across basal lobes	2.0

Description. Cephalon elliptical in outline, strongly convex in both directions. Glabella pyriform, narrowing little towards back, rising high above cheeks, strongly convex in both directions. Frontal lobe almost half length of glabella, strongly rounded anteriorly; longitudinal median furrow shallow, extending backward from preglabellar furrow for one-fifth length of glabella. Posterior lobe short, marked off by posterior lateral furrows which are faintly connected across central lobe; anterior and middle lateral lobes faintly defined by short furrows on steep lateral slopes of glabella, middle lobes slightly longer than anterior. Occipital ring short, strongly arched transversely. Occipital furrow shallow, transverse. Axial furrows deep and narrow; apodemes proximally at points of junction with middle and posterior lateral and occipital furrows; deep fossulae at forefront. False preglabellar field flattened, short. Preglabellar furrow deep and broad. Fixed cheeks convex, sloping inwards proximally. Positions of eye ridges indicated by absence of pitting. Palpebral lobes small, elevated, situated opposite hind part of middle lateral lobes, near mid-width of cheeks. Posterior borders short (exsag.), depressed, directed straight outwards. Posterior border furrows narrow. Laterally posterior borders widen slightly, and join short lateral borders; fixiginal spines slender, moderately long, directed outwards and more or less strongly backwards. Anterior branches of facial sutures run obliquely forwards and inwards from eyes, cutting axial furrows immediately anterior to fossulae and meeting in front of false preglabellar field; posterior branches curve outwards and slightly backwards.

Eye lobe elongatedly oval, moderately high; lens surface convex, half height of lobe, marked off by a shallow furrow on internal moulds. Inner area of free cheek weakly convex, almost three times width of border. Pseudoglabellar area and anterior border fused, continuing curve of lateral border. Lateral border convex, weakly rounded in outline. Lateral border furrow deep and broad, slightly stronger anteriorly than posteriorly. Doublure convex, as wide as border.

Hypostome subtriangular, anterior outline strongly rounded. Middle body oval, strongly swollen; longitudinal median lobe short, widening rapidly backwards. Maculae

indistinct. Anterior border moderately broad, flexed upwards. Anterior wings slope dorsally upwards. Lateral borders horizontally extended, widening slowly backwards. Posterior tongue pointed, comparatively short. Surface granular; parts of middle body shallowly pitted.

Pygidium triangular, strongly convex, composed of twelve or more axial rings and six pairs of pleurae. Axis occupies about half maximum width of pygidium, convex longitudinally, with comparatively long post-axial ridge. Ring furrows continuous but faint mesially at back. Axial furrows straight, strongly convergent, becoming faint posteriorly. Pleural lobes narrow, sloping gently outwards with weak convexity. Successive pleural ribs directed increasingly backward; first four pairs of pleurae end in short, out-turned free points; fifth pair subparallel, sixth pair indistinctly marked off from axis, hardly reaching margin. Inter-pleural furrows broad, moderately deep. Articulating facets weakly developed. Doublure narrow, sloping steeply downwards.

Cephalon within borders, including pseudoglabellar area, sparsely covered by comparatively small tubercles of various sizes; a pair of conspicuous tubercles placed between basal lateral lobes. Inner areas of cheeks closely pitted, fixed cheeks more strongly so than free cheeks. Palpebral lobes and occipital ring smooth; posterior borders with a few small tubercles. Pseudoglabellar areas of free cheeks finely tuberculate; anterior and lateral borders granular, devoid of tubercles. Surface of pygidium granular; a few large granules on axial rings. Doublure finely granular.

Remarks. The squat pygidium, with broad axis, distinguishes *E. obesus* from all described species except *E. fallax* (Reed 1899, pp. 753-5, pl. 49, figs. 9-12) from the Tramore Limestone, which it closely resembles in many respects. The main differences are that the eye lobes are situated further apart and further back, the tuberculation is weaker, the pygidium is more strongly convex, and the sixth pair of pleurae are less developed in *E. obesus*.

Encrinuroides sp.

Plate 82, figs. 29-31

Material. One cranium, two free cheeks, four pygidia.

Description. Glabella weakly convex, rising no higher than cheeks. Basal lateral lobes exceptionally short; lateral furrows short and broad. Palpebral lobes situated near mid-width of cheeks, not quite as far back as in *E. obesus*. Fixigenal spines comparatively long and stout, curving outwards and backwards.

Free cheek gently convex; eye stalk incomplete. Inner area broad. Pseudoglabellar area and anterior border fused, set at an angle to lateral border, which narrows towards back. Lateral border furrow becomes weaker posteriorly. Surface of inner area sparsely tuberculate and shallowly pitted; pseudoglabellar area and lateral border granular.

Pygidium narrow, strongly vaulted. Axis narrow compared with pleurae, convex longitudinally, composed of about fourteen rings. Six pairs of pleurae, last pair short; first four pleurae end in long horizontally extended free points. Pleural ribs narrow, strongly swollen, rib furrows broad. Surface smooth except for a few low tubercles on axial rings.

Remarks. This species differs conspicuously from *E. obesus* in the less convex glabella, the outline of the free cheek, and narrow, vaulted pygidium.

Genus CYBELE Lovén 1846

Cybele ? sp.

Plate 83, fig. 1

Material. One incomplete cranium.

Description. Glabella unknown except for swollen middle and posterior lateral lobes, standing higher than fixed cheek. Fixed cheek broad, weakly convex. Palpebral lobe elevated, placed far forwards. Eye ridge almost transverse, moderately long (tr.). Posterior border short (exs.), furrow broad, flat bottomed, bordered on anterior side by a raised ridge. Surface granular. Inner area of cheek except for eye ridge and posterior ridge shallowly and closely pitted. Entire inner area of cheek very sparsely tuberculate.

Remarks. The unpitted ridge at the back of the inner area of the fixed cheek is an unusual feature, which occurs also in *Cybele bellatula* Dalman (see Öpik 1937, pp. 120-1, text-fig. 34), a species in which the eye ridges are similarly developed. The specimen is not sufficiently complete to justify an unqualified determination.

Genus QUINQUECOSTA gen. nov.

Diagnosis. Glabella widens steadily forwards, strongly convex. Frontal lobe at least half length of glabella. Three pairs of lateral glabellar lobes; posterior pair much the smallest with lateral nodes; anterior lateral glabellar furrows bifurcate, anterior branches short. Anterior border short, swollen laterally, dying out mesially. Eyes moderately large, placed opposite middle lateral furrows and close to glabella. Pygidium composed of about twelve axial rings and five pairs of backwardly directed pleural ribs which terminate bluntly on the arc of a circle.

Type species. *Q. williamsi* sp. nov.

Remarks. *Quinquecosta* is most closely related to certain members of the Subfamily Cybelinae; *Atractopyge xiphères* (Öpik 1925, pp. 11, 12; pl. 1, figs. 10, 11; 1937, p. 121, pl. 7, fig. 3; pl. 21, figs. 3, 4), for instance, presents a comparable bifurcation of the anterior lateral glabellar furrows, and the free cheeks are similarly constructed. The five pairs of pygidial ribs (unfurrowed pleurae) distinguish *Quinquecosta* from *Cybele*, which has five pairs of furrowed pleurae, and from *Atractopyge*, which has four pairs of pleurae or ribs. Pygidia of *E. quinquecostatus* Männil 1958 and *E. pilisiverensis* Rosenstein 1941 possess only five pairs of ribs, but the new genus is quite different in the longer, less divergent ribs, quadrate rather than triangular outline, and absence of axial tubercles.

Certain features are evocative of the family Phacopidae—for instance, the glabella widening steadily forwards; long frontal lobe; apodemes on middle and posterior, not the anterior, lateral furrows; short posterior lateral glabellar lobes, with lateral nodes. The general stamp of the cranium, and the five pairs of long pygidial ribs suggest a pliomnerid relationship, and as such this form was recorded in Williams's monograph (1962, p. 47).

Quinquecosta williamsi gen. et sp. nov.

Plate 83, figs. 2-10

Diagnosis. Glabella as long as wide. Lateral lobes wide; middle lateral lobes almost as large as anterior pair. Occipital ring long, as wide as base of glabella.

Holotype. A. 5918a, b (cranium). Plate 83, figs. 2a, b.

Paratypes. A. 5920 (free cheek); A. 5923a, b (hypostome); A. 5924 (pygidium).

Other material. Twenty-five cranidia, forty-five free cheeks, seven hypostomes, twenty-nine pygidia.

Material from other horizons. Cranidia, hypostomes, and pygidia from the *superstes* Mudstones, Aldons.

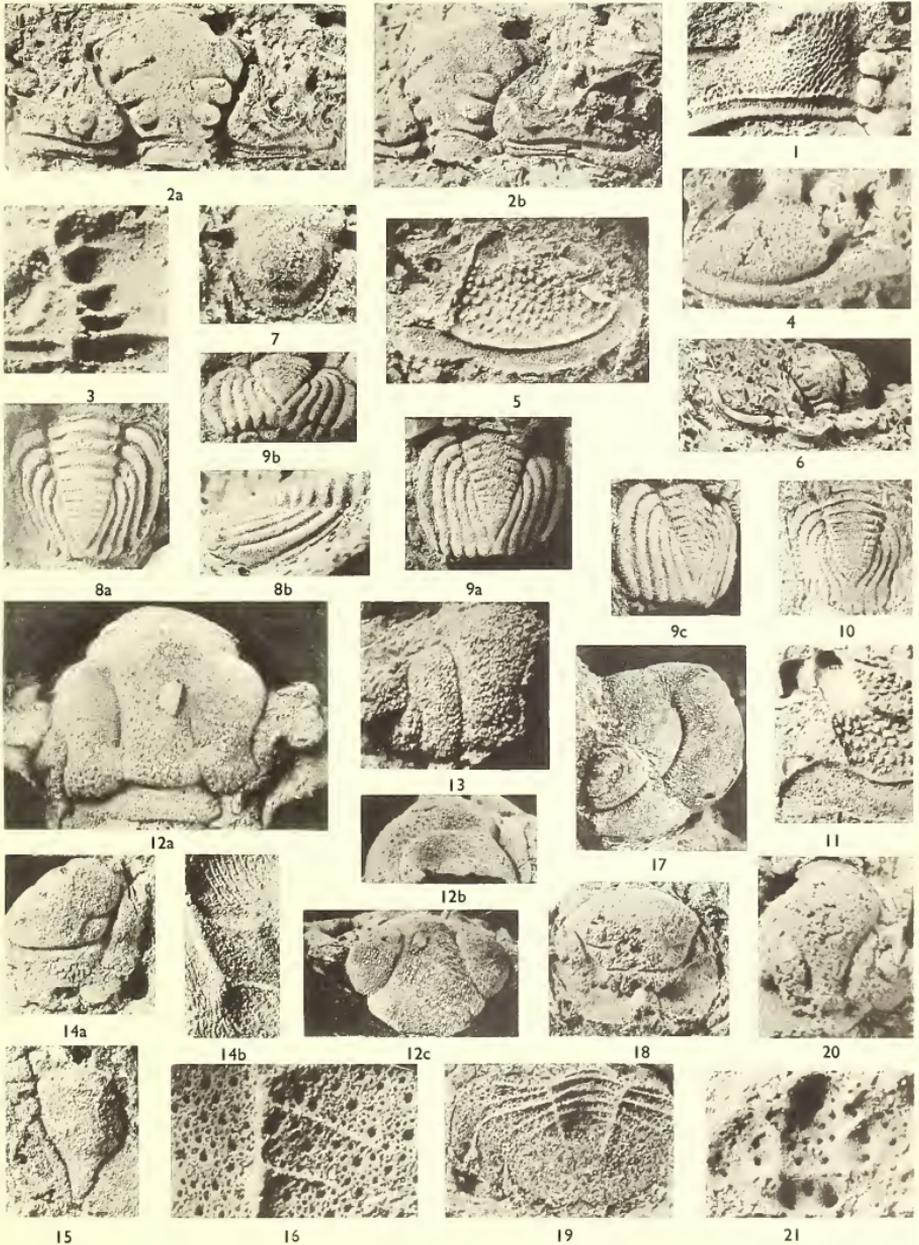
Dimensions of holotype (in mm.)

Length of cranium	6.5
Width of cranium	14.5
Length of glabella	5.5
Width of glabella across frontal lobe	6.1
Width of glabella across basal lobes	3.4

Description. Glabella subpentagonal in outline, evenly convex in both directions. Frontal lobe half length of glabella (sag.); a shallow median pit near mid-length; antero-lateral angles sharply rounded. Lateral glabellar lobes wide, with some independent convexity but continuous with central lobe; anterior pair narrower proximally than distally; posterior pair much the shortest, expanding laterally. Anterior lateral furrows bifurcate within short distance; anterior branches short, convergent forwards, posterior branches long, transverse, shallow. Middle lateral furrows short and deep, converging forwards. Posterior lateral furrows directed inwards and backwards for a short distance, then bending forwards. Occipital ring moderately long (sag.) and convex, as wide as basal lobes; occipital tubercle centrally placed, low. Occipital furrow shallow, bowed forwards. Transversely elongate apodemes at distal extremities of middle and posterior lateral furrows; rounded apodemes at extremities of occipital furrow. Axial furrows narrow, much deeper than lateral furrows; deep, rounded fossulae opposite anterior border furrow. Anterior border extremely short, well defined and swollen laterally,

EXPLANATION OF PLATE 83

- Fig. 1. *Cybele* ? sp. Cranium (A. 5917), showing ridge running alongside posterior border furrow, $\times 4$.
- Figs. 2–10. *Quinquecosta williamsi* gen. et sp. nov. 2a, b, Cranium (holotype, A. 5918a). Dorsal and oblique lateral views, $\times 3.75$. 3, Cranium (A. 5919b). External mould, $\times 8$. 4, Right free cheek (A. 5920), $\times 4$. 5, Right free cheek (A. 5921). External mould, $\times 6$. 6, Cranium and reversed thoracic segment (A. 5922a). Oblique lateral view, $\times 2.5$. 7, Hypostome (A. 5923a), $\times 8$. 8a, b, Pygidium (A. 5924). Dorsal and lateral views; axis extends almost as far as posterior margin, $\times 3.5$. 9a–c, Pygidium (A. 5925). Latex cast from external mould. Dorsal, postero-ventral, and oblique lateral views; note short axis and post-axial ridge, $\times 4$. 10, Small pygidium (A. 5926b). Latex cast from external mould; note short axis and incurved pleurae, $\times 6$.
- Fig. 11. Encrinuridae indet. Right free cheek (A. 5927b). External mould, $\times 5$.
- Figs. 12–16. *Amphilichas priscus* sp. nov. 12a, Cranium (holotype, A. 5928b). Latex cast from external mould. Dorsal view, $\times 4$. 12b, c, The same. Lateral and frontal views, $\times 3$. 13, Small cranium (A. 5929), $\times 10$. 14a, Hypostome (A. 5930a), attributed to this species, $\times 5$. 14b, The same, external mould (A. 5930b), $\times 10$. 15, Pygidium (A. 5931a), attributed to this species, $\times 6$. 16, Pygidium (A. 5932), attributed to this species. External mould, $\times 12$.
- Figs. 17–19. *Amphilichas* sp. 17, Cranium (A. 5933a). Lateral view, $\times 3$. 18, Hypostome (A. 5934) attributed to this species, $\times 3$. 19, Pygidium (A. 5935b) attributed to this species. External mould, $\times 8$.
- Fig. 20. *Hemiarges* sp. Cranium (A. 5936a), $\times 10$.
- Fig. 21. *Ceratocephala* sp. Cranium (A. 5937). External mould, $\times 10$.



becoming indistinct mesially, cut off by axial furrows. Anterior border furrow well marked laterally, becoming shallow mesially, where indistinguishable on internal moulds. Outline of anterior border transverse for median one-quarter width, oblique and gently embayed laterally. Fixed cheeks proximal to eyes narrow, strongly convex transversely, extending to anterior extremities of cranidium; postero-lateral areas short and broad (tr.). Palpebral lobes moderately large, about anterior width of glabella apart, extending from opposite mid-length of anterior lateral lobes almost to posterior border furrows, sloping steeply inwards. Palpebral furrows start near mid-length of palpebral lobes and curve round posterior extremities of eyes. A large pit at mid-point of lobe. Posterior borders short, strongly convex longitudinally, not depressed, bending sharply downwards and slightly backwards at two-fifths width, widening near genal angles which are rounded. Posterior border furrows deep and wide. Anterior branches of facial sutures run almost straight forwards at first, curving inwards and converging at anterior extensions of free cheeks, presumably joining rostral suture mesially; posterior branches long, almost transverse except for a backward sigmoidal bend at lateral border. Glabella and fixed cheeks within borders finely and sparsely granular. Occipital ring and posterior borders smooth. Anterior border strongly granular. Fixed cheeks coarsely pitted.

Lens surface occupies two-thirds of short eye-lobe, marked off by a furrow on internal moulds only. Free cheek within border broad, gently convex. Border convex, narrow, strongly rounded in outline, widening forwards; anterior extensions large, strongly convex, bent at an angle to border, almost vertical. Border furrow uniformly narrow and shallow. Doublure two-thirds width of border, upcurved. External surface of inner area shallowly and densely pitted, and sparsely granular; border and doublure closely granular.

Hypostome subtriangular. Middle body oval, convex, not clearly defined. A pair of small maculae just posterior to mid-length. Anterior border narrow and flattened mesially, widening rapidly laterally and marked off from middle body by a broad furrow. Anterior wings large, steeply inclined. Lateral borders narrow anteriorly, widening slightly and joining posteriorly, horizontally extended, rounded in outline. Middle body granular.

Axis one-quarter total width of thorax, strongly arched transversely. Articulating furrow broad, with deep, rounded apodemes near extremities. Axial furrows deep and narrow. Pleurae straight and horizontally extended to fulcra at mid-width, curving downwards and slightly backwards laterally, free points tapered. Pleural ribs strongly swollen proximally, becoming narrower (exs.) to fulcra, expanding and less swollen laterally. Anterior bands short (exs.), depressed. Pleural furrows sharp on external, broad on internal moulds, curving forwards and dying out half-way beyond fulcra. Surface granular.

Pygidium as long as wide. Axis almost half maximum width, tapering rapidly to a pointed termination near posterior margin, strongly convex transversely at front, flattened posteriorly; in some specimens hind-part of axis is replaced by a post-axial ridge. Twelve rings, ring furrows transverse, deepest laterally, successively shallower towards back, deeper on internal than on external moulds. Axial furrows sharp. Pleural lobes convex, steep. Articulating facets extend for full width of lobes, marked off by broad furrows; anterior slopes of first ribs widen markedly laterally. Five pairs of

unfurrowed pleural ribs directed backwards for most of their length, terminating bluntly. Successive ribs increasingly convergent, and extending slightly further backwards. First four pairs of ribs correspond with axial rings. Interpleural furrows deep and broad, extending successively more lightly across doublure. Doublure uniformly narrow, horizontally extended, arcuate in outline. Pygidium granular, median area of axis coarsely so.

Remarks. Only one other species is known—a form with broader glabella from the platy upper Stinchar Limestone, Auchensoul Hill.

Encrinuridae indet.

Plate 82, fig. 32; Plate 83, fig. 11

Material. One free cheek, one pygidium.

Description. One free cheek bears some resemblance to that of *Quinquecosta* but the eye lobe is much taller, the inner area is smaller, and, to judge by the course of the facial suture, the eye must have been forwardly placed and close to the glabella.

Pygidium strongly convex. Axis narrow, composed of numerous well-defined rings. Axial furrows deep and narrow. Five (?) pairs of pleural ribs extend successively further backwards; fifth pleurae long, convergent. First three pairs of pleurae correspond with first three axial rings. Ribs widen laterally. Rib furrows deep and broad. Surface smooth.

Remarks. Although the posterior part of the pygidium is lacking, it seems unlikely that more than five pairs of ribs were developed. Nevertheless, the affinities of both free cheek and pygidium are equivocal, and it is possible that both belong to some encrinurid genus.

Family LICHIDAE Hawle and Corda 1847

Genus AMPHILICHAS Raymond 1905

Amphilichas priscus sp. nov.

Plate 83, figs. 12-16

Diagnosis. Cranium moderately convex. Central glabellar lobe weakly expanded anteriorly. Lateral lobes narrow posteriorly. Longitudinal furrows shallow throughout. Basal lateral furrows faintly indicated.

Holotype. A. 5928a, b (cranium). Plate 83, figs. 12a-c.

Other material. Five cranidia [four hypostomes, four pygidia].

Dimensions of holotype (in mm.).

Length of cranium	9.0
Maximum width of glabella	9.0
Width of central lobe opposite eyes	2.9
Width of lateral lobes opposite eyes	2.7

Description. Cranium weakly convex for most of its length, more strongly so at front. Frontal lobe projects strongly anterior to lateral lobes, swollen, not expanded to full width of glabella, narrowing rapidly backwards, widening slowly posteriorly. Lateral lobes broad and swollen anteriorly, narrowing opposite posterior extremities of palpe-

bral lobes, where narrower than central lobe, widening posteriorly and extending backwards far beyond central lobe; posterior lateral angles broadly pointed. Longitudinal furrows much deeper on internal than on external moulds. Basal lateral furrows represented by deep notches formed by axial furrows at one-quarter length from back, and by independent convexity of basal lateral lobes. Axial furrows deep, bowed inwards. Occipital ring long, narrowing rapidly behind lateral lobes, not extending sideways beyond them. Occipital furrow deep and narrow. Anterior border ill defined. Palpebral lobes large, horizontally extended, slightly more than their own length from posterior border. Palpebral furrows lacking. Fixed cheeks slope outwards. Cranium closely covered with tubercles of various sizes; occipital ring more weakly tuberculate, a single large tubercle placed posteriorly.

[Hypostome three-quarters as long (exs.) as wide, broadly rounded anteriorly. Middle body five-eighths length of hypostome, extending to anterior margin, moderately convex. Posterior lobes slightly swollen. Middle furrows short (tr.), narrow, bending abruptly backwards proximally, dying out before reaching posterior furrow. Lateral furrows deep, extending some way across posterior border. Lateral borders convex anteriorly; posterior wings and posterior lobes narrow. Posterior border long, weakly convex, with a median embayment extending for about one-third the length (sag.). Doublure of posterior border extends to posterior furrow, convex except in front of median embayment where a flattened channel reaches almost to anterior margin. Surface of antero-lateral parts of central body and lateral borders with anastomosing, sharply raised lines, convergent backwards.]

[Fragmentary pygidium weakly convex; axis pointed, contracting abruptly posteriorly, with one ring clearly defined. Short pleural furrows on first and second pleurae.]

Remarks. The closest resemblance is to *A. wahlenbergi* Warburg (1925, pp. 315-19, pl. 8, figs. 27-35, 26?, 41?) from the Kallholn Limestone; the new species differs mainly in the greater anterior width of the lateral lobes, and in the vestiges of the basal lateral lobes. Hypostomes and pygidia provisionally attributed to *A. wahlenbergi* and to *A. priscus* are comparable.

Amphilichas sp.

Plate 83, figs. 17-19

Material. Two cranidia, one hypostome, three pygidia.

Description. Cranidia differ markedly from *A. priscus* in much stronger longitudinal convexity, wide expansion of the frontal lobe and deep longitudinal furrows which die out abruptly before reaching occipital furrow. Hypostome attributed to this form wider, particularly postero-lateral borders, and middle furrows do not bend backwards; anastomosing raised lines fainter. Pygidium attributed to this species has axis tapering backwards but undefined posteriorly; three axial rings strongly marked and a fourth faintly. Axial furrows straight. First and second pairs of pleurae broad, strongly furrowed, ending in long free points. Third pair of pleurae fused, unfurrowed, extending backwards much further than tips of second pleurae, gently embayed for a short way mesially, but without free points. Surface strongly tuberculate.

Remarks. Hypostome and pygidium have been attributed to this species on the grounds of their greater width, compared with *A. priscus*.

Genus *HEMIARGES* Gürich 1901*Hemiarges* sp.

Plate 83, fig. 20

Material. Three crania.

Material from other horizons. Crania from the *superstes* Mudstones, Aldons.

Remarks. The long, rounded frontal lobe and small bicomposite lobes are distinctive features of this small species. Identical crania from the *superstes* Mudstones, Aldons, are better preserved, and justify specific description.

Family ODONTOPLEURIDAE Burmeister 1843

Genus *CERATOCEPHALA* Warder 1838*Ceratocephala* sp.

Plate 83, fig. 21

Material. Two crania.

Description. Glabella broad posteriorly narrowing forwards, ill defined; longitudinal convexity strong. Central lobe with independent transverse convexity. Anterior lateral lobes obsolete. Middle and posterior lateral lobes and furrows ill defined except for apodemes. Occipital ring moderately long, strongly convex longitudinally, fused with fixed cheeks laterally, without posterior band. A pair of strong, divergent occipital spines at back of ring with prominent median tubercle anterior to them. Fixed cheeks only slightly wider than basal lobes. Palpebral lobes elevated, placed opposite middle lateral lobes; a row of small tubercles just above base of lobe. Eye ridges comparatively short. Larger tubercles on cranium are symmetrically arranged as follows: six pairs of tubercles on central lobe of glabella, fourth pair from back placed on a transverse ridge, and two tubercles one behind the other on middle and posterior lobes.

Remarks. This form bears some resemblance to a new species from the platy upper Stinchar Limestone, but differs (1) in having cranial tubercles smaller; (2) only one pair of tubercles on central lobe placed on a transverse ridge, compared with the upper Stinchar species in which all six pairs are situated on ridges; (3) two pairs of tubercles on the lateral lobes.

Unassigned free cheek

Plate 81, fig. 15

Material. Three free cheeks.

Description. Free cheek extremely broad, strongly rounded in outline, gently convex. Eye (incomplete) short, weakly rounded. Inner area much wider posteriorly than anteriorly. Lateral border widens towards back. Short (exs.), wide (tr.) subgenal notch indents posterior border laterally. Lateral and posterior border furrows shallow, meeting at an acute angle. Librigenal spine continuous with lateral border in curvature, tapering steadily. Inner area of cheek finely and closely tuberculate.

Remarks. It seems unlikely that the free cheek figured belongs to any of the genera recorded in this paper.

Unassigned hypostome

Plate 81, fig. 16

Material. One hypostome.

Description. Hypostome elongate. Middle body oval, moderately swollen, extending to anterior border. Posterior lobe short, strongly defined laterally, weakly demarcated mesially. Lateral and posterior border furrows deep. Anterior wings small. Lateral borders consists of narrow bands anteriorly, widening slowly and becoming more convex backwards. Posterior border long (exs.), flattened, with rounded median indentation (best seen on external mould) extending half-way across border. Area anterior to indentation swollen. Longitudinal raised lines on anterior parts of lateral borders; remainder of surface smooth.

Remarks. This hypostome does not seem to be attributable to any one of the foregoing genera. A pygidium of *Carrickia* is closely associated with this specimen, but there is no evidence that they are part of one individual, although appropriate in size. Ross (1951, pl. 16, figs. 21–29) figured five unassigned hypostomes from the same horizon as *Gonio-phrys*, but none of these has an embayed posterior border.

CONCLUSIONS

1. The Albany mudstones with calcareous nodules yield a shelly fauna, without graptolites, in which both trilobites and brachiopods are moderately common. All the specimens occur as isolated parts, but the preservation is good, and there is no sign of abrasion. None of the species described has been recognized outside the Girvan area.
2. Williams (1962, p. 58) correlated the fossiliferous beds of the Albany Group with the top of the Stinchar Limestone. The trilobite fauna is most closely allied to that from nodules in the *superstes* Mudstones at Aldons Quarry. The following species occur at both horizons:

<i>Carrickia pelagia</i> gen. et sp. nov.	<i>Sphaerexochus</i> sp.
<i>Nileus</i> sp.	<i>Quinquecosta williamsi</i> gen. et sp. nov.
<i>Raymondaspis</i> sp.	<i>Hemiarges</i> sp.
<i>Ceraurinella</i> sp.	

The following are closely allied to forms from the *superstes* Mudstones:

<i>Trinodus</i> sp.	<i>Dimeropyge hystrix</i> sp. nov.
<i>Remopleurides</i> sp. B.	<i>Toernquistia</i> sp. A.
<i>Hypodicranotus</i> sp.	<i>Encrinuroides obesus</i> sp. nov.
<i>Hibbertia whitingtoni</i> sp. nov.	

All the genera except *Bumastoides*, *Mesotaphraspis*, and *Ceratocephala* occur in the *superstes* Mudstones, Aldons. However, the *superstes* is a much larger fauna, and the degree of relationship cannot be assessed until work on the Lower Barr trilobites has been completed.

3. The Albany mudstone fauna consists mainly of genera which occur earlier in the

- district. The only new appearances of any significance are *Nileus* and *Toernquistia*, the former widely dispersed at earlier horizons, the latter a first record.
4. Outside the Girvan area the closest relations are with the lower Edinburg Formation of the Appalachian Valley of the U.S.A., as is the case with all the Lower Barr trilobite faunas. Seventeen genera are common to both horizons, the most significant being *Mesotaphraspis*. There is a possible link with the Kukruse Stage (C_{11}) of Estonia (*Dimeropyge*, *Quinquecosta*), but no connexion with contemporary Anglo-Welsh faunas.
 5. The new genus *Carrickia* constitutes the only record of the rare family Komaspidae in the Girvan district. The most closely allied genus is *Gontophrys* from the Garden City Formation. The second new genus *Quinquecosta* provides an interesting link between the Encrinuridae, Pliomeridae, and Phacopidae. Unlike *Carrickia*, it does not appear to have North American antecedents. *Hypodicranotus* occurs considerably earlier in the Girvan District than in North America, as far as is known at present.

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SENSORY SPINES IN THE JURASSIC BRACHIOPOD *ACANTHOTHIRIS*

by M. J. S. RUDWICK

ABSTRACT. The rhynchonelloid *Acanthothiris* has tubular external spines similar to the spines of productoids and chonetoids. Their structure, arrangement and mode of growth are described in detail, on the basis of a study of exceptionally well-preserved specimens of *A. spinosa*. They are compared to the spines of the related genus *Acanthorhynchia*, and to those of the living oyster *Crassostrea echinata*. On the basis of the known sensory physiology of living brachiopods, it is inferred that the spines near the valve-edges of *Acanthothiris* contained extensions of the mantle, and that their tips bore portions of the highly sensitive mantle-edge tissue. These sensitive spine-tips could have provided the brachiopod with effective 'early warning' protection against potentially harmful agents in the environment; and the radiating spines themselves could have formed a protective grille straddling the apertures leading into the mantle cavity. Spines further from the valve-edge are blocked, and are regarded as having been superseded functionally. This interpretation is discussed in relation to the spines of other brachiopods and *Crassostrea*, and in relation to the ontogeny, ecology and phylogeny of *Acanthothiris*.

TUBULAR external spines were developed in great abundance and diversity in one sub-order of the Brachiopoda, namely the Upper Palaeozoic Productoidea. Similar spines, developed only in one particular position on the shell, characterize another Upper Palaeozoic suborder, the Chonetoidea. Outside these two suborders, tubular spines are rare and sporadic. This paper is concerned with one of the best known of these anomalous genera, the Jurassic rhynchonelloid *Acanthothiris*. This is separated by a span of about 100 million years from the last of the spiny productoids and chonetoids, and is even more decisively separated from them by morphology and taxonomy. In all characters except the spines, it is a 'normal' rhynchonelloid. It thus illustrates a common phenomenon in brachiopod evolution: a structure characteristic of some major group is often found to have been evolved independently by one or a few anomalous genera which clearly belong (on every other criterion) to a quite different group (cf. Williams 1956). A functional analysis of the spines of *Acanthothiris* may help to throw light on this phenomenon.

Material. For this study, I have used a small collection of very well-preserved specimens of *A. spinosa* (Schlothheim), the genotype, from the Inferior Oolite (Middle Jurassic) of 'Collier's Lane, nr. Bath' (Sedgwick Museum, Cambridge, SM J57751-71), together with some similar specimens from another old collection, labelled 'Gt. Oolite, Bath' (Museum of Comparative Zoology, Harvard, MCZ 5794). Despite the difference of labelling, all these specimens may come from the same locality. 'Collier's Lane' is unfortunately not mentioned by name in Richardson's (1907) account of the stratigraphy of the Inferior Oolite around Bath. Richardson records *A. spinosa* from most units of the Inferior Oolite; but the matrix suggests that the specimens came from the Upper Trigonion Grit. The matrix is a hard oolitic limestone, but it has weathered in pockets to a much softer material which, with care, can be dissected away from the spines. Normally only the stumps of the spines are preserved.

For comparative purposes, I have also studied the closely related species *Acantho-*
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rhynchia senticosa (von Buch) from the Inferior Oolite of Dorset. There are no living brachiopods with true tubular spines. But the mollusc *Crassostrea echinata* (Quoy and Gaimard) is a possible functional analogue. I have collected this oyster from intertidal localities on the Queensland coast and offshore islands, and studied it alive in a small aquarium.

The photographs in this paper were taken with a Leitz Aristophot on Ilford Pan F film; all except Plate 86, fig. 5 were lightly coated with ammonium chloride.

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STRUCTURAL ANALYSIS

General description. The shells of *Acanthothiris* (the 'corrected' spelling *Acanthothyris* is invalid: see Ager 1960) are typically 'rhynchonelloid' in form. They are strongly biconvex in profile, broadly elliptical in plan, and have a non-strophic hinge. There is a small incurved ventral umbo; the dorsal umbo is tucked inside the delthyrium. There is a dorsal median deflexion in the commissure, a low median fold on the dorsal valve, and a shallow median sulcus on the ventral. The surface of each valve is covered with a pattern of fine costellae radiating from the umbo. On most specimens, the costellae appear to be swollen at intervals into small pustules (Pl. 84, fig. 1); but well-preserved specimens show that these pustules are in fact the broken stumps of slender spines.

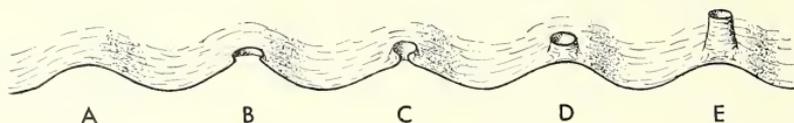
The whole array of spines covers almost all parts of the valve-surfaces. The spines are arranged in rows corresponding to the costellae from which they project, radiating from the umbo of each valve towards the valve-edge. The number of rows, like the number of costellae, increases progressively in this direction. Within each row, the spines project from the costella at fairly regular intervals (Pl. 84, figs. 1-3; Pl. 85, figs. 1, 3, 4). They are not arranged regularly in concentric fashion, but it will be convenient to refer to a *set* of spines as those projecting from any narrow concentric zone of the valve-surface (cf. Rudwick 1959). On most parts of the shell the spines project almost tangentially from the curved surface of the valves; but in the lateral sectors, and especially near the commissure, they project at higher angles and even perpendicularly (Pl. 84, fig. 5).

The spines are very rarely preserved to their full length; some have been dissected from the matrix to a length of 8 mm. (Pl. 85, fig. 5) but were certainly longer than this. They are cylindrical; at the base they are about 0.5 mm. in diameter, but they taper gradually to about 0.2 mm. diameter on those preserved to the greatest length (Pl. 84, fig. 6; Pl. 85, figs. 1, 5; Pl. 86, figs. 1, 5). They are straight or slightly curved. They are composed of an external sheath of dense primary-layer shell, of matt appearance, within which there is generally an almost solid core of shiny fibrous secondary-layer shell. The contrast between the two layers is easily seen at the broken tips of the spines (Pl. 86, fig. 5) or on the broken stumps (Pl. 85, fig. 2).

Mode of growth of spines. Since the spines are sheathed in primary-layer shell, which is continuous with that of the rest of the valve, it is clear that they are derivatives of the valve-edge, at which the primary-layer was secreted. Their mode of growth can be

reconstructed from a study of individual spines preserved at various stages of growth, and from the growth-lines on the primary-layer.

The commissure was affected throughout ontogeny by a serial deflexion of small wavelength and low amplitude. Thus the valve-edges were slightly crinkled and interlocked with one another (Pl. 84, fig. 2; Pl. 86, figs. 6, 7), while the cumulative effect of the deflexion was to produce the costellae on the valve surfaces. Each spine first appeared at the valve-edge on one of the crests (text-fig. 1A) of the deflexion. Initially it was marked only by a slight expansion of the valve-edge at this point (text-fig. 1B). Successive increments of primary-layer accentuated this into a small 'collar' (text-fig. 1C). At the next stage observed the 'collar' had been completed into a shelly ring surrounding a small foramen, while the main growing-edge had resumed its normal form (text-fig. 1D). In other words, a small circle of valve-edge had, in effect, been 'budded off' from the



TEXT-FIG. 1. Initial stages in the growth of a tubular spine at a valve-edge in *Acanthothis*. For further explanation, see text. Semi-diagrammatic, about $\times 20$.

rest of the valve-edge. Thereafter it grew independently, adding circular increments of primary-layer, which lengthened the ring into a tube; while the continued growth on the main growing-edge isolated the base of the incipient spine further from the valve-edge (text-fig. 1E). All these early stages in the growth of a spine can be recognized near the valve-edges of well-preserved specimens (Pl. 84, figs. 3, 4; Pl. 86, figs. 2, 3, 4). Further growth at the distal end of the spine, with a gradual reduction in the diameter of the circle of growing-edge, would have produced the long, gently tapering form of the full-grown spines.

Relation of spines to mantle-tissue. These growth-stages can be interpreted in terms of the secretory activity of the mantle-tissue by using the standard homological relation between shell and mantle as known in living brachiopods (cf. Williams 1956). Thus the budding-off of a ring of valve-edge material reflects an identical budding-off of a ring of mantle-edge tissue, by which the primary-layer was secreted. Each hollow-growing spine must have been lined with an inner tube (or possibly a solid cylinder) of mantle-tissue, connecting the distal ring of mantle-edge tissue to the rest of the mantle. Obviously the spine could have grown in length only so long as this connexion was maintained.

If the spines are examined in cross-section near the base (e.g. where they have all been broken off) it is clear that their walls were progressively thickened with secondary-layer, until the central lumen was constricted to vanishing point. Only the spines nearest the valve-edge (i.e. the youngest spines) have a clear central lumen; those further from the valve-edge (formed earlier in ontogeny) are blocked with concentric layers of shell-material (Pl. 84, fig. 3; Pl. 85, figs. 1, 2; Pl. 86, fig. 4). This secondary-layer material must have been secreted by the inner tube or core of mantle-tissue, which must thereby have been progressively constricted. Ultimately the tissue must have been abandoned; the spine could then have grown no more. The completion of this process is seen also in

the blocking of the internal foramina leading into the spines: these are clearly open near the valve-edges, but are blocked further in from the valve-edges (Pl. 86, figs. 2, 3, 6, 7).

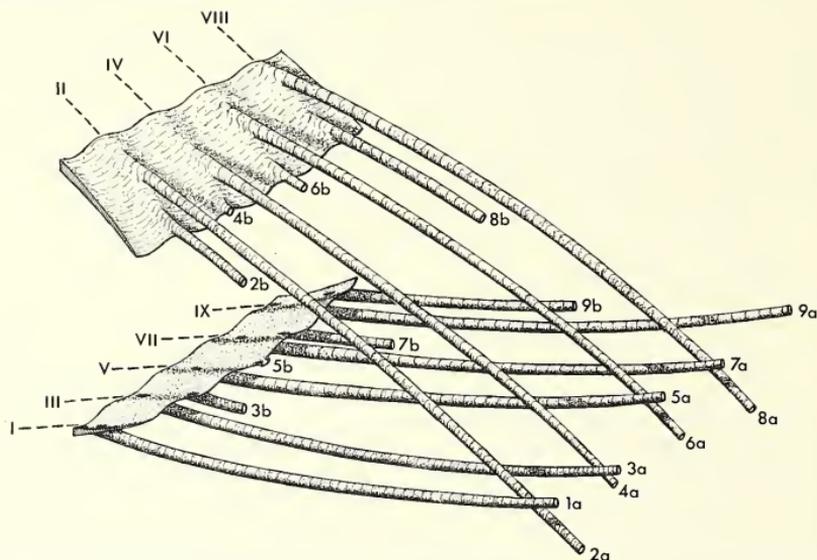
Time-sequence of growth of spines. This distinction between *open* and *blocked* spines leads to an interpretation of the time-relations of the whole array of spines. The spines in each row are those that were successively budded off, during ontogeny, from the same crest of the serial deflexion. The spines in each set, lying on or near any single growth-line on the valve-surface, are those that were formed all round the valve-edge at or about the same time during ontogeny. In any given row, at the moment when a new spine began to be formed at the valve-edge, the immediately preceding spines would still be open, but the earlier ones would have been blocked. On the valve as a whole, at any given moment in ontogeny, the most recently formed set or sets of spines, all round the valve-edge, would still be open, but all those nearer the umbo would have been blocked (Pl. 86, figs. 6, 7). Although a spine might have remained open after ceasing to grow, the converse is of course impossible; hence the actively growing spines must also have been restricted to the peripheral zone of each valve. Each individual spine must therefore have grown relatively quickly to its full length.

Orientation and arrangement of spines. If the shell is described 'statically', the orientation of the spines appears to be rather haphazard: especially in the lateral sectors they seem to project at many different angles (Pl. 84, fig. 2). A more 'dynamic' description, taking into account the time-relations of the spines, reveals a simpler and more orderly arrangement. Seen in plan, each spine projects perpendicularly from the growth-lines on the valve-surface at its base (Pl. 84, fig. 2; Pl. 85, figs. 1-4); in other words, during the time of its formation and growth it projected *radially* from the valve-edge. Seen in profile, each spine projects obliquely from the valve-surface and curves gently towards the opposite valve (Pl. 84, fig. 6; Pl. 86, fig. 1); during the time of its formation and growth it would have projected at a low angle across the plane of the commissure. The most recently formed sets of spines on the two valves would thus have projected radially and interdigitated with each other (text-fig. 2). Since all the spines were formed from the crests of the serial deflexion, and the crests necessarily alternate in position on the two valves, the projecting spines would have alternated likewise, and therefore would not have obstructed the closing of the shell. The spacing of the spines around the valve-edges was markedly uniform at any given growth-stage. In the later stages there was generally a gap of about 0.7 mm. between the bases of adjacent spines. Since the spines diverge and also taper, this spacing would obviously have increased away from the valve-edge.

Ontogeny of spines. The formation of radiating spines began very early in ontogeny. On large shells the stumps of the earliest spines are preserved very close to the umbo of each valve (Pl. 84, fig. 1; Pl. 85, fig. 2). The growth-lines show that they correspond to a stage at which the shell was only about 1.5 mm. broad. A rough estimate from the size of the stumps suggests that the spines themselves were about 0.15 mm. in diameter near the base, and were there separated from each other by spaces about 0.25 mm. across.

During the next stage of ontogeny the diameter and spacing of the spines increased rather rapidly to the adult size (Pl. 84, fig. 2). Thereafter, notwithstanding the progressive increase in the size of the shell, both the diameter and the spacing of the spines remained remarkably constant. This probably reflects a similar constancy in the original length of the spines. The average spacing of the peripheral spines (about 0.7 mm. at the base) was

maintained, in spite of the increasing length of the valve-edges, by the progressive introduction of new rows of spines (borne on new costellae) intercalated between the earlier rows. The effect of this is to be seen in the overall appearance of the whole shell: the bases of the spines appear to be scattered at a uniform density over all parts of the valve-surfaces (Pl. 84, figs. 1-3, 5; Pl. 85, figs. 1-4).



TEXT-FIG. 2. Reconstruction of parts of the valve-edges in *Acanthothiris*, gaping apart as in life, showing grille of spines straddling the aperture, and sensitive spine-tips projecting outwards from the shell; about $\times 10$.

Only the peripheral zone of 'open' spines is shown: note apertures on inner surface of lower valve. Costellae I, III, ... on one valve alternate with costellae II, IV, ... on the other; hence spine-rows 1, 3, ... interdigitate with spine-rows 2, 4, ... In each row there is one fully-grown 'open' spine (*a*); spines of the next set (*b*), which would ultimately supersede them, are at various stages of growth (*9b* and *8b* are most advanced, *5b* and *4b* least; *1b* has not yet appeared).

The spacing between successive spines in a single row was also kept remarkably constant during ontogeny. This is particularly striking if a row on the anterior sector of the

EXPLANATION OF PLATE 84

Figs. 1-6. *Acanthothiris spinosa* (Schlotheim); Inferior Oolite (Middle Jurassic); Bath, England.

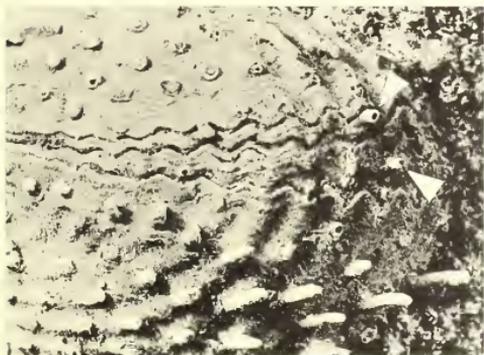
1. Left postero-lateral view of SM J57759, $\times 3$, showing general form of shell, costellae, and stumps of broken spines.
2. Spines on left antero-lateral sector of dorsal valve of SM J57757, $\times 6$.
3. Spines on left lateral sectors of MCZ 5794a, $\times 6$, showing short 'active' or 'open' spines near commissure (two with white pointers), and 'blocked' stumps of earlier spines.
4. Fragment of valve-edge MCZ 5794c, $\times 6$, showing two very young spines.
5. Spines on left postero-lateral sector of SM J57757, $\times 6$, showing radial orientation of later spines (one complete young spine with white pointer).
6. Row of spines on left lateral sector of dorsal valve of SM J57753, seen in profile (valve broken), $\times 6$, showing slight curvature towards commissure.



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shell is compared with one of the much shorter rows on the postero-lateral sectors. The total number of spines projecting from a long row is much greater than from a short row, although both of course represent the same span of time. Yet the spacing between successive spine-bases is approximately the same (about 1.2–1.5 mm.). This implies that a new spine began to be formed at the valve-edge whenever the preceding spine had become distant from the edge by that amount, regardless of the length of time that had elapsed since the preceding spine was formed.

Comparison with spines in other shells. The related genus *Acanthorhynchia* has spines which are closely similar to those of *Acanthothiris*, except that they are on a smaller scale. Thus, where only the stumps of the spines are preserved, they form a similar but much finer pattern on the valve-surface (Pl. 87, fig. 2; compare Pl. 84, fig. 1, at same magnification). The spines themselves are very similar in appearance, but are only about 0.1 mm. in diameter near the base, though they reach over 4 mm. in length (Pl. 87, fig. 1; compare Pl. 85, fig. 2, at same magnification).

No other rhynchonelloid has comparable spines. The living species *Tegulorhynchia döderleini* (Davidson) has radial rows of very short projections, scarcely deserving the name of spines, each of which is a short incomplete tube with a slit or seam on the side nearest the valve-edge (Leidhold 1922, Taf. XIII). In this they resemble the earliest stage in the formation of a true tubular spine; but the budded-off portion of the valve-edge evidently fails to fuse into a complete isolated ring. As Leidhold pointed out, such short spines have more resemblance to the short spines of some bivalve molluscs (e.g. *Pinna*) than to the tubular spines of fossil brachiopods.

Hölder (1958) has likewise emphasized the fundamental difference between such molluscan spines and the spines of *Acanthothiris*. Nevertheless, at least one mollusc shows a moderately close, though imperfect, analogy. This is the oyster *Crassostrea echinata* (Quoy and Gaimard), which in the juvenile stage develops moderately long quasi-tubular spines. They are not truly tubular, for they invariably have a narrow slit or seam on the side nearest the valve-edge (Pl. 87, figs. 6, 8); but they may reach a length of 5 mm. at an external diameter of about 0.7 mm. They are formed by the development of an upturned 'collar' of valve-edge (Pl. 87, figs. 1, 2), which fails to fuse into a complete ring; but the further addition of incomplete rings of shell-material builds up a cylinder which, from the side furthest from the valve-edge, appears to be a complete tube (Pl. 87, figs. 5, 7). The spines project almost perpendicularly from the surface of the free (uncemented) right valve of the oyster. They are not arranged in regular radial rows, but generally occur in roughly concentric sets. Each set consists of spines which, at their time of formation, were spaced at fairly regular intervals around the edge of the valve. The set nearest the valve-edge has open apertures to the interior; earlier sets have been blocked off at the base (Pl. 87, figs. 4, 6, 8).

Rather similar spines seem to have developed in one orthoid brachiopod, *Spinorthis geniculata* Wright (1964), of Upper Ordovician age. These spines are arranged in radial rows and concentric sets, and project almost perpendicularly from the valve-surfaces. They are short, and appear to be incomplete tubes. Spines with a greater similarity to those of *Acanthothiris* have been found in an atrypoid brachiopod, *Atrypa cf. aspera*, of Middle Devonian age (Jux 1962). They are arranged in radial rows, and seem to have been long and tapering; it is not clear whether they were true or incomplete tubes.

Apart from such sporadic occurrences, the only genuine structural analogues to the spines of *Acanthothiris* are the spines of productoids and chonetoids. These are truly tubular spines, and were apparently formed in an identical manner, by the 'budding-off' of small portions of the valve-edge. The spines of some spiriferoids, which may be 'double-barrelled' and bear hooks or barbs, do not seem to be comparable.

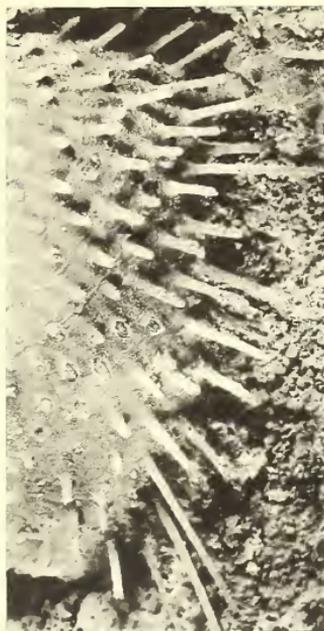
FUNCTIONAL ANALYSIS

Rejected interpretations. Many functional interpretations have been suggested for spines in general, or for the spines of brachiopods in particular. Most of them, however, are clearly inapplicable to the spines of *Acanthothiris*. These are so narrow in bore, and would have been even narrower when lined with an inner tube of mantle-tissue, that it is inconceivable that they could have acted as channels for the water-currents flowing through the mantle-cavity. For the same reason, and since few of them were open at any given growth-stage, it is inconceivable that they could have increased significantly the area of mantle-tissue available for gaseous exchange. Moreover, as Hölder (1958) has pointed out, *Acanthothiris* is generally found in calcareous sediments, which are unlikely to have been deposited in poorly aerated conditions. The spines are fragile (at least in the fossil state: they would have been less so when the organic component of the shell-material was still present); and once they were broken they could not be repaired (unless they were still 'open'). It is therefore difficult to believe that they performed any porcupine-like function of protection against large predators. On the other hand, it is perhaps possible that they might have served to camouflage the shell, by breaking up its otherwise sharp and distinctive outline. This fails to account, however, for most of the detailed characteristics of the spines. Finally, whatever the natural orientation of the shell, most of it must have been above the level of the substratum, in order to provide the apertures with clear access to food- and oxygen-bearing water. Hence only a few of the spines (probably the earliest, in the umbonal region) could ever have served to anchor the shell in a soft substratum (cf. text-fig. 3B). Unlike the rhizoid spines of productoids (Muir-Wood and Cooper 1960), the spines of *Acanthothiris* have never been found cemented to substratal material.

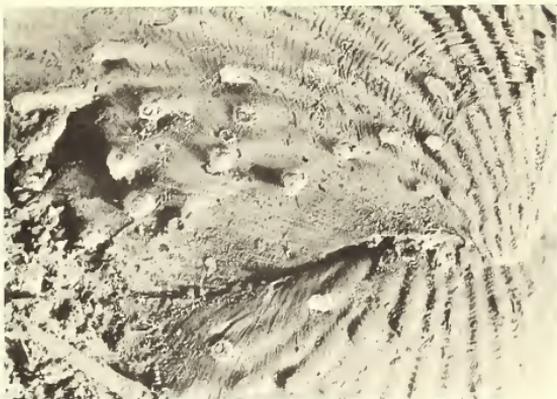
Spines as a sensory mechanism. A more promising interpretation can be derived from knowledge of the sensory mechanisms of living articulate brachiopods. Although the exact nature of the sensory receptors is at present unknown, they are apparently confined to the extreme edge of the mantle. The mantle-edge is highly sensitive to touch, light, and some chemical stimuli, and is richly supplied with nerve-endings. (If setae are present, they too are sensitive, but only to tactile stimuli.) A simple reflex nerve circuit from the mantle-edge causes the shell to be snapped shut in response to stimuli (Rudwick

EXPLANATION OF PLATE 85

Figs. 1-5. *Acanthothiris spinosa* (Schlotheim); Inferior Oolite (Middle Jurassic); Bath, England. 1. Later spines on dorsal valve of SM J57756, $\times 6$, showing radial orientation and gently tapering form. 2. Umbonal region and right postero-lateral sectors of SM J57759, $\times 9$, showing structure of stumps of spines, and their early origin. 3. Spines on left lateral sector of dorsal valve of MCZ 5794a, $\times 6$, showing radial orientation. 4. The same, on SM J57757, $\times 6$. 5. Later spines on anterior sector of (broken) dorsal valve of MCZ 5794b, $\times 6$, showing gently tapering form.



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1961). Hence any modification of the form of the mantle-edges can be considered as a possible modification of this protective system. For example, sharply zigzagged valve-edges would have reduced the distance between the sensitive mantle-edges without any corresponding reduction in the area of the apertures (Rudwick 1964*a*). This would have improved the quality of protection at the apertures, but would not have given the brachiopod any *earlier* warning of the approach of potentially harmful agents. Early warning could only be provided by extending the sensitive mantle-edges, or parts of them, outwards away from the rest of the shell. This would have been precisely the effect of the spines of *Acanthothiris*. Each of the 'open' spines would have carried at its tip a small piece of the sensitive mantle-edge tissue (and possibly, but not necessarily, one or more setae). Assuming only that at least one of the many peripheral nerve-fibres extended along each spine, the tip would have formed a highly sensitive 'outpost' of the brachiopod's protective system, giving early warning of the approach of harmful agents and enabling the shell to be snapped shut well in advance.

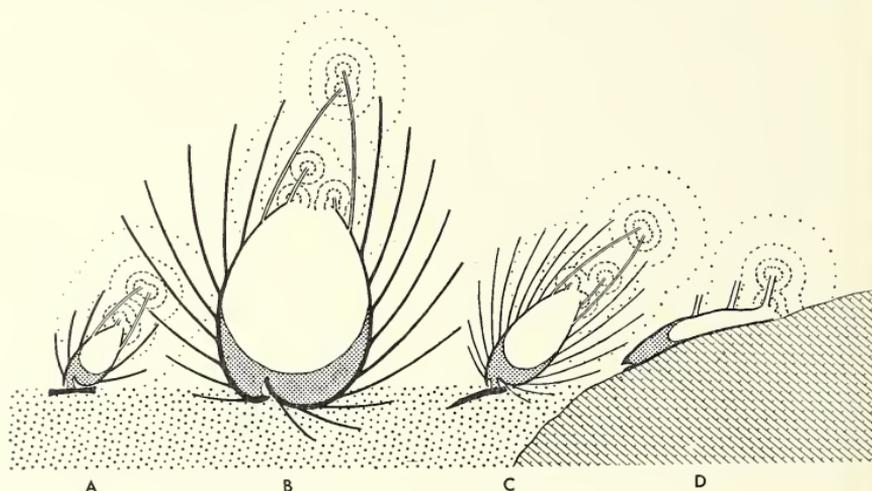
The paradigm, or optimal specification for this function (Rudwick 1964*b*), is fairly easy to determine. Ideally the tips of the spines might be situated very far from the shell, but in reality the length of the spines would presumably be limited by the supply of material available for their construction and by the strength of the material itself. They would need to be as slender as possible, consistent with strength, since they would otherwise tend to obstruct the free flow of the water-currents in and out of the mantle-cavity. A cylindrical form is of course the most effective shape by which to combine strength with economy. Their sensitive tips would be disposed most effectively if they were situated at uniform intervals all round the approaches to the apertures. With the continuing growth of the shell, the tips of these 'active' spines would inevitably be shifted further and further from the apertures, and would gradually become less effective; and they would need to be replaced by new spines, projecting from the valve-edges in their new position.

The observed structure and arrangement of the spines of *Acanthothiris* fit this specification very well. If the tips of the 'open' spines are identified as the points of chief functional importance, much that is otherwise obscure about the spines becomes intelligible. This interpretation explains the radial orientation and regular spacing of the spines in each set; the time-sequence of growth and blockage that marks each row; and their slender cylindrical form. It implies that only the most recently formed sets of spines were fully functional at any given growth-stage; and that all the earlier spines had been superseded and had become functionally redundant through the inevitable shift in their relative position (text-fig. 3*A*, *B*).

The range of sensitivity around each spine-tip would depend on the sensitivity of the mantle-edge tissue. This in turn would probably depend on properties at the cellular level, which would be unlikely to change in proportion to the growth of the whole organism. There would therefore be certain optimal distances for the spacing of adjacent spine-tips, both between spines in adjacent rows, and between successive spines in the same row; and these optimal values would remain relatively constant during ontogeny. Although the validity of this aspect of the paradigm cannot be demonstrated conclusively, it is at least probable, and it would explain the remarkable constancy in the spacing of the spines.

This interpretation is compatible with another, slightly different, concept of protection.

The peripheral spines, by their orientation and slight curvature towards the opposite valve, would have interdigitated when the shell was closed. When the valves gaped apart through a small angle (as they do in living brachiopods), and water-currents were being pumped by the lophophore through the mantle-cavity, the same spines would therefore have straddled the apertures with a protective grille (text-fig. 2). No 'particle' (e.g. a swimming animal or piece of floating debris) larger than the spaces between



TEXT-FIG. 3. Reconstructions of *Acanthothiris* (A, B) and *Acanthorhynchia* (C), with analogous section of *Crassostrea* (D), showing functional interpretation of spines as sensory 'antennae'. Note peripheral 'open' spines and earlier 'blocked' spines. 'Contours' of chemo-sensitivity (radii arbitrary) shown around open spine-tips and mantle-edges; for tactile sensitivity all the spines would be operative, and the protection would surround the whole shell. Reconstructions based on conservative estimates of original length of spines. 'Body' of animals close-stippled; lophophore, gills, &c., omitted. About $\times 1.5$.

A, young *Acanthothiris*, with pedicle attached to shell fragment. B, adult *Acanthothiris*, with pedicle atrophied, resting loosely on unconsolidated substratum. C, *Acanthorhynchia*, with similar but more slender spines, and smaller shell. D, young *Crassostrea echinata*, with broad tubular spines on upper (right) valve, left valve cemented to rock surface.

EXPLANATION OF PLATE 86

Figs. 1-7. *Acanthothiris spinosa* (Schlotheim); Inferior Oolite (Middle Jurassic); Bath, England.

1. Rows of spines on right antero-lateral sectors of SM J57757, $\times 6$, showing slight curvature towards commissure.
2. Interior of right antero-lateral sector of dorsal valve of SM J57753, $\times 6$, showing broad peripheral zone of unblocked spine-apertures.
3. Oblique view of same valve-edge, $\times 6$, showing connexion between two marginal apertures and their respective spines.
4. Very young spines on peripheral part of left antero-lateral sector of dorsal valve of SM J57756, $\times 6$.
5. Close-up of spines on anterior sector of dorsal valve of SM J57757, $\times 18$, showing shell-structure and growth-lines (not whitened).
6. Interior of left antero-lateral sector of MCZ 5794b, $\times 6$, showing narrow peripheral zone of unblocked spine-apertures.
7. The same, anterior sectors, $\times 6$.



1



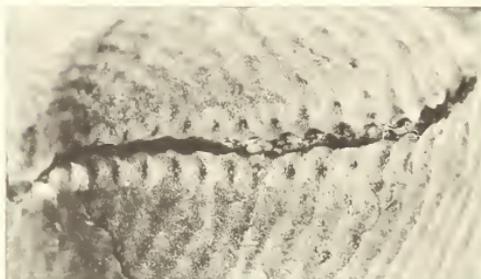
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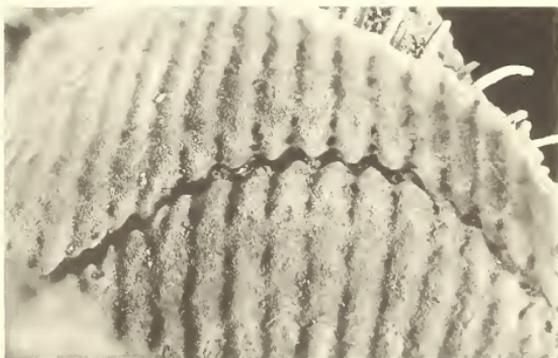
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adjacent spines could have penetrated to the apertures. The slender and uniformly spaced spines would have been highly effective as a protective grille of this kind.

In living brachiopods the shell itself is often highly sensitive to tactile stimuli (apparently by transmission of vibrations through the shell to the receptors in the mantle-edge). Thus another animal, alighting or crawling on to the brachiopod, even some way from the shell edge, may cause an immediate and rapid protective closure of the shell. In *Acanthothiris*, assuming the same properties, this type of tactile sensitivity would have extended to the whole length of the spines, *in addition to* the broader sensitivity (including photo- and chemo-sensitivity) of the mantle-edge tissue at the tips of the spines. Thus the protective grille of spines would have been more than a passive sorting device, barring the passage of particles larger than a certain size. Any but the lightest particles that collided with any part of any of the spines forming the grille would probably have caused a closure of the shell, and the grille would thus have acted as a protective warning device. (Even the 'blocked' spines further from the apertures could, of course, have acted in this way.)

It is not possible to decide conclusively between these two related interpretations of 'protection', because their paradigms are so similar (cf. Rudwick 1964*b*). In any case, given the validity of the anatomical reconstruction suggested here, the spines must necessarily have provided both varieties of protection, simply by virtue of their form and arrangement.

Functional analogues. The spines of *Crassostrea echinata* appear to serve a similar function of early warning protection. In the younger growth-stages, this species is cemented by the whole of its left valve to a substratum such as a rock surface or the root of a mangrove. When the shell is open, therefore, its apertures are immediately adjacent to the substratum. The peripheral set of spines projects perpendicularly from the edge of the right valve, and encloses quasi-tubular extensions of the right mantle. At the tip of each of these 'open' spines is a portion of the mantle-edge, which, as in brachiopods, is highly sensitive. Hence the peripheral set of spines extends the sensitivity of the oyster away from the shell in the most strategic direction, that is, away from the surface of the substratum (text-fig. 3*D*). When, during the growth of the shell, a set of spines is no longer close to the valve-edge, a new set is formed and the older set is blocked off at the base. This oyster provides a fairly close functional analogue to the interpretation suggested here for the spines of *Acanthothiris*.

The spines that Jux (1962) has described on a Devonian atrypid may also have been analogous in function. Though they are more irregular than the spines of *Acanthothiris*, they are roughly radial and would have interdigitated; and Jux suggests that they could have formed a grille guarding the apertures and excluding larger particles of shell-debris, &c. On the present interpretation this grille would have been not merely a kind of sieve but an active sensory device, causing the protective closure of the shell.

The tubular spines of productoids are diverse in form and arrangement, and were probably equally diverse in function, though all seem to have been formed in essentially the same manner. Of the varieties distinguished by Muir-Wood and Cooper (1960), the *rhizoid* spines manifestly served to anchor the shell to the substratum, and the *halteroid* spines are reasonably interpreted as serving to stabilize the shell on or in a soft substratum. The spines most closely analogous to the spines of *Acanthothiris* are the *prostrate*

spines, which are generally slender and project radially at a low angle to the valve-surface. These are interpreted as 'serving partly for protection or as a strainer when radiating out from the anterior of the shell' (p. 16). This statement is not amplified, and is not entirely clear. 'Protection' seems to imply protection by camouflage, or else what I have termed porcupine-like protection. A 'strainer' probably implies a structure similar to what I have termed a protective grille. But the primary function assigned to these spines in *Waagenoconcha*, which is one of the best examples, is 'to prevent the shell from sinking into soft mud' (p. 17). This could not be applied, however, to the prostrate spines on the dorsal valve, which are structurally identical to those on the ventral (assuming the shell lay on the convex ventral valve). But if they are interpreted instead as providing early warning protection, their distinctive arrangement becomes intelligible. They are very slender (about 0.15 mm. diameter) but relatively long (preserved to 5 mm. length or more); and they are arranged radially, projecting outwards around both valve-edges, even posteriorly across the hinge-line (Muir-Wood and Cooper 1960, pl. 90). If the peripheral sets of spines were 'open' and contained extensions of the mantle, with sensitive mantle-edge tissue at the tip of each, they could have provided this productoid with efficient all-round early warning protection.

The complex spines of some spiriferoids are different in structure, and presumably in mode of growth, from those of *Acanthothiris*. But they might have been similar in function. They are generally oriented radially, and are spaced uniformly all round the valve-edges.

The internal marginal spines of *Uncinulus* and *Hypothyridina* covered the apertures with a protective grille (Schmidt 1937), but could not have given early warning protection.

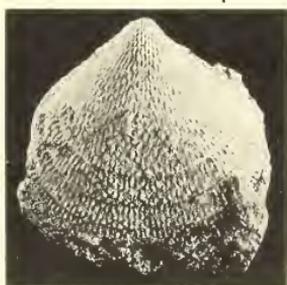
Ecology of Acanthothiris. Young shells of *A. spinosa* have a hypothyrid pedicle foramen, and were evidently attached to the substratum by a pedicle (text-fig. 3A). In larger shells, however, the ventral umbo has become tightly incurved towards the dorsal valve, leaving no space for the emergence of the pedicle. Thus the pedicle probably atrophied during ontogeny, and the adult brachiopods would have lain freely on the substratum. They were probably stabilized in orientation by shell-thickening in the umbonal region, and perhaps, adventitiously, by some of the earliest and superseded spines. The commissural plane was probably held in an oblique or even vertical orientation, so that all the apertures were clear of the substratum (text-fig. 3B). The current system may have been the same as in adult living rhynchonelloids (Rudwick 1962), the water entering the mantle-cavity laterally and being ejected through an anterior aperture corresponding in position

EXPLANATION OF PLATE 87

- Figs. 1-2. *Acanthorhynchia senticosa* (von Buch); Inferior Oolite (Middle Jurassic); Loder's Hill, near Bridport, Dorset, England. 1. Spines on right lateral sector of dorsal valve of specimen in collection of M. J. Collins, $\times 9$. 2. Ventral valve of same specimen, $\times 3$, showing arrangement of stumps of spines at all growth-stages.
- Figs. 3-8. *Crassostrea echinata* (Quoy and Gaimard); Recent; intertidal rock-surfaces at Eimeo, near Mackay, Queensland. (SM). 3, 4. External and internal views of right (free) valve of young shell, $\times 6$, showing one set of 'open' spines, with previous set blocked. 5, 6. External and internal views of part of right valve of another young shell, $\times 6$, showing 'seam' on outer side of each spine. 7, 8. External and internal views of ventral edge of right valve of a larger shell, $\times 6$, showing several sets of blocked spines.



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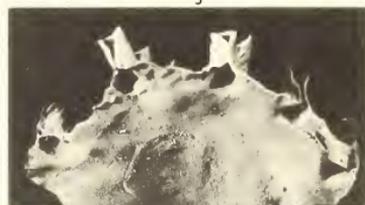
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to the median deflexion of the commissure. In any case, whatever the arrangement of the apertures around the commissure, it is clear that the spines provided the same degree of putative protection to all the apertures.

It is impossible to infer, with any supporting evidence, the exact nature of the 'harmful agents' against which the protection would have been effective. They might have included 'particles' as diverse as saltating shell-fragments, sand-grains or ooliths, pieces of organic debris in suspension, and small floating or swimming animals. Any of these might have clogged the delicate ciliary feeding apparatus of the brachiopod. The tips of the spines might also have been able, through the chemosensory properties of the mantle-edge, to detect the approach of potential predators, noxious water-conditions, &c.

If *Acanthothiris* was equipped with such an effective sensory apparatus, it is perhaps surprising that it is generally found in association with other, more 'normal' brachiopods (rhynchonelloids and terebratuloids without spines). This, however, overlooks the fact that such sensory apparatus as a brachiopod may possess is necessarily co-ordinated with other functional systems, especially the rejection mechanisms, which leave no structural trace in the fossil state. It is therefore invalid to assert that *Acanthothiris* must have been better adapted to its particular environment than the more 'normal' brachiopods with which it is associated, or (conversely) that since it is so associated its spines cannot have been an effective adaptation.

Phylogeny of Acanthothiris. Buckman (1907) asserted that a spiny shell was the phylogenetic terminal stage of a trend from a smooth shell through a stage in which the shell was ribbed. In the case of *Acanthothiris* there would seem to be no evidence for this. Its evolutionary origin is in fact obscure. Throughout its ontogeny (except in the earliest stage of growth), it seems to have been equipped with fully functional sensory spines. Unless some other rhynchonelloid is found, in which spines are less well developed or confined to a shorter part of ontogeny, it may be necessary to infer that the ancestor of *Acanthothiris* was a brachiopod of very small adult size, i.e. that it evolved by paedomorphosis.

The development of an early warning protective system in *Acanthothiris* was made possible by the evolution of the capacity for forming tubular spines at the valve-edges. This enabled portions of the sensitive mantle-edges to be extended outwards from the shell. This capacity had not, apparently, been evolved previously among the rhynchonelloids, and only rarely (e.g. productoids and chonetoids) in the whole history of the brachiopods. Considering the great adaptational potential of tubular spines (as shown in the history of the productoids), it is surprising that the development of spines in this rhynchonelloid stock should have been so short-lived and 'unsuccessful'. Possibly *Acanthothiris* and its allies became extinct, through the chances of environmental change, too soon for that potential to be realized. Possibly the many ecological niches that were open to the productoids in the Upper Palaeozoic were no longer open by the Jurassic, having been occupied perhaps by the bivalve molluscs. In any case, this is a problem that deserves closer analysis.

Without the capacity for forming spines, it would be difficult for a brachiopod to evolve an effective early warning system. One possibility, which appears to have been realized on two separate occasions, involved the formation of long narrow projections

of the mantle- and valve-edges. This gave rise to the well-known and astonishingly close homoeomorphic resemblance between the Middle Triassic athyracean *Tetractinella* and the Upper Jurassic terebratellacean *Cheirothyris* (Cloud 1941, Rudwick 1965). Given the limited anatomical 'materials' out of which any brachiopod adaptation must be formed, the only other means of providing early warning protection would be by the use of the sensitive setae projecting from the mantle-edge. This possibility is in fact utilized by several living brachiopods, and was almost certainly exploited by many fossil groups; but it suffers from the inherent limitation that the setae are only sensitive to tactile stimuli.

CONCLUSION

The structure and arrangement of the spines of *Acanthothiris* accord with a functional interpretation based on the known sensory properties of the mantle-edge in living brachiopods. On this interpretation, the spines projecting from the periphery of each valve acted like inflexible antennae, projecting outwards from the shell into the environment, and enabling the brachiopod to receive early warning of the approach of potentially harmful agents. They would also have straddled all parts of the gape into the mantle-cavity with a protective grille. The brachiopod would have had this protection throughout life; the spines formed earlier in ontogeny were progressively superseded by those formed later, the functional spines remaining close to the valve-edges.

Such spines would have been an effective adaptation in any brachiopod. Yet in fact they seem to have been evolved only once among the rhynchonelloids, and even on that occasion the adaptation had a relatively short history. They may have been evolved sporadically in other groups of brachiopods at other times, but were only common among the Upper Palaeozoic productoids. In view of their adaptive utility, their relative rarity needs some explanation. Their formation depended on the ability of the shell and mantle to form tubular spines, and this may have been a property that was only rarely evolved. But this fails to account for their generally short history, once they had been evolved. This problem may remain insoluble, until the ecological environment of these brachiopods has been rigorously analysed.

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SOME NORTH AMERICAN SPECIES OF THE DEVONIAN TETRACORAL *SMITHIPHYLLUM*

by A. E. H. PEDDER

ABSTRACT. The tetracoral genus *Smithiphyllum* is emended. It is shown to be closely related to *Tabulophyllum* and consequently is transferred from the Spongophyllidae to the Endophyllidae.

Additional material of the type species, *S. imperfectum* (Smith), is described and three new Frasnian species, *S. belanskii* from Iowa, *S. kindlei* from Alberta, and *S. whittakeri* from the Northwest Territories, are erected.

SPECIES now assigned to *Smithiphyllum* were first erected for specimens from Timan, at the turn of the century. Since then, others have been named for North American specimens, but recent workers have referred these to quite different genera and even families.

Apart from the description of new species, the purpose of this paper is to redefine the genus and elucidate its relationships.

The following abbreviations are used:

GSC for Geological Survey of Canada (Ottawa) type number
SUI for State University of Iowa (Iowa City) type number
N.W.T. for Northwest Territories.

SYSTEMATIC PALAEOLOGY

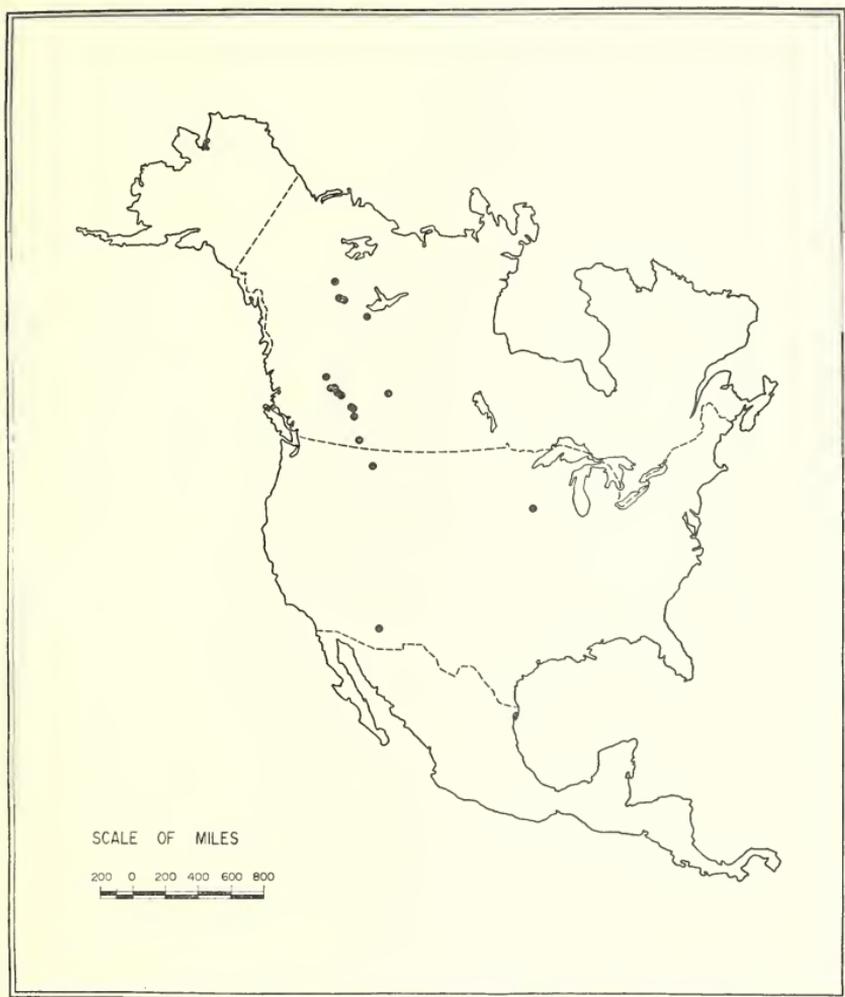
Family ENDOPHYLLIDAE Torley 1933

Genus SMITHIPHYLLUM Birenheide 1962, emend.

Type species (original designation). *Spongophyllum imperfectum* Smith. See below, p. 622.

Description. Fasciculate to subcerioid tetracorals with a relatively thick wall. The septa are radially arranged, typically smooth and clearly differentiated into two orders. The major may be withdrawn both axially and peripherally and the minor are commonly represented merely by ridges on the interior of the wall and short crests on the dissepiments. The dissepimentarium is narrow and may be lonsdaleoid; in some species, including the type, it is only intermittently developed. The tabulae are broad and in narrow corallites many are complete. They are generally gently sinuous in longitudinal section and are commonly downturned peripherally.

The minute skeletal structure is imperfectly preserved in much of the material studied. The skeletal material of the wall is almost entirely lamellar. As seen in transverse section the lamellae are deflected towards the axis at the bases of the septa and in longitudinal section they lie oblique to the wall surfaces with their upper edge away from the periphery. A thin dark line (axial plate of Flower 1961, p. 28) separates contiguous corallites; however, no trace of this is present in most free corallites. Fibre fascicles have not been observed, but sparse, dark, and apparently structureless spine-like bodies within the septa and walls may represent trabeculae.



TEXT-FIG. 1. Known distribution of *Smithiophyllum* in North American Frasnian beds. Occurrences indicated by a black circle.

Additional species assigned

Smithiophyllum belanskii sp. nov. See below, p. 623.

Smithiophyllum kindlei sp. nov. See below, p. 625.

Spongophyllum lituus Smith 1945, p. 56, pl. 11, figs. 5a-d. Redknife Formation (late Frasnian), Jean Marie River, N.W.T.

Spongophyllum martinense Stumm 1948, p. 41, pl. 11, figs. 9, 12; pl. 12, fig. 6. Martin Limestone (Middle Frasnian), Dear Creek Valley, Arizona.

Cyathophyllum stuckenbergii Lebedew 1902, pp. 179, 180, pl. 2, figs. 21-24. Uchta River, Timan. Probably Frasnian.

Cyathophyllum weberi Lebedew 1902, p. 178, pl. 4, figs. 49-53. Uchta River, Timan. According to Soshkina (1952, p. 70) this occurs in the Middle Frasnian D₃¹ 2-3 beds.

Smithiophyllum whittakeri sp. nov. See below, p. 626.

Species requiring further description

Spongophyllum expansum Stumm 1937, pp. 436, 437, pl. 53, fig. 11; pl. 55, figs. 6a, b. Basal 500 feet of the Nevada Limestone, Eureka region, Nevada. Stumm considered this to be a lower Middle Devonian species; it is now thought to be Emsian (Johnson 1962).

Spongophyllum nevadense Stumm 1937, pp. 435, 436, pl. 53, fig. 10; pl. 55, figs. 5a, b. Basal 500 feet of the Nevada Limestone (Emsian), Eureka region, Nevada.

Calophyllum tschernyschewi Lebedew 1902, p. 148, pl. 2, figs. 29-31. Uchta River, Timan. Probably Frasnian. See under the discussion of *S. imperfectum*.

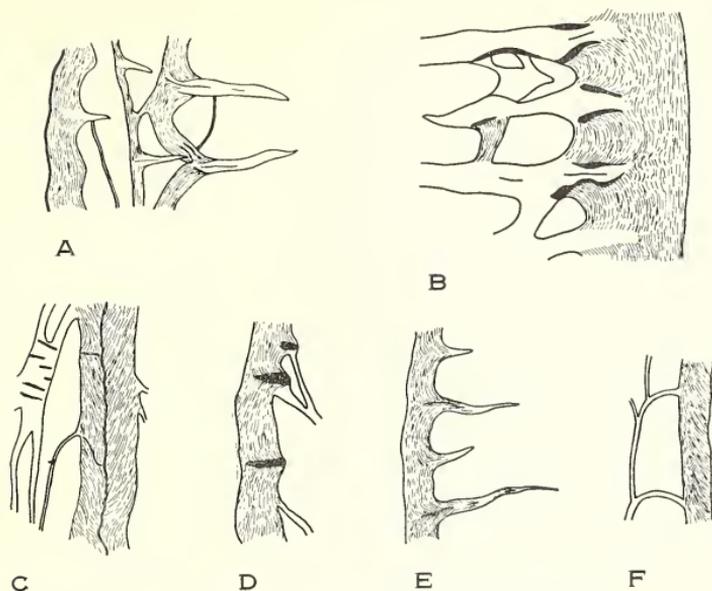
Distribution. At present the genus is known definitely only from the Frasnian of North America and Timan. Its distribution in the former is indicated in text-fig. 1. In addition to the described species the figure indicates the occurrence of some undescribed forms as well as others listed by Sloss and Laird (1945), Crickmay (1962, p. 4), and by McLaren and Mountjoy (1962, pp. 8, 23).

Discussion. Birenheide (1962, p. 82) included completely cerioid species, such as *Spongophyllum alpenense* Ehlers and Stumm, *S. brevisseptatum* Stumm, and *S. missouriense* Ehlers and Stumm, in the genus. The present writer prefers to regard these species as constituting either a new genus, or at least a subgenus. Another species included in *Smithiophyllum* by Birenheide is *Spongophyllum pax* Smith. This is based on a specimen found in a river boulder and is therefore of unknown stratigraphical origin. Crickmay (1960, pp. 878, 879) listed it in Givetian faunas from British Columbia, but Norford (1962, p. 27) has suggested that the species is Silurian and placed it in *Columnaria*.

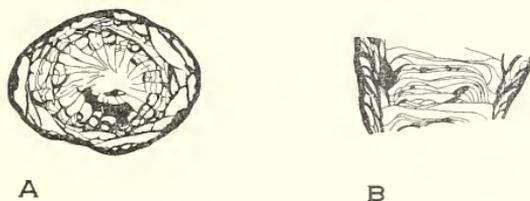
In recent years the species now grouped in *Smithiophyllum* have most frequently been referred to *Spongophyllum*. The latter cannot be said to be a fully understood genus since the minute structure of the type species is imperfectly known, but it does differ from *Smithiophyllum* in being cerioid and by having essentially concave tabulae and a well-developed dissepimentarium, even in very narrow corallites.

Smithiophyllum is close to *Tabulophyllum* (text-figs. 2B, D; 3A, B) and in fact Soshkina (1952, p. 70) assigned *S. weberi* to *Tabulophyllum*. Both genera possess a lamellar wall, broad typically peripherally downturned tabulae, and similar septa. Furthermore, the discontinuity, which is seen in the dissepimentarium of such species as *Smithiophyllum imperfectum* and *S. belanskii*, has also been figured in various species of *Tabulophyllum* (e.g. Frech 1885, pl. 10, fig. 2; Sloss 1939, pl. 11, fig. 18). *Smithiophyllum* is distinguished from *Tabulophyllum*, which is solitary, by its fasciculate to subcerioid form.

Birenheide (1962, p. 69) placed *Smithiophyllum*, and also doubtfully *Tabellaephyllum*, in the Spongophyllidae. However, this writer feels that the discontinuous crest-like septa and the peripherally downturned tabulae indicate a closer relationship with the Endophyllidae.



TEXT-FIG. 2. Minute skeletal structure (as far as preserved) in *Smithiphyllum* and *Tabulophyllum*. All $\times 15$. A, C. *Smithiphyllum belanskii* sp. nov., A from a transverse section of the paratype, SUI 11617, C from a longitudinal section of the holotype, SUI 11616. B, D. *Tabulophyllum mccoynelli* (Whiteaves), B from a transverse section of topotype, GSC 17547, from the Escarpment Formation (middle Frasnian) on Hay River, N.W.T. D from a longitudinal section of GSC 17548 from the Ferques Limestone (middle Frasnian) in the Parisienne Quarry, near Ferques, Boulogne region, France. E, F. *Smithiphyllum imperfectum* (Smith), from transverse and longitudinal sections, respectively, of GSC 17543.



TEXT-FIG. 3. *Tabulophyllum rotundum* Fenton & Fenton, $\times 2$. Based on topotype GSC 17549 from Cerro Gordo Member of the Lime Creek Formation at Rockford, Iowa. This specimen combines features considered by Fenton and Fenton (1924) as being diagnostic of both *T. rectum*, the type species of *Tabulophyllum*, and *T. rotundum*. A, transverse section. B, longitudinal section.

Smithiophyllum imperfectum (Smith 1945)

Plate 88, fig. 7; Plate 89, figs. 1-3, 10-12; text-figs. 2E, F, 4A-1

1945 *Spougophyllum imperfectum* Smith, pp. 55, 56, pl. 11, figs. 3a-g.

Holotype. GSC 6307. Upper Devonian, about one mile below the upper end of the middle gorge of Jean Marie River, N.W.T. In current stratigraphical terms (Belyea and McLaren 1962, pp. 6, 7) this specimen was obtained from the Redknife Formation (late Frasnian).

Other material. GSC 17543. Kakisa Formation (late Frasnian), 4 miles (direct) above the mouth of Poplar River, N.W.T. Collected by the writer in 1960 with *Endothyra* sp., *Mictophyllum modicum* Smith, *M. semidilatatum* Smith, *Hexagonaria magna* (Webster and Fenton), *Disphyllum* sp., *Tabulophyllum* sp. close to *T. mcconnelli* (Whiteaves), *Thamnopora* spp., *Alveolites* sp., *Syringopora* sp., *Schizophoria* sp., *Nervostrophia* sp., *Atrypa* sp., *Cyrtospirifer* sp., *Cranaena* sp., and *Scutellum* sp.

Description. The growth form is dendroid; in most cases the offsets diverge widely from the parent corallite so that the corallum has the appearance of being well spread out. Specimen GSC 17543, which was not completely collected, measured about $150 \times 100 \times 70$ mm. before sectioning. The corallites are sub-cylindrical and have an adult diameter of between 7 and 9 mm. Increase is lateral. The exterior of the exposed corallites bear rugae, but not interseptal ridges.

Although the wall is generally about 0.4 mm. thick, it varies between 0.25 and 0.75 mm. (Smith gives the range as 0.5 to 0.75 in the holotype); it consists of a very thin dark outer axial plate and an inner much thicker lamellar layer.

The septa are smooth, radially disposed and well differentiated into two orders. The major taper towards their axial extremity where they are very thin; most are continuous lamellae typically extending from one- to two-thirds the distance to the axis; some are peripherally withdrawn. The minor septa are very short, most are less than 0.5 mm. long and in young corallites they may be almost imperceptible. Number of major septa ranges from nineteen at 6.5 mm. diameter to twenty-two at 9.0 mm. diameter.

The dissepimentarium is intermittently developed and is entirely absent in some longitudinal sections; where it is developed it consists of a single row of elongate dissepiments numbering about ten in 10 mm.

The tabulae are broad and may be predominantly complete. Some are very nearly flat, but most are very gently sinuous as seen in longitudinal section.

Discussion. The synonymy and distribution of the species is fully treated elsewhere (Predder in press) and is not repeated here.

The cylindrical corallite described by Lebedew (1902, p. 148, pl. 2, figs. 29-31) under the name *Calophyllum tschernyschewi* is similar to isolated corallites of *S. imperfectum*.

EXPLANATION OF PLATE 88

All figures $\times 2$

Figs. 1-3, 5. *Smithiophyllum belauskii* sp. nov. from the Shellrock Formation, Iowa. 1-3, Holotype, SUI 11616. 5, Paratype, SUI 11617.

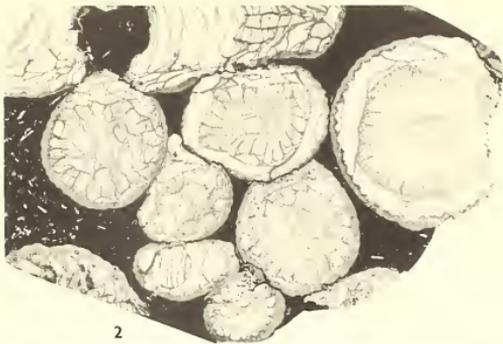
Fig. 4. *Smithiophyllum whittakeri* sp. nov. from the Redknife Formation, N.W.T. Holotype, GSC 17545.

Fig. 6. *Smithiophyllum kiudlei* sp. nov. from the Mount Hawk Formation, Alberta. Holotype, GSC 17544.

Fig. 7. *Smithiophyllum imperfectum* (Smith) from the Redknife Formation, N.W.T. GSC 17543.



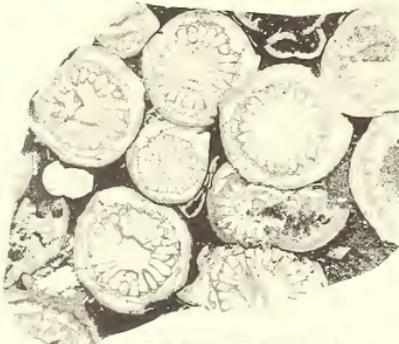
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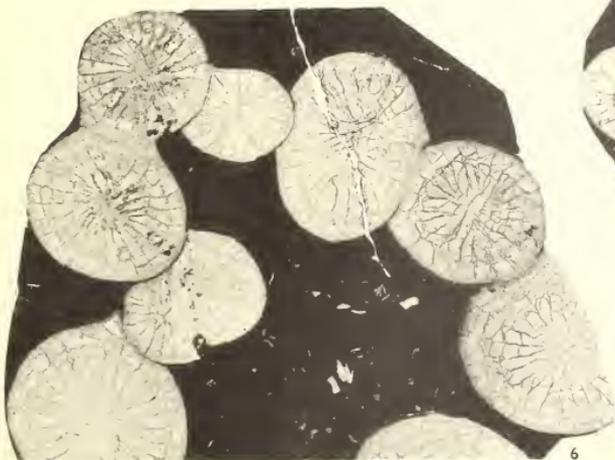
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4



5

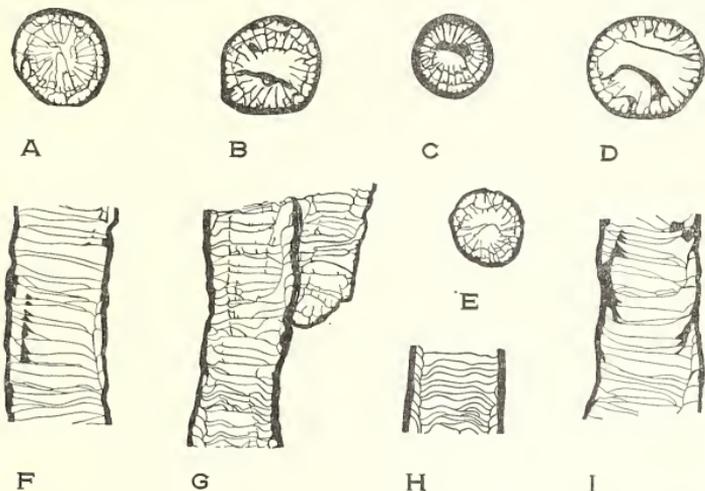


6



7

If Lebedew's species is based on an individual corallite of a fasciculate corallum, it appears to differ from *S. imperfectum* only in having as many as twenty-seven major septa at its full diameter of 9 mm.



TEXT-FIG. 4. *Smithiphyllum imperfectum* (Smith), $\times 2$. Based on figures given by Smith and Birenheide of the holotype, GSC 6307, and original figures based on GSC 17543. A-C, E, transverse sections of the holotype. D, transverse section of GSC 17543. F, I, longitudinal sections of GSC 17543. G, H, longitudinal sections of the holotype.

Smithiphyllum belanskii sp. nov.

Plate 88, figs. 1-3, 5; Plate 89, figs. 13, 16; text-figs. 2A, C; 5A-D

Name derivation. The species is named for the late C. H. Belanski in recognition of his contribution to the study of the Shellrock Formation and its fauna.

Holotype. SUI 11616. Mason City Member of the Shellrock Formation (early Frasnian) at Nora Springs, Floyd County, Iowa. Collected by the writer in 1956 with calcispheres, stromatoporoids and *Phillipsastrea websteri* (Belanski).

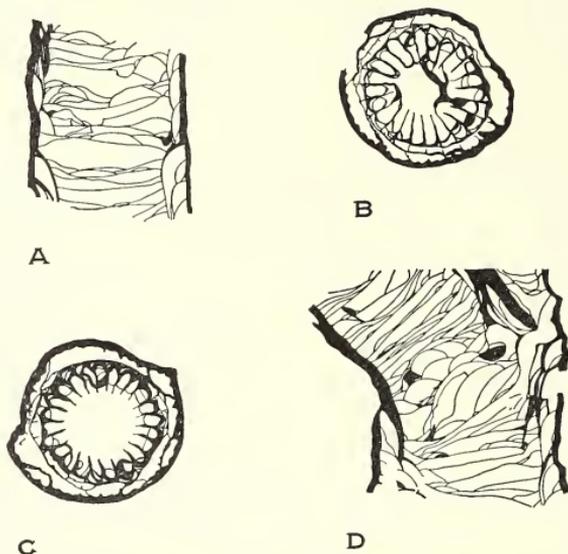
Paratype. SUI 11617. Same horizon, locality, and collector as the holotype.

Diagnosis. Maximum corallite diameter about 14 mm. Major septa up to twenty-five in number and withdrawn both axially and peripherally. Minor septa very suppressed. Dissepimentarium discontinuous.

Description. The corallum is dendroid to phaceloid. The largest specimen studied is the holotype, which was incompletely collected and measured about $100 \times 90 \times 60$ mm. before sectioning. Free corallites are subcylindrical, but contiguous ones may have their shape modified by pressure from adjacent corallites. They appear to have attained their full diameter of from 14 to 16 mm. slowly, so that most transverse sections show numerous

corallites of less than maximum diameter. Increase is lateral. The external features of the type specimens are completely masked by matrix.

The wall consists of an inner lamellar layer and a dark outer axial plate; the latter is extremely thin and only clearly visible between touching corallites. The thickness of the wall varies between 0.2 and 1 mm.



TEXT-FIG. 5. *Smithiphyllum belanskii* sp. nov., $\times 2$. Based on the holotype, SUI 11616 and the paratype, SUI 11617. A, D, longitudinal sections of the holotype. B, transverse section of the holotype. C, transverse section of the paratype.

The septa are meagrely developed, radially arranged, and are highly differentiated into two orders. The major are smooth and spring from either the interior of the wall or a dissepiment; in addition to being peripherally discontinuous, they are withdrawn axially, so that few extend more than two-thirds the distance to the axis and many

EXPLANATION OF PLATE 89

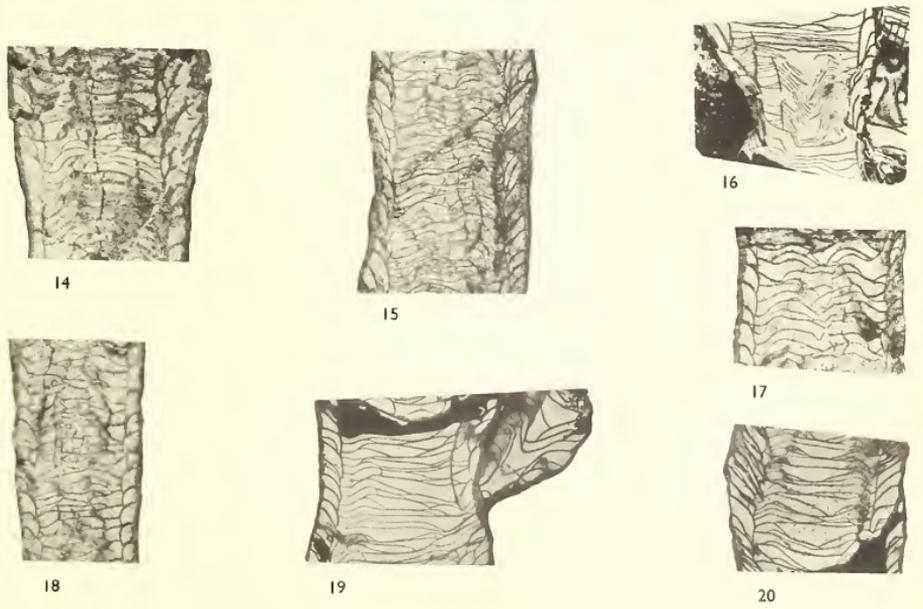
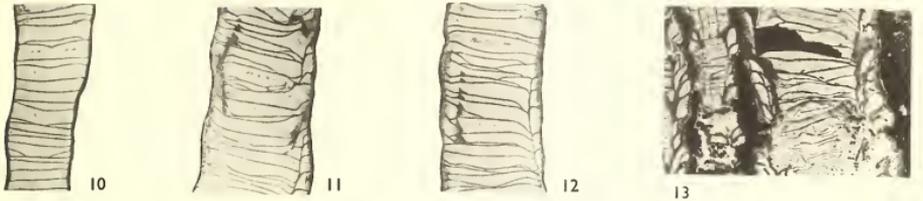
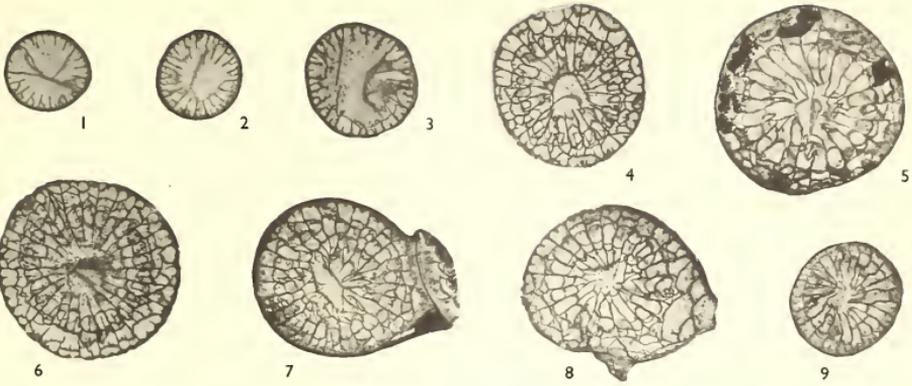
All figures $\times 2$

Figs. 1-3, 10-12. *Smithiphyllum imperfectum* (Smith) from the Redknife Formation, N.W.T. GSC 17543.

Figs. 4, 6, 19, 20. *Smithiphyllum whittakeri* sp. nov. from Redknife Formation, N.W.T. 4, 6, 20, Paratype, GSC 17546. 19, Holotype, GSC 17545.

Figs. 5, 7-9, 14, 15, 17, 18. *Smithiphyllum kindlei* sp. nov. from the Mount Hawk Formation, Alberta. Holotype, GSC 17544.

Figs. 13, 16. *Smithiphyllum belanskii* sp. nov. from the Shellrock Formation, Iowa. 13, Paratype, SUI 11617. 16, Holotype, SUI 11616.



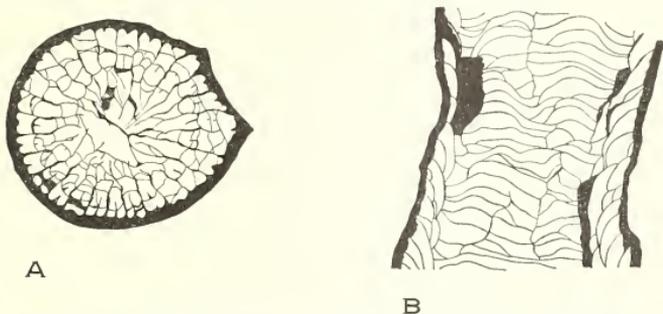
considerably less. The minor septa are mere ridges on the interior of the wall and some are totally suppressed. Number of major septa ranges from none at 3 mm. diameter to twenty-five at 15.5 mm. diameter.

The dissepimentarium is lonsdaleoid and as viewed in longitudinal section typically consists of a single row of elongate dissepiments; two rows occur in parts of some corallites and in places the dissepimentarium is entirely absent.

The tabulae are broad and many are quite complete; in longitudinal section they are mostly very slightly convex or slightly sinuous.

Discussion. The new species resembles *Smithiphyllum weberi* (Lebedew), particularly specimens figured by Soshkina (1952, pl. 4, fig. 16). It is distinguished by having a slightly more persistent dissepimentarium and by having fewer septa, which number up to seventy in *S. weberi*.

S. martinense (Stumm) differs from *S. belanskii* in being slightly smaller and having fewer and considerably less differentiated septa.



TEXT-FIG. 6. *Smithiphyllum kindlei* sp. nov., $\times 2$. Based on the holotype, GSC 17544. A, transverse section. B, longitudinal section.

Smithiphyllum kindlei sp. nov.

Plate 88, fig. 6; Plate 89, figs. 5, 7-9, 14, 15, 17, 18; text-figs. 6A, B

Name derivation. From the late E. M. Kindle in recognition of his work on the succession of faunas in the Jasper Park region.

Holotype. GSC 17544. Mount Hawk Formation, 350 to 370 feet above base, Roche Ronde, Bosche Range, Jasper National Park, Alberta, $53^{\circ} 14' N.$, $118^{\circ} 01' W.$ Collected by P. B. Jones in 1960. Elements of the *Calvinaria albertensis* fauna, including *Thamnophyllum colemanense* (Warren) and *Smithiphyllum imperfectum* (Smith) were collected above and below the type horizon.

Diagnosis. Known maximum width of corallite 15 mm. Maximum septal count fifty. Major septa long and commonly not withdrawn. Dissepimentarium well developed.

Description. The corallum is dendroid. Before sectioning the incomplete fragment of the holotype measured about $90 \times 65 \times 55$ mm. The corallites are subcylindrical where free and have adult diameters of from 12 to 15 mm. Increase is lateral. External features in the type material are largely obscured by matrix but the poorly preserved surface of one corallite bears traces of rugae.

The wall, consisting of a very thin axial plate and an inner lamellar layer, is about 0.4 or 0.5 mm. thick in the regions farthest from the septal bases.

The septa are thin, smooth, and gently to moderately sinuous; their arrangement is radial and they are strongly differentiated into two orders. The major septa are generally well developed, some are peripherally discontinuous, and a few are entirely withdrawn from the dissepimentarium. Most, however, are continuous lamellae extending variably from about one-half to the entire distance to the axis. The feebly developed minor septa are typically represented by low crests on the dissepiments and to a lesser extent the tabulae, or by ridges on the interior of the wall. Numbers of major septa range from fourteen at 4 mm. diameter to twenty-five at 15 mm. diameter.

The dissepimentarium is from 1 to 3 mm. wide; in places the dissepiments are limited to a single row as seen in longitudinal section, elsewhere they may be up to three deep; they number about ten in 10 mm.

The tabulae are broad and may be quite complete; in some cases their median profile is irregularly sinuous, in others it is peripherally downturned, or there is a peripheral trough.

Discussion. *Smithiphyllum kindlei* does not closely resemble any previously described species. It is, however, close to an undescribed species also occurring in the Frasnian of Alberta. *S. kindlei* is smaller, has fewer septa and a less pronounced dissepimentarium, furthermore the septa in *S. kindlei* are less withdrawn both axially and peripherally.

Smithiphyllum whittakeri sp. nov.

Plate 88, fig. 4; Plate 89, figs. 4, 6, 19, 20; text-figs. 7A, B

Name derivation. From the late E. J. Whittaker, the pioneer geologist and collector on Jean Marie and neighbouring rivers.

Holotype. GSC 17545. Redknife Formation (late Frasnian), middle Jean Marie Gorge, N.W.T., about 60° 24' N., 121° 10' W. Collected by R. de Wit in 1957. Specimens of *Tabulophyllum* sp. close to *T. mcconnelli* (Whiteaves), *Smithiphyllum imperfectum* (Smith), *Devonoproductus* sp., *Atrypa ciliipes* Crickmay, *Spiratrypa* sp., *Vandergrachtella kobayashii* Crickmay, and *Paracyclas?* sp. were also present in the collection.

Paratype. GSC 17546. Same horizon, &c. as holotype.

Diagnosis. Corallum probably loosely aggregate. Corallite wall thin. Corallites up to 14.5 mm. in diameter. Major septa number up to twenty-seven, regularly withdrawn axially. Minor septa comparatively well developed. Dissepimentarium narrow, but regular.

Description. Fragments only of the corallum are available and it is not known whether the coral is weakly aggregate or truly fasciculate. The corallites are subcylindrical and have an adult diameter of from 12 to 14.5 mm. Increase is lateral. Fine rugae are present on the exterior, but there are no interseptal ridges.

The wall consists of a very narrow exterior axial plate and a lamellar layer; in the parts furthest from the septal bases it is about 0.5 mm. thick.

The septa are thin, smooth, and most are gently sinuous as seen in transverse section; a few, however, are crenulate. They are radially arranged and clearly differentiated into two orders. The major septa are typically continuous lamellae, although some are

discontinuous in the dissepimentarium; they are withdrawn from the axis leaving a region from 2 to 4 mm. wide devoid of septa. The minor septa, which are mere ridges in young stages, become well developed in later stages; in adult corallites they are about one-half as long as the major and occur as discontinuous crests on the dissepiments and tabulae. Numbers of major septa range from nineteen at 4.5 mm. diameter to twenty-seven at 14.5 mm. diameter.

As seen in longitudinal section the dissepimentarium is typically a single row of comparatively large dissepiments, numbering from ten to twelve in 10 mm.; it is about 2 mm.



A

B

TEXT-FIG. 7. *Smithiphyllum whittakeri* sp. nov. $\times 2$. Based on the holotype, GSC 17545. A, transverse section. B, longitudinal section.

wide and fairly constant, although it is absent immediately below a lateral offset in the holotype.

The tabulae are broad and many are quite complete; in median profile they tend to be flat, or gently sloping, in the axial region, and sigmoidal at the periphery.

Discussion. The species is reminiscent of *Smithiphyllum weberi* (Lebedew), but differs in having considerably more prominent minor septa and a less lonsdaleoid dissepimentarium.

Acknowledgements. The Canadian specimens described in this paper were collected by geologists working for Triad Oil Co. Ltd., Calgary, Alberta, and were originally studied by the writer while employed by the same company. The management of the company has consented to the publication of this work and has kindly allowed the type specimens to be transferred to the collection of the Geological Survey of Canada. B. Whan of the technical staff of the Department of Geology of the University of New England drafted text-fig. 1.

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ARCOSCALPELLUM COMPTUM (WITHERS), A SPECIES OF CIRRIPEDE NEW TO THE GAULT

by J. S. H. COLLINS

ABSTRACT. A species of cirripepe, *Arcoscalpellum comptum* (Withers), hitherto known only from terga and carinae from the Lower Greensand, is here recorded from the Gault. Further valves are attributed to this species and the present known vertical and geographical distribution is tabulated.

WITHERS (1910) founded his species *Scalpellum comptum* on two terga (I 13403—holotype, and I 13404—paratype, in the collection of the British Museum (Natural History)) from the Lower Greensand of Sevenoaks, Kent. In 1935 he referred it to the genus *Arcoscalpellum* Hoek, and in 1945 described further terga and two carinae (C. W. and E. V. Wright Coll.) from the 'Crackers' of Atherfield, Isle of Wight.

A comparison of these specimens with valves from the Gault collected by the author reveals that they belong to the same species. Although there are distinct differences between the terga (the commonest valves found) of *A. comptum* and those of *A. arcuatum* (Darwin), a well-known Gault species, their superficial similarity is undoubtedly the reason why the presence of *A. comptum* in the Gault has been overlooked until now.

The scutum and upper latus, here described, are sufficiently distinct from the corresponding valves of *A. arcuatum* and any other known Gault species, yet so resemble in structure and ornament the terga and carinae of *A. comptum* that they may with certainty be included within that species.

DESCRIPTION

1910 *Scalpellum comptum* Withers, p. 153, fig. 5.

1935 *Scalpellum (Arcoscalpellum) comptum* Withers, p. 202, pl. xxiii, figs. 7, 8.

1945 *Arcoscalpellum comptum* (Withers), p. 552, pl. ii, figs. 1, 2.

Terga. (Plate 90, figs. 1–5.) All the terga examined from the Gault agree closely with the types and have, as Withers (1935) states, a prominent ridge extending from the apex to the middle of the scutal margin, on either side of which the valve is almost smooth or with only weakly developed longitudinal ridges. The number of these ridges on the carinal side and on the extreme occludent side of the valves varies slightly among individuals. The length of the valve slightly exceeds twice its width.

The terga closely resemble those of *A. arcuatum* (Darwin), but may at once be distinguished by the smaller number of longitudinal ridges. Moreover, while in *A. arcuatum* these ridges are sometimes bifurcated, and shorter finer ridges which do not extend to the apex are always intercalated, the holotype of *A. comptum* (I 13403) and all the terga examined from the Gault have uninterrupted ridges that pass continuously from the apex to the margin of the valve. In the paratype of *A. comptum* (I 13404), however, two of the ridges on the carinal side are bifurcated.

The terga of both species have the same size range and the inner side is similar.

Carina (Plate 90, figs. 6a, b, 7). The specimens figured by Withers from the 'Crackers' of Atherfield are embedded in matrix and Withers was of the opinion (1945) that the intraparietes, which are hidden, were inflected at right angles, causing the upper part of the valve to be solid. A further small carina (21512, C. W. Wright Coll.) from the 'Crackers' of Atherfield, and the author's specimens from the Gault show that this is not so. In these a weakly developed ridge separates the parietes from the intraparietes, which are narrow, being at their widest part equal in width to the parietes. They are short and sometimes faintly longitudinally striated, and are inflected inwards to about 45°, the valve remaining open almost to the apex. The inner margin is thickened.

The Gault specimens examined are larger than those recorded from the 'Crackers' and range in length from 9 to 13 mm., and are about four times longer than wide.

The carina is distinguished from that of *A. arcuatum* by the rounded tectum, the laterally visible intraparietes and the general absence of ridges.

Scutum (Plate 90, figs. 10, 11). The scutum, which is trapezoidal in outline, is about twice as long as wide. It is moderately convex transversely, the convexity being slightly accentuated towards the occludent margin. The apex is acute and somewhat produced. The apico-basal ridge is moderately developed and becomes splayed out a little towards the base; its margins are rounded throughout its length and it is slightly produced at the basi-lateral angle. The basal margin may be either convex or slightly concave, and at right angles to the lower part of the occludent and lateral margins. The rostral angle is very slightly produced downwards. The occludent margin is regularly convex and there is a shallow depression parallel to its edge. The tergal margin, which is short, may be either slightly convex or concave and the edge is slightly arched. The tergo-lateral angle is barely produced and is inclined with the lateral margin at about 40°. (In *A. arcuatum* this angle averages 36°.) There is a lateral depression parallel to the tergal margin. The lateral margin is regularly convex, except close to both the tergo-lateral and basi-lateral angles, where it is slightly excavated.

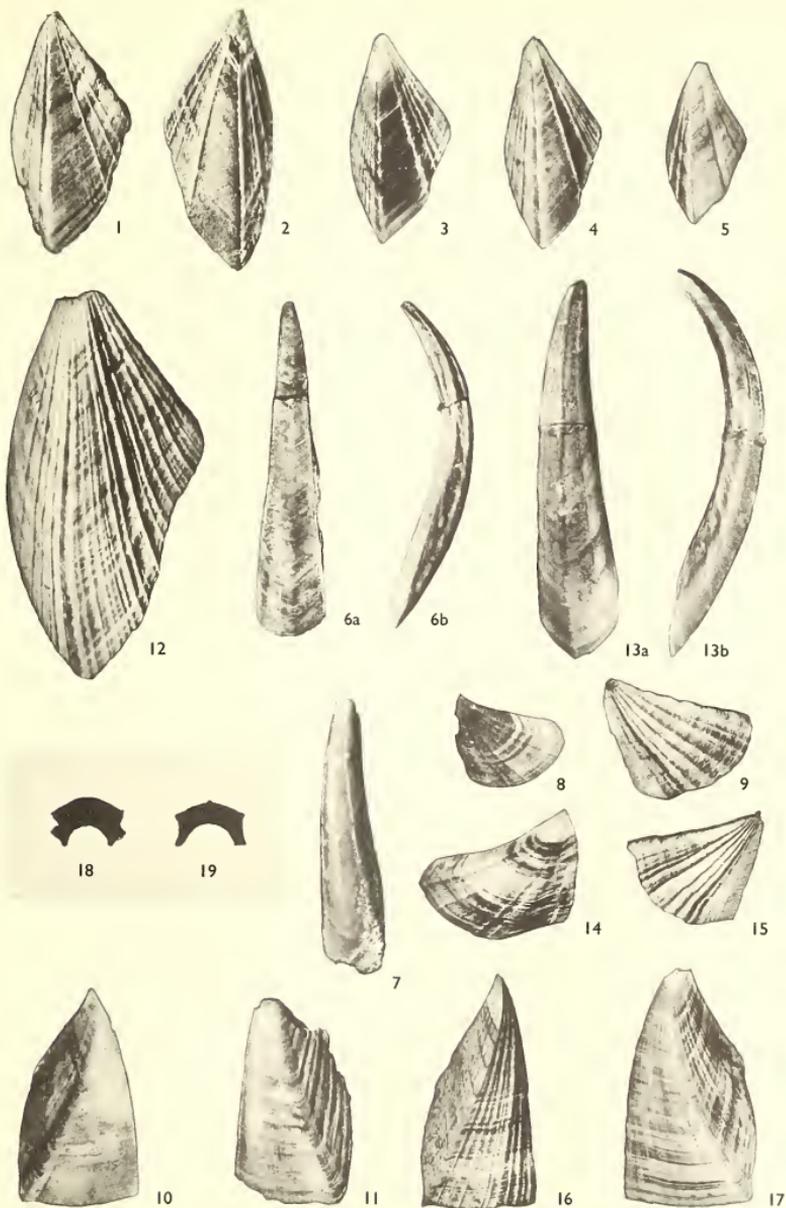
Generally there are longitudinal ridges on the lateral side and a few on the extreme part of the occludent side of the valve. Other valves may be almost smooth, although there is a tendency for the ridges on the extreme lateral side to remain. None of the valves examined shows intercalated or bifurcated ridges.

EXPLANATION OF PLATE 90

All specimens, except Fig. 11, are from the Upper Albian, *H. orbigny* subzone (between Beds 50 and 64 of Milbourn 1963), Rugby Portland Cement Co., Ford Place, Wrotham, Kent. Fig. 11 is from the Middle Albian, *D. cristatum* subzone, of the same locality. All photographed specimens $\times 3$. Specimens deposited in Palaeontological Department, British Museum (Natural History).

Figs. 1-11, 18. *Arcoscalpellum comptum* (Withers). 1, Tergum, left, In64248. 2, Tergum, right, In64249. 3, 4, 5, Terga, left, In64250-2. 6a, b, Carina, outer and side views, In64253. 7, Carina, outer view, In64254. 8, Upper latus, left, In64255. 9, Upper latus, right, In64256. 10, Scutum, left, In64257. 11, Scutum, right, In64258. 18, Carina, transverse section $\times 5$, 8 mm. from apex, just below maximum development of the intraparietes, In64265.

Figs. 12-17, 19. *Arcoscalpellum arcuatum* (Darwin). 12, Tergum, left, bifurcated and intercalated longitudinal striae clearly seen on occludent side of valve, In64259. 13a, b, Carina, outer and side views, In64260. 14, Upper latus, left, In64261. 15, Upper latus, right, In64262. 16, Scutum, left, In64263. 17, Scutum, right, In64264. 19, Carina, transverse section $\times 5$, 7.5 mm. from apex, In64266.



On the inner surface a prominent pit, inclined towards the occludent margin, extends above the adductor muscle pit to the apex. As growth advances a pit, bounded by a sharp ridge extending along the tergal margin, is developed.

Upper latus (Plate 90, figs. 8, 9). The valve is thin and subtriangular in outline. It is slightly inclined towards the scutum, almost flat transversely, and slightly convex longitudinally. The umbo is slightly produced with a thickened ledge, which is more pronounced on the scutal side, and which thins out towards the lateral angles. The tergal margin is slightly convex and is shorter than the scutal margin, which is moderately concave. The angle enclosed by two lines drawn from the apex to the lateral angles is approximately 65° . The basal margin is boldly convex; the portion occupying the distance from a poorly developed apico-basal ridge to the sharp basi-tergal angle, is almost straight. The basi-scutal angle is bluntly rounded. The portion of the valve on the tergal side of the apico-basal ridge is slightly raised and a pronounced ridge extends parallel to the scutal margin. A few very fine uninterrupted ridges complete the surface ornament. The growth-lines are distinct and present a slightly overlapping appearance. On the thickened edges of the scutal and tergal margins the growth-lines are upturned, forming fine longitudinal ridges.

CONCLUSIONS

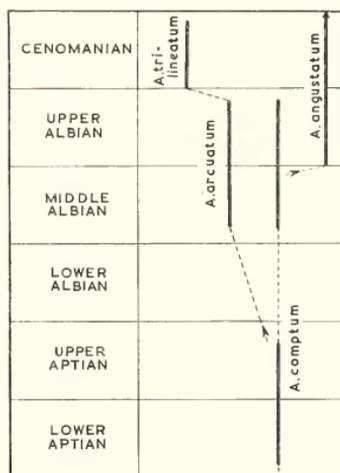
Withers (1910) compared the terga of *A. comptum* with those of *A. arcuatum* and *A. fossula* (Darwin) and, with knowledge of the carina, further implied (1945) that *A. comptum* was the ancestor of *A. arcuatum*. With better preserved specimens from the Gault, it is possible to advance these opinions further.

As stated above, the length of the terga of *A. comptum* slightly exceeds twice the width, a feature approaching the valves of *A. angustatum* (Geinitz) of the *A. fossula* group. The terga of *A. arcuatum* are generally just twice as long as wide. The ridge extending from the apex to the scutal margin is, to a greater or lesser degree, present in both groups (contrary to Withers's statement (1910) that it is never present in *A. arcuatum*).

The presence of small, laterally visible intraparietes in the carina of *A. comptum*, together with the rounded tectum devoid of a median ridge in all but the earliest stage of growth, are both characteristic of the *A. fossula* group. The intraparietes of *A. arcuatum*, which are turned under, are not visible in the lateral view, and the tectum is strongly arched with a median ridge.

The outline of the scutum is similar to that in both groups, but the valve resembles that of *A. angustatum* in being nearly devoid of ridges.

The upper latus is flatter, thinner, and smoother than that of *A. arcuatum* and in this



TEXT-FIG. 1. Evolution of *Arcoscalpellum comptum* (Withers) and allied species.

respect approaches that of *A. angustatum*. The concave scutal margin and broadly rounded basi-scutal angle also suggest that this valve more nearly approaches the *A. angustatum* form than the *A. arcuatum*.

The latest known occurrence of *A. comptum* in the Upper Gault, *H. varicosum* subzone, overlaps the lowest known record of *A. angustatum* (Withers 1935, and specimens in author's collection). The earliest record of *A. arcuatum* is from the *A. intermedius* subzone, from where it continues at least to the *H. varicosum* subzone.

From the evidence thus far available, it would seem that *A. comptum* was more probably the ancestral form of the *A. fossula* group, as originally suggested by Withers (1910) rather than that of the *A. arcuatum* group. Both groups presumably arose from a common ancestor, yet to be found.

TABLE 1. Vertical and geographical distribution of *Arcoscalpellum comptum* (Withers) in the Gault.

Subzones	Ford Place, Kent (Rugby Portland Cement Co.)	Reservoir Pit, Ford Place, Kent	Folkestone, Kent	Greatness Lane, Kent	Small Dole, Sussex
<i>H. varicosum</i>	T				
<i>H. orbigny</i>	CLST	CLST	T	T	
<i>D. cristatum</i>	T	ST		CST	
<i>A. daviesi</i>					
<i>E. nitidus</i>					
<i>D. doris</i>	T				
<i>E. neglectus</i>					
<i>D. niobe</i>	T			CT	
<i>A. intermedius</i>	CT			T	T
<i>H. spathi</i>					

C: carinae, L: latera, S: scuta, T: terga.

Subzones after Milbourn 1963.

Range (Table 1). The earliest valves of *A. comptum* so far recorded from the Gault are terga and a carina collected from the *A. intermedius* subzone of Ford Place, Wrotham, Kent, and it is evident that the upward range extends at least as far as the *H. varicosum* subzone. In some subzones the tergum (the commonest valve found) occurs fairly frequently. For example, from the lower part of the *H. orbigny* subzone (Beds 50-64 of Milbourn 1963) of Ford Place, one tergum of *A. comptum* was collected to about ten of *A. arcuatum*. The greatest development of *A. comptum* appears to have occurred in the *H. orbigny* subzone.

Acknowledgements. I wish to thank the Officers of the British Museum (Natural History) for providing access to specimens; Mr. C. W. Wright for the opportunity to examine his specimens and for valuable advice; Mrs. J. I. Collins, Messrs. A. T. Buffery, R. A. Milbourn, and N. Stevens for assistance in the field; and Mr. E. Kentish for preparing the photographs.

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AN ALMOST COMPLETE SKULL ROOF AND PALATE OF THE DIPNOAN *DIPNORHYNCHUS SUSSMILCHI* (ETHERIDGE)

by K. S. W. CAMPBELL

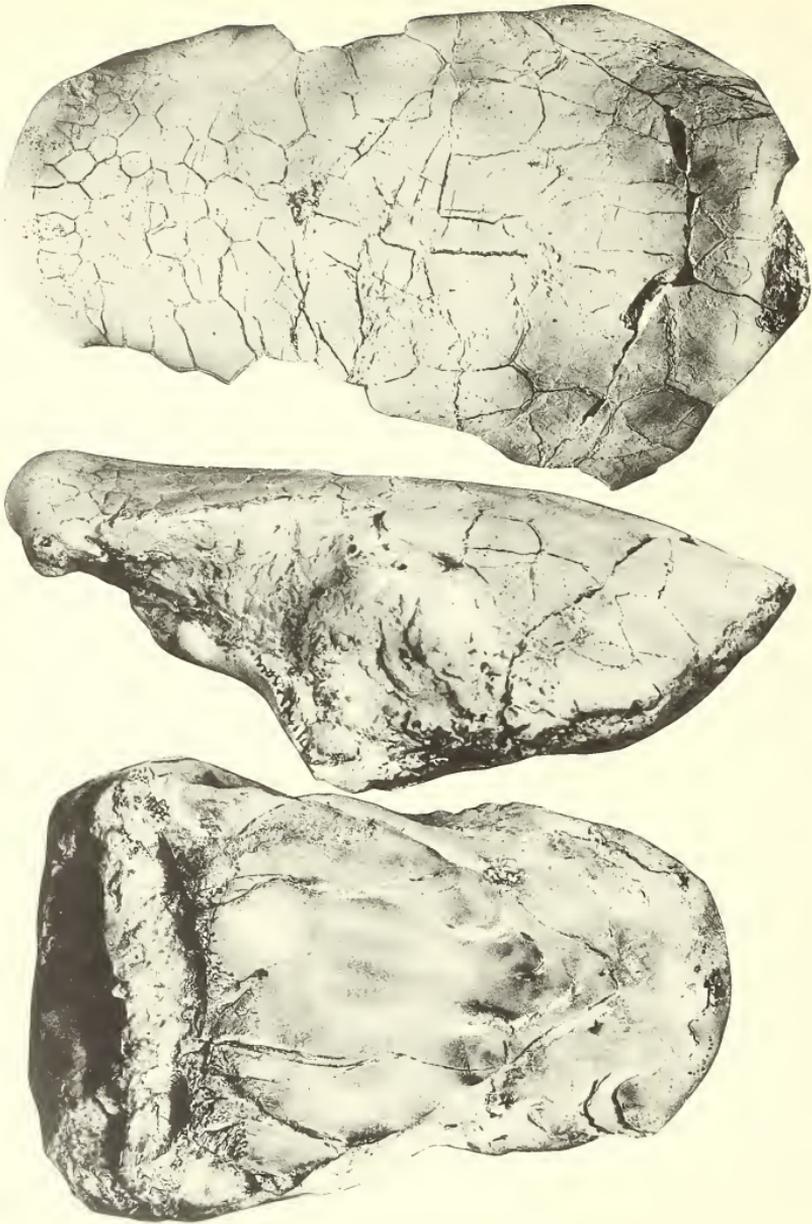
ABSTRACT. A preliminary account is given of the cranial structure of *Dipnorhynchus sussmilchi* (Etheridge) based on a newly found topotype from the Middle Devonian of Taemas, New South Wales.

UP till now the Devonian Dipnoan genus *Dipnorhynchus* Jaekel has been known from two specimens only, one *D. lehmanni* Westoll (Lehmann and Westoll 1952; Lehmann 1956) from the Lower Devonian Hunsrückschiefer of Germany, and the other *D. sussmilchi* (Etheridge 1906; Hills 1933, 1941) from the Middle Devonian of Taemas, New South Wales. The genus is of particular interest since it is the oldest known member of the Order Dipnoi, and the structure of its skull table displays many primitive features which have been of value in comparative studies of the Dipnoi and the Rhipistidia, as well as in studies of dipnoan evolution (Westoll 1949).

A new specimen of *D. sussmilchi* has been discovered in the 'Spirifer yassensis Limestone' at the locality known as Shearsby's Wallpaper, Taemas, Burrinjuck Dam, close to the locality at which the original specimen was obtained. The skull roof is almost complete, and is only slightly distorted. The only parts missing are the bones 4+X and the postero-lateral tips of the bones H (for terminology see Westoll 1949). The bones of the snout, which are covered by a layer of cosmine obliterating the sutures in the other two specimens, can be seen with great clarity. There are no cheek bones. Most of the palate is present, and a large part of the quadrate ramus appears to be embedded in the matrix on one side.

Little has yet been done to prepare the specimen, but from a preliminary study the following conclusions can be drawn:

1. The relative length of the otic region is even greater than had been anticipated in the reconstructions of Hills (1941, fig. 6). This is a primitive feature in which *D. sussmilchi* is now known to be very similar to *D. lehmanni*.
2. This relative increase in length is due to the larger size of bones 'H' and 'I'. 'H' especially is larger, and in this it differs from the same bone in *D. lehmanni*.
3. There is no bone 'A' as was inferred by both Hills (1941) and Westoll (1949), but the bones 'I' join medially as Westoll was able to show (by means of X-ray photographs) in the case of *D. lehmanni*. However, a more or less symmetrical gap in the medial portion of the back of the skull may have been the site of a loosely articulated bone 'A'.
4. Although the bones 'B₂' are medially fused in the type specimen (Hills 1941, p. 51), they are divided by a clear suture in this individual.
5. Bones 'J₁', 'J₂', 'J₃', 'K', 'L₁', 'L₂', 'M', 'N', and 'Q' are all present as separate entities as in the type specimen, and show no sign of fusions. There is only one minor difference—the enlargement of 'L₂' on the right side.



CAMPBELL, *Dipnorhynchus* from Australia

6. There is one lateral line bone anterior to 'Q', and three or four lying medially to this one. All these bones are irregularly shaped and as yet have not been named. Another set of unnamed bones—three on the left side and four on the right—lie in front of bone 2. This latter bone is itself split into two elements on the right side.

7. Between the lateral line bones and anterior to B_2 there are twenty-nine separate irregularly shaped bones which are only roughly symmetrically arranged. This is by far the greatest number known in any member of the Dipnoi. On their exposed surfaces the bones show the same characters as the others and there is no reason to believe that they are histologically different in any way (cf. Westoll 1949, p. 141).

8. The anterior tip of the snout is very thick and is cosmine covered. It shows the characteristic depressions for the external nares.

9. From the arrangement of the sensory pores both sub- and supra-orbital lateral line canals are inferred to be present and show a pattern similar to that of the type. However, in many places it is not possible to identify the position of the canals with precision, and this must await further preparation of the specimen. The anterior part of the supra-orbital canal is somewhat more flexed than that of the type (compare text-fig. 1a with Hills 1941, figs. 5–6). The sub-orbital canal appears on the snout in the position indicated on Westoll's diagram (1949, fig. 5A). It can be traced as a line of very coarse pores running around the under edge of the snout across the top of the external naris and gradually dying out toward the mid-line.

10. The occipital commissure of the lateral line system is not clearly marked, but the presence of several large pores near the postero-medial corners of the bones 'I' suggests that it probably passes out of these bones in this region. This supports the view that a movable bone 'A' was originally present in this region, but further preparation is needed.

11. It is difficult to distinguish between fine cracks and pit lines in some areas, but the pit lines shown in text-fig. 1 are definite.

12. The bone of the palate is an enormously thick structure and its edges are knobbed where they were embedded in cartilage. All the bones are fused, and while the vomers can be distinguished from each other and from the pterygoids by emarginations and deep grooves, it is not possible to separate the pterygoids and the parasphenoids. The vomers are short and do not reach to the snout. At the posterior end of the palate the bone thins out rapidly and rises abruptly. There is clearly no parasphenoidal stalk. In general form the palate is very similar to that of *D. lehmanni*, though in that species Westoll (1952, fig. 4B) claimed to be able (with difficulty) to delineate a narrow parasphenoid.

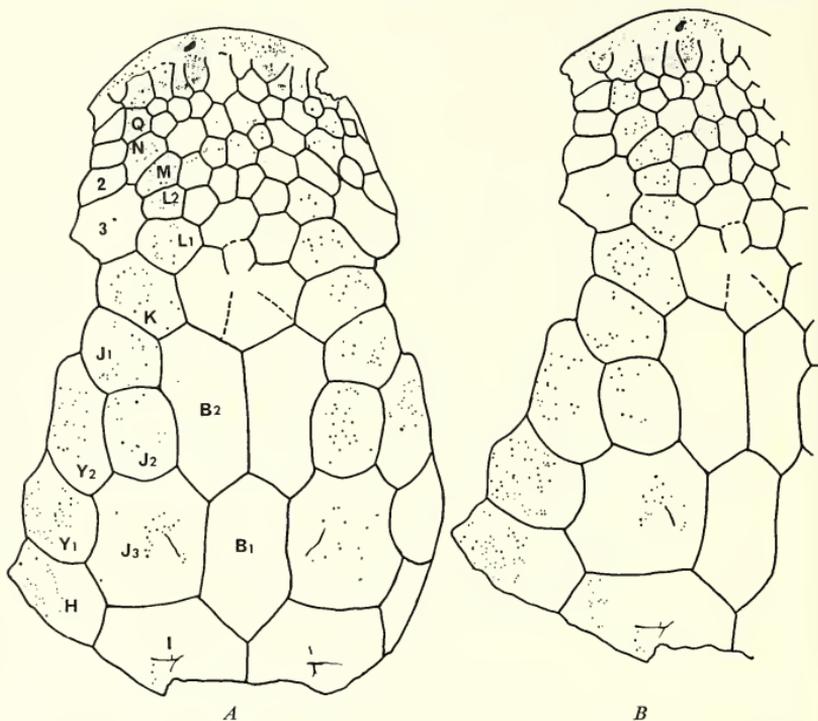
13. There is no ceratodont dentition. The teeth form three large, slightly elongate bulbous masses. The central one is the most anterior and is itself subdivided into three segments by the remnants of the sutures between the vomers and the pterygoids, and between the two pterygoids themselves. Where the sutures join there is a deep pit. The two lateral teeth are at the antero-lateral margins of the pterygoids and are formed entirely from these bones. Teeth of this shape and the massive palatal bones suggest that

EXPLANATION OF PLATE 91

Figs. 1–3. *Dipnorhynchus sussmilchi* (Etheridge), dorsal, ventral, and lateral views of the skull. The dorsal view was photographed with the long axis horizontal, and the ventral view with the palate horizontal. All approx. $\times 1$.

the animal was a shell feeder. The plate figured by Hills (1933, pl. 12, fig. 4) is not a tooth plate of *Dipnorhynchus*.

14. The associated fauna is very rich and consists mainly of brachiopods, orthoconic cephalopods, high spired gastropods, bivalves, and trilobites. These undoubtedly indicate a marine environment. As has been suggested by Hills (1958) the fine state of



TEXT-FIG. 1A-B. Dorsal and dorso-lateral views of the skull prepared by inking in the sutures and the sensory pores on enlarged photographs, and then bleaching them.

preservation of the fish fauna in the Murrumbidgee limestones in general indicates that they probably have not been transported far after death. The interpretation of the structure of the teeth and palate given above supports the view that it was a marine organism.

Work on the specimen is proceeding and it is intended to produce a more complete account as soon as possible.

Note. Throughout this paper the bone nomenclature originated by Foster-Cooper (1937) and developed for *Dipnorhynchus* by Westoll (1949), has been used without modification for the sake of simplicity. It is *not* implied that this nomenclature is accepted in its entirety.

All except the posterior bones of the skull were found on the one piece of rock. During a search at a subsequent date these bones were found in place only a few feet from the original site by Mr. R. W. Day of this department. His assistance is gratefully acknowledged.

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SOME EUROPEAN PROVIVERRINI (MAMMALIA, DELTATHERIDIA)

by LEIGH VAN VALEN

ABSTRACT. A generic revision of the Proviverrini is made, with special attention to European material from the middle Eocene. Phylogeny and parallel evolution are discussed. *Proviverra* is made identifiable; *Sinopa*, *Geiseloitherium*, *Leonhardtina*, and *Prorhyzaena* are synonymized with it. Specimens of the Miacidae and Oxyaenidae, and one of unknown affinities, are described from the Eocene of Europe. New taxa are the following: Deltatheridia, new order; *Arfia*, new genus; *Prototomus torvidus*, *Cynhyaenodon trux*, *Prodissopsalis phonax*, *P. theriodis*, and *Miacis? macintyri*, new species.

WHILE in Europe in 1963 I had the opportunity to examine material of a number of species of European creodonts, especially middle Eocene proviverrines. The following account, together with another paper (Van Valen, in press) and one by R. J. G. Savage (in press), provides the framework for a revision of the known Old World proviverrines. Early Eocene specimens recently collected by D. E. Russell, D. E. Savage, and P. Louis will provide further information when described. I have elsewhere (Van Valen, in press) reduced the subfamily Proviverrinae to the rank of a tribe in the Hyaenodontinae, family Hyaenodontidae, which I include in a new order, Deltatheridia. Because the publication date of that long paper is still uncertain although it was submitted for publication in the spring of 1962, I will give here a brief diagnosis of the Deltatheridia. The drawings of teeth were made on quadrille paper using a reticule in a binocular microscope unless otherwise stated. The following abbreviations are used: BM, British Museum (Natural History), Department of Palaeontology; MME, Museum für Mitteldeutsche Erdgeschichte, Halle/Saale; NMB, Naturhistorische Museum, Basel.

Acknowledgements. I am indebted to a number of people for hospitality and access to collections during this study. These are especially Prof. H.-W. Matthes of Halle, Dr. H. Schaefer and Prof. J. Hürzeler of Basel, Dr. D. E. Russell of Paris, M. P. Louis of Reims, Dr. A. J. Sutcliffe of London, and Dr. R. J. G. Savage of Bristol. Part of this study was supported by a NATO post-doctoral fellowship.

Order DELTATHERIDIA, nov.

Diagnosis. Insectivorous or carnivorous placental mammals usually with the following characters: tall cusps on the teeth; distinct paraconid; relatively close paracone and metacone; relatively wide styler shelf; persistent embrasure shear on the molars, which have a prominent metastyle and no hypocone; no interradicular crests; premolars not molariform; fissured ungual phalanges; primitive placental pattern of internal carotid circulation; alisphenoid canal present.

Included groups. The order is based equally on the Palaeoryctidae (including Deltatheridiidae), Hyaenodontidae (including Limnocyonidae), and Oxyaenidae, with ordinal rank separate from the Insectivora because of the inclusion of the latter two families and separate from the Carnivora because close phyletic affinity with the Miacidae is improbable and predation clearly originated independently in the two groups. The Didy-

moconidae are also included, and the Micropternodontidae and some or all zalambdodonts, especially the Tenrecidae (including Potamogalidae and Apternodontidae) and Chrysochloridae, may also fall here. The origin of the Oxyaenoidea from the Palaeoryctidae is shown by Van Valen (in press), where other phylogenetic and anatomical matters are also discussed.

GENERA AND SPECIES OF PROVIVERRINI

The following genera and species have previously been described or are described in the present paper. Taxa I regard as of uncertain validity are preceded by a question mark; type species of genera considered valid are preceded by an asterisk. Only papers giving original information or interpretations are cited.

?*Prototomus* Cope 1874, p. 13 [? = *Protoproviverra* (not *Protoviverra*) Lemoine 1891 (May), p. 272; not *Protoproviverra* Ameghino 1891 (August), which was replaced by *Amphiproviverra* Ameghino 1891, and is now included in *Thylacodictis* Mercerat, 1891], validation of name pending.

**Prototomus viverrinus* Cope 1874, p. 13. Early Eocene, Wasatchian; New Mexico and Wyoming. See also Cope (1877, pp. 109, 112), Matthew (1901, p. 27), Matthew (1909, p. 470), Matthew (1915, p. 83), McKenna (1960, p. 92), Gazin (1962, p. 54), Van Valen (in press). Validation of the name is pending.

Prototomus nutlicuspis (Cope 1875, p. 10). Early Eocene, Wasatchian; New Mexico and Wyoming. See also Cope (1877, pp. 112, 116), Matthew (1901, p. 27), Matthew (1915, p. 80), Gazin (1962, p. 55).

?*Prototomus vulpecula* (Matthew 1915, p. 80). Early Eocene, Wasatchian; Wyoming and Colorado. See also Gazin (1952, p. 53), Robinson (1960, p. 1), Gazin (1962, p. 55).

Prototomus mordax (Matthew 1915, p. 73). Early Eocene, Graybullian; Wyoming. See also Denison (1938, p. 241), Van Valen (in press).

?*Prototomus secundaria* (Cope 1875, p. 9). Early Eocene, Wasatchian; New Mexico, ?Wyoming. See also Cope (1877, p. 115), Matthew (1901, p. 27), Matthew (1915, p. 82), McKenna (1960, p. 91), Van Valen (in press).

Prototomus palaeonictides (Lemoine 1880, p. 5) [= *Protoproviverra pomelii* Lemoine (1891, p. 265), based on the same specimen]. Early Eocene, late Ypresian; France. See also Teilhard (1921, p. 50 or 58), Louis (1963, p. 87), Van Valen (in press).

Prototomus torvidus, new species. Middle Eocene, Lutetian; Switzerland.

Arfia, new genus.

**Arfia opisthotoma* (Matthew 1901, p. 28). Early Eocene, Graybullian; Wyoming. See also Matthew (1915, p. 73).

?*Arfia shoshoniensis* (Matthew 1915, p. 73). Early Eocene, Graybullian; Wyoming.

Tritenmodou Matthew (1906, p. 25).

Tritenmodon strenua (Cope 1875, p. 10). Early Eocene, Wasatchian; New Mexico and Wyoming. See also Cope (1877, p. 117), Matthew (1901, p. 26), Matthew (1915, p. 74), Gazin (1952, p. 54), Gazin (1962, p. 56).

Tritenmodon hians (Cope 1877, p. 118). Early Eocene, Wasatchian; New Mexico and Wyoming. See also Matthew (1901, p. 25), Matthew (1915, p. 75).

Tritenmodon whitiae (Cope 1882, p. 161). Early Eocene, Lostcabinian; Wyoming. See also Cope (1884, p. 292), Matthew (1901, p. 26), Matthew (1906, pp. 207, 209), Matthew (1915, p. 84).

**Tritenmodou agilis* (Marsh, 1872, p. 204) [= *Stypolophus brevicaratus* Cope (1872*b*, p. 469); = *Sinopa gracilis* Wortman (1902, pp. 17, 201)]. Middle Eocene, Bridgerian; Wyoming. See also Cope (1884, p. 291), Matthew (1901, p. 24), Wortman (1902, p. 437), Matthew (1906, pp. 207, 209), Matthew (1909, p. 475), Thorpe (1923, p. 37).

Proviverra Rüttimeyer 1862, p. 80 [= *Sinopa* Leidy 1871, p. 116; = *Stypolophus* Cope 1872*a*, p. 1;

- = *Prorhyzaena* Rüttimeyer 1891, p. 105; = *Leonhardtina* Matthes 1952, p. 223; = *Geiselotherium* Matthes 1952, p. 225].
- Proviverra rapax* (Leidy 1871, p. 116). Middle Eocene, Bridgerian; Wyoming. See also Wortman (1902, p. 435), Matthew (1906, pp. 207, 209), Matthew (1909, pp. 464, 465, 471).
- ?*Proviverra rapax lania* (Matthew 1909, p. 472). Middle Eocene, Bridgerian; Wyoming.
- ?*Proviverra grangeri* (Matthew 1906, p. 206). Middle Eocene, Bridgerian; Wyoming.
- ?*Proviverra pugens* (Cope 1872a, p. 1). Middle Eocene, Bridgerian; Wyoming. See also Cope (1884, p. 291), Matthew (1901, p. 24), Wortman (1902, p. 436), Matthew (1906, p. 209), Matthew (1909, p. 472).
- ?*Proviverra minor* (Wortman 1902, p. 17). Middle Eocene, Bridgerian; Wyoming. See also Matthew (1906, pp. 207, 209), Matthew (1909, p. 473), Thorpe (1923, p. 35). If this species is shown to be valid and if both it and Filhol's *Cynohyaenodon minor* prove referable to *Proviverra*, then Wortman's species must be renamed as it would be a secondary homonym. Probably at least one Bridgerian species other than *P. rapax* is valid, but which this (or these) may be is now uncertain.
- ?*Proviverra major* (Wortman 1902, p. 18). Middle Eocene, Bridgerian; Wyoming. See also Matthew (1906, pp. 207, 209), Matthew (1909, p. 473), Thorpe (1923, p. 36).
- **Proviverra typica* Rüttimeyer 1862, p. 80 [= *Prorhyzaena egerkingiae* Rüttimeyer, 1891, p. 105]. Middle Eocene, Lutetian; Switzerland. See also Schlosser (1887, p. 213), Rüttimeyer (1891, p. 102).
- Proviverra gracilis* (Matthes 1952, p. 223) [= *Geiselotherium pilzi* Matthes 1952, p. 225]. Middle Eocene, Lutetian; Germany.
- Proviverra minor* (Filhol 1877, p. 28). Late Eocene, Ludian; France. See also Schlosser (1887, p. 216), Filhol (1888, p. 191), Martin (1906, pp. 417, 420, 421).
- Cynohyaenodon* Filhol 1873, p. 87 [= *Pseudosinopa* Depéret 1917, p. 172].
- Cynohyaenodon trux*, new species. Middle Eocene, Lutetian; Switzerland.
- Cynohyaenodon ruetimeyeri* (Depéret 1917, p. 172). Middle Eocene, Lutetian; Switzerland.
- **Cynohyaenodon cayluxi* (Filhol 1873, p. 87). Late Eocene, Ludian; ?Early Oligocene, ?Sannoisian; France. See also Filhol (1877, p. 7), Gaudry (1878, p. 20), Cope (1884, p. 289), Schlosser (1887, p. 217), Filhol (1888, p. 190), Smith (1902, p. 400), Martin (1906, pp. 420, 422), Matthew (1906, p. 209), Edinger (1929, p. 151), Russell and McKenna (1962, p. 277).
- Cynohyaenodon leenhardtii* Martin 1906, p. 420. Late Eocene, Ludian; France.
- Prodissoptalis* Matthes 1952, p. 206 [= *Imperatoria* Matthes 1952, p. 214].
- **Prodissoptalis eocaenicus* Matthes 1952, p. 206 [= *Imperatoria gallwitzii* Matthes 1952, p. 214; = *Imperatoria hageni* Matthes 1952, p. 220; = *Geiselotherium robustum* Matthes 1952, p. 228]. Middle Eocene, Lutetian; Germany.
- Prodissoptalis phonax*, new species. Middle Eocene, Lutetian; Switzerland.
- Prodissoptalis theriodis*, new species. Middle Eocene, Lutetian; Switzerland.
- Paracynohyaenodon* Martin 1906, p. 424.
- **Paracynohyaenodon schlosseri* Martin 1906, p. 426. Late Eocene, Ludian; France.
- ?*Metasinopa* Osborn 1909, p. 423.
- Metasinopa ethiopia* (Andrew 1906, p. 233). Late Eocene, lower Fluvio-marine beds; Egypt. See also Schlosser (1911, p. 77), Van Valen (in press).
- **Metasinopa fraasi* Osborn 1909, p. 423. Early Oligocene, upper Fluvio-marine beds; Egypt. See also Schlosser (1911, p. 77).
- Propterodon* Martin 1906, p. 455.
- **Propterodon morrisi* (Matthew and Granger 1924, p. 1) [= *P. iridinensis* Matthew and Granger 1925, p. 4]. Late Eocene, Irдин Manha Formation; Mongolia. See also Van Valen (in press).
- cf. *Propterodon*
- Propterodon minutus* (Douglass 1901, p. 19). Early Oligocene, Chadronian; Montana. See also Matthew (1903, p. 208), Scott and Jepsen (1936, p. 53), Van Valen (in press).

Dissopsalis Pilgrim 1910, p. 64.

**Dissopsalis carnifex* Pilgrim 1910, p. 64. Early Pliocene, Chinji beds, West Pakistan. See also Pilgrim (1914, p. 267), Pilgrim (1932, p. 11), Colbert (1933, p. 1), Colbert (1935, p. 75).

?*Dissopsalis ruber* Pilgrim 1910, p. 64. Locality and references as for *D. carnifex*.

Quercitherium (not *Quercytherium*) Filhol 1880, p. 48.

**Quercitherium tenebrosium* Filhol 1880, p. 48. Late Eocene, Ludian; France. See also Filhol (1882, p. 30; reprint of Filhol 1880), Filhol (1892, p. 135), Martin (1906, p. 429), Depéret (1917, p. 165), Piveteau (1935, p. 84), Russell and McKenna (1961, p. 277); Van Valen (in press).

The following genus and species have most recently been referred to the Proviverrini (as a subfamily or family) but are here not recognized as such:

Galethylax Gervais 1850. The type specimen is of uncertain relationships but is apparently not a proviverrine. See Van Valen (in press).

Proviverra americanus (sic) Scott 1892, is an artiodactyl (cf. Van Valen, in press).

The foregoing classification has a number of innovations, in addition to the new taxa. These may be summarized as follows. The type species of *Sinopa* is placed in *Proviverra* and other species are placed in *Proviverra* and three other genera. *Prototomus* is provisionally revived; it is probably a senior synonym of *Protoproviverra*. *Pseudosinopa* is synonymized with *Cynohyaenodon*, and *Prorhyzaena*, *Geiselotherium*, and *Leonhardtina* are synonymized with *Proviverra*; the synonymy of species in *Proviverra* is also new. *Geiselotherium robustum* is synonymized with *Prodissopsalis eoceanicus*, *Cynohyaenodon minor* is transferred to *Proviverra*, and *Paracynohyaenodon morrissi* is made conspecific with *Propterodon iridinensis*. *Propterodon* does not include the species on which it was originally based; see below.

GENERIC DIAGNOSES

The lower dentition is known for all species of proviverrines, but the upper dentition is unknown in a number of species. For this reason I will emphasize characters of the lower teeth. The skull, most of which is unknown in several genera, does not as yet provide characters that are clearly diagnostic at the generic level except for *Quercitherium* and *Dissopsalis*, genera that are recognizable at a glance from the teeth. All relative statements used in the diagnoses can be interpreted from published figures of the genera involved.

Prototomus, as tentatively used here, is known mainly from American species. It is the most primitive known genus of proviverrines and was probably the stem genus of the entire family Hyaeodontidae. For this reason the allocation of some species to *Prototomus* or other genera is arbitrary. Intergradation is particularly evident on the basis of species now known with *Tritemnodon*, which is, however, generically distinct at least by the middle Eocene. In the lower molars of *Prototomus* the metaconid is not or is only slightly reduced; it is larger than or equal to the paraconid, and may be considerably larger. The paraconid is not shifted anteriorly. The labial height of the protoconid above the talonid is about the same as the length of the trigonid. The molar talonids are two-thirds to fully as long as the trinonids, and the talonid rim is high or moderately high. The size of the trigonid of M_1 is less than or usually equal to that of M_2 , which is about the same as that of M_3 but may be somewhat larger or smaller. The existence and length of diastemata between the canine and P_3 are variable. P_3 is relatively narrow and high:

its width is about a third of its length, and its labial height (above the base of the enamel on the roots) is two-thirds to four-fifths its length. The paracone and metacone of the upper molars are more or less close together but are not twinned, and are of about the same size as each other on M^1 and M^2 (either may be slightly larger). The European species *P. palaenictides* is distinguished especially by the low angle (about 60°) that the posterolingual corner of the trigonid of at least M_1 makes with the horizontal plane of the tooth, and the fact that the metaconid of at least M_1 is about as tall as the protoconid when the sides of the trigonid are taken as vertical; one or occasionally both of these characters are present also in some American specimens.

Arfia has M_1 and M_2 with structure similar to that of *Prototomus*, but on M_3 the metaconid is moderately reduced and is somewhat smaller than the paraconid, which has shifted anteriorly to a variable degree. The M_3 protoconid height is variable with respect to the trigonid length. The molar talonids vary from as long as the trigonids to a little over half that length; their rims are high on M_1 and M_2 , but reduced on M_3 . The trigonid of M_3 is much larger than that of M_2 , which is moderately larger than that of M_1 . There are no diastemata or only one short one between the canine and P_3 . P_3 is moderately wide and high; its width is two-fifths to half its length and its height is four-fifths of its length. The paracone and metacone of the upper molars are about as separated as in *Prototomus* and are of about equal size on M^1 and M^2 . P^4 differs from that of all other proviverrines for which the upper dentition is known except *Quercitherium* in the reduction of the metastyle, which is a weak crest not more than a fifth of the labial length of the tooth.

Tritemnodon has lower molars with the metaconid slightly to (middle Eocene) much reduced; at least on M_3 the metaconid is smaller than or equal to the paraconid, and is almost always smaller. The paraconid is not to moderately shifted anteriorly. The labial height of the protoconid above the talonid is greater than or equal to the length of the trigonid, distinctly greater in the middle Eocene. The molar talonids are half to three-fourths as long as the trigonids in the early Eocene, not more than a third as long in the middle Eocene. The talonid rim, moderate to high in the early Eocene, becomes much reduced. The trigonid of M_1 is smaller than that of M_2 , which is about the same size as that of M_3 but may be slightly larger or smaller. There are moderate diastemata between the canine and P_3 . P_3 is narrow and low: its width is one-third to two-fifths of its length and its height is three-fifths of its length. The paracone and metacone of the upper molars are moderately to (middle Eocene) highly connate; the paracone is larger than the metacone, considerably larger in the middle Eocene.

Proviverra has a lower dentition like that of *Prototomus*; the molar talonids are sometimes even longer than the trigonids. The only consistent structural difference I have found between the genera, if they are regarded as distinct, is the greater separation of the paracone and metacone in *Proviverra*.

Cynhyaenodon has lower molars with the metaconid slightly to moderately reduced and the paraconid moderately to not shifted anteriorly. The M_3 protoconid height is slightly less than the trigonid length. The talonids are two-fifths to two-thirds the length of the trigonids, and have moderately high rims. The trigonids increase moderately and regularly in size from M_1 to M_3 . There are no diastemata in the premolar region. P_3 is relatively wide and high: its width is about half its length and its height is about four-fifths its length (three-fifths in *C. trux*). The paracone and metacone of the upper molars

are only moderately (Lutetian) to closely appressed and are similar to each other in size on M^1 and M^2 .

Prodissopsalis has the metaconid of the lower molars moderately to much reduced, it being smaller than the paraconid, which has shifted far anteriorly. The protoconid of M_3 is somewhat lower than the length of the trigonid. The talonids are a third to a half the length of the trigonids, and have low or intermediate rims. There is a moderate and progressive increase in the size of the trigonids from M_1 to M_3 . Diastemata are absent. P_3 is relatively wide and low: its width is about half its length and its height is about three-fifths its length. The paracone and metacone of the upper molars are only moderately close together; the metacone is distinctly larger than the paracone on M^1 and M^2 .

Paracynhyaenodon has the metaconid of the lower molars only slightly reduced on M_1 and M_2 , moderately reduced on M_3 . The paraconid is moderately to far anterior; the height of the protoconid of M_3 is probably about the same as the trigonid length. The talonids are half to two-thirds of the trigonid length, and have moderate to high rims. The trigonid of M_1 is moderately smaller than that of M_2 , which is much smaller than that of M_3 . The nature of the anterior and upper dentition is unknown.

Metasinopa is not certainly distinct at the generic level from *Paracynhyaenodon*. The metaconid of the lower molars is much reduced on M_1 and M_2 , and nearly absent on M_3 . The paraconid is moderately to far anterior; the height of the protoconid of M_3 is about the same as the trigonid length. The talonids are a third to a half the trigonid length, and have moderately high rims (at least on M_2). The trigonid of M_1 is moderately smaller than that of M_2 , which is much smaller than that of M_3 . Diastemata are absent. The P_3 is wide, its width in *P. fraasi* being about three-fifths its length. The height of P_3 and the nature of the upper dentition are unknown.

Propterodon has much reduced metaconids on the molars, and the paraconid is far anterior. The height of the protoconid of M_3 is unknown, but by analogy with M_1 and M_2 would be about the same as the trigonid length, perhaps slightly less. The talonid of M_1 is about four-tenths the length of the trigonid, that of M_2 three-tenths, and that of M_3 one-tenth. The talonid rim is moderately high labially and posteriorly, but is absent lingually. There is a considerable but regular increase in the size of the trigonid from M_1 to M_3 . There are no diastemata in the premolar region. P_3 is relatively wide and high: its width is half its length and its height is four-fifths its length. The paracone and metacone of the upper molars are unknown.

Dissopsalis has the metaconid of M_1 moderately reduced, that of M_2 much reduced, and that of M_3 absent. It should be noted that the only known M_1 is from a different individual than the M_2 and M_3 . The paraconid of M_1 is only slightly shifted anteriorly, while that of M_2 and M_3 is far anterior. The protoconid of M_3 is incompletely known but was probably considerably lower than the length of the trigonid. The talonid of M_1 and M_2 is about half the length of the trigonid, while that of M_3 is less than a fifth. The talonid rim is high or moderately high on M_1 and M_2 , and nearly absent on M_3 . The trigonid of M_2 is somewhat larger than that of M_1 , and that of M_3 is considerably larger than that of M_2 . The lower premolars anterior to P_4 are unknown, but by analogy with the maxilla there were probably one or two diastemata. P_4 is relatively wide. The paracone and metacone of the upper molars are not particularly close together; the paracone is much smaller than the metacone on M^1 and especially M^2 . The greatly enlarged anteroposterior shearing surface on M^2 is diagnostic.

Quercitherium is immediately recognizable by its greatly enlarged and bulbous pre-molars, especially the second, which are larger than the molars. The metaconids of M_2 and M_3 are only slightly reduced; that of M_1 has not been described. The paraconids of M_1 and M_2 are not or are only slightly shifted anteriorly, while that of M_3 is moderately far anterior. The protoconid of M_3 is considerably lower than the length of the trigonid. The talonids of M_1 and M_2 are two-thirds to three-fourths the length of the trigonid, while that of M_3 is more or less a third the trigonid length. The talonid rim is high on at least M_1 and M_2 . There is a moderate and progressive increase in the size of the trigonids from M_1 to M_3 . Diastemata are absent. P_3 is tall and very wide: its width is about two-thirds its length and its height is about four-fifths its length. The paracone and metacone of the upper molars are not particularly close together; the paracone is smaller than the metacone on M^1 and especially M^2 .

ADAPTATION, PHYLOGENY, AND PARALLELISM

Of the genera here included in the Proviverrini, only *Dissopsalis*, *Propterodon*, and *Metasinopa* are derivable from any other genus (except *Prototomus*) without invoking a reversal and subsequent re-establishment of carnassial specialization. The major criterion I use for a genus in proviverrines (aside from probable monophyly) is a significant difference in adaptive specializations from the most recent possibly ancestral genus.

Prototomus may be regarded as a primitive proviverrine in all characters. *Quercitherium* is specialized in its crushing premolars (with concomitant changes in the skull and mandible), with moderate carnassial specialization in the anterior paraconid of M_3 and the size of the metacone of M^2 . *Proviverra* has somewhat less carnassial specialization than *Prototomus*. This difference is not great and is perhaps not of generic rank, but it represents a definite trend in opposition to that of all other proviverrines. *Proviverra minor* (Filhol) has crushing premolars, but these are not as large as those of *Quercitherium* and there are no indications of the carnassial specialization of the latter genus; in fact the molars of *P. minor* (Filhol) are nearly inseparable from those of *P. typica*. It is possible that the European and American species of *Proviverra* are independent developments from the stage of *Prototomus*, but this is simply speculation. Even evolutionary classification must follow the dictates of static morphology until reasonable evidence for a phylogeny is available.

At least five of the remaining eight genera present an interesting picture of independent adaptations to increase the efficiency of shear between the upper and lower molars. Each of the five has one or more specializations that are not present in any of the other four genera taken individually, although a single specialization may not distinguish a genus from all the other four genera taken together. This pattern is in fact an important reason for my recognizing these groups as genera.

Arfia is characterized especially by the enlargement and specialization of M_3 without particular carnassial specializations on the other lower teeth. *Tritemnodon* has tall trigonids with much reduced metaconids and talonids, moderately anterior paraconids, and connate paracone and metacone with the metacone reduced. *Cynohyaenodon* has only moderately reduced metaconids and talonids and moderately anterior paraconids, but has connate paracone and metacone by the Ludian. *Prodissopsalis* has reduced metaconids and anterior paraconids as its main specializations. *Paracynohyaenodon*,

as yet known from only one specimen, has a relatively anterior paraconid and an enlarged M_3 ; the metaconid of M_3 is less reduced than that of *Arfia*.

Metasinopa could have evolved from either *Arfia* or an early *Paracynohyaenodon*. It is similar to the latter, differing especially in its more reduced metaconids. The metaconid of M_3 of at least most specimens of *Arfia* is smaller than that of *Paracynohyaenodon* even in the Gray Bull. *Propterodon* could have been derived most easily from either *Cynohyaenodon* or *Prodissoisalis*; it is advanced in all known respects except that the M_3 is not notably enlarged. *Dissopsalis* seems almost equally well derivable from *Prodissoisalis* (perhaps the most likely candidate), *Paracynohyaenodon*, *Metasinopa*, Lutetian species of *Cynohyaenodon*, or even *Arfia*. It should, however, be noted that the upper teeth of *Paracynohyaenodon* and *Metasinopa* are unknown. The three genera discussed in this paragraph could easily have originated directly from *Prototomus* via unknown intermediates. The phylogeny of hyaenodonts is poorly known, and parallelism is so prevalent in demonstrable cases that it very possibly occurred in cases in which it cannot now be shown.

This last conclusion is particularly relevant to the Hyaenodontini (*Pterodon*, *Hyaenodon*, *Hemipsalodon*, *Metapterodon*, *Ischnognathus*, and just possibly *Apterodon*, a probable mesonychid). The Hyaenodontini is defined exclusively on the basis of the degree of carnassial specialization, and it seems probable that the threshold was reached more than once. In particular, it is difficult to see how *Metapterodon* could have evolved from an ancestor in the Hyaenodontini. Even the genera *Pterodon* and *Hyaenodon* are defined largely on the basis of degree of carnassial specialization, and polyphyletic origin of them would not be surprising (but it is not yet proved). The ancestors of the Hyaenodontini are unknown, although *Prodissoisalis*, *Cynohyaenodon*, or an early *Propterodon* are probably the most likely candidates among described genera; *Metasinopa* is also quite possible. One or more species from the middle Eocene of Egerkingen ('*Hyaenodon*' *schlosseri* and others not certainly distinct) are already of the hyaenodontine grade; '*H.*' *schlosseri* lacks a metaconid of M_3 and the talonid is nearly absent on this tooth. It is probable that *Tritemnodon*, at least by the Bridgerian, was too divergent to give rise to any other known genus.

EGERKINGEN PROVIVERRINI

The geology of the fissure-fillings of Egerkingen has been summarized by Stehlin (1903, 1905). J. Hürzeler, who has also collected there, kindly provided some additional information. Three localities have been collected from since 1896; these are designated α , β , and γ . Quarries α and β are of late Lutetian age, while γ is of early or middle Lutetian age. The specimens collected before 1896 are largely or entirely from the early and middle Lutetian. I found only one specimen of a proviverrine (of *Prototomus torvidus*, from β) which was from either α or β ; presumably all the species described here were nearly or quite contemporaneous, despite their number. One or more species of miacid and one or two of a form resembling the Hyaenodontini are also present in Egerkingen γ . The latter species are probably not referable to a described genus (cf. Martin, 1906). My schedule, arranged in advance under the belief that there were only about two species of Egerkingen proviverrines, was inflexible and did not permit complete analysis of the available material at Basel. It nevertheless seems desirable to present the information

obtained. The species were first distinguished on the basis of the upper dentition; the separation so obtained was confirmed by the lower dentition. Upper and lower teeth are referred to the same species on the basis of size, degree of carnassial specialization, and direct occlusal manipulation. There is only one mandible for *Prodissopsalis phonax*; in all other cases several to many specimens are available for both upper and lower dentitions.

Proviverra typica Rüttimeyer

Text-figs. 1B, 2A, 3A, 4A

Proviverra typica Rüttimeyer 1862, p. 80.

Prorzyhaena egerkingiae Rüttimeyer 1891, p. 105.

Discussion. This species is the smallest and most abundant Egerkingen proviverrine. It is moderately although not excessively variable; this variation was regarded by Rüttimeyer (1891) as indicating the presence of two species and even of two genera. No specimen in the Basel Museum labelled *Prorzyhaena* gives any indication of the structure of the premolars anterior to P⁴, and from Rüttimeyer's figure (1891) this has probably always been true despite statements about them in the literature. P⁴ is not enlarged; that of the type of *Prorzyhaena egerkingiae* differs from that of the type of *Proviverra typica* mainly in the presence of two cuspules rather than one on the lingual lobe. The talonid of M₁ is as wide as the trigonid. The widest part of P₃ is just posterior of the middle. The alveolar length from the posterior end of the upper canine to the posterior end of P⁴ is 18.0 and 17.7 mm. on the two sides of the type; to the posterior end of M³ it is 28.3 mm.

Rüttimeyer's various figures of the teeth are highly inaccurate. His partly corrected figures of the somewhat crushed skull (Rüttimeyer 1862, pl. 5) are better, but the skull was probably somewhat deeper; text-fig. 3A of the present paper supplements them. The type skull of *P. typica* now contains the root of the right canine, the base of the crown of the left P¹, all of both P⁴s, both M¹s without most of the paracone and metacone and the distal end of the metacrista, the lingual half of the right M², and the left M³ without the surface of the crown of the labial half.

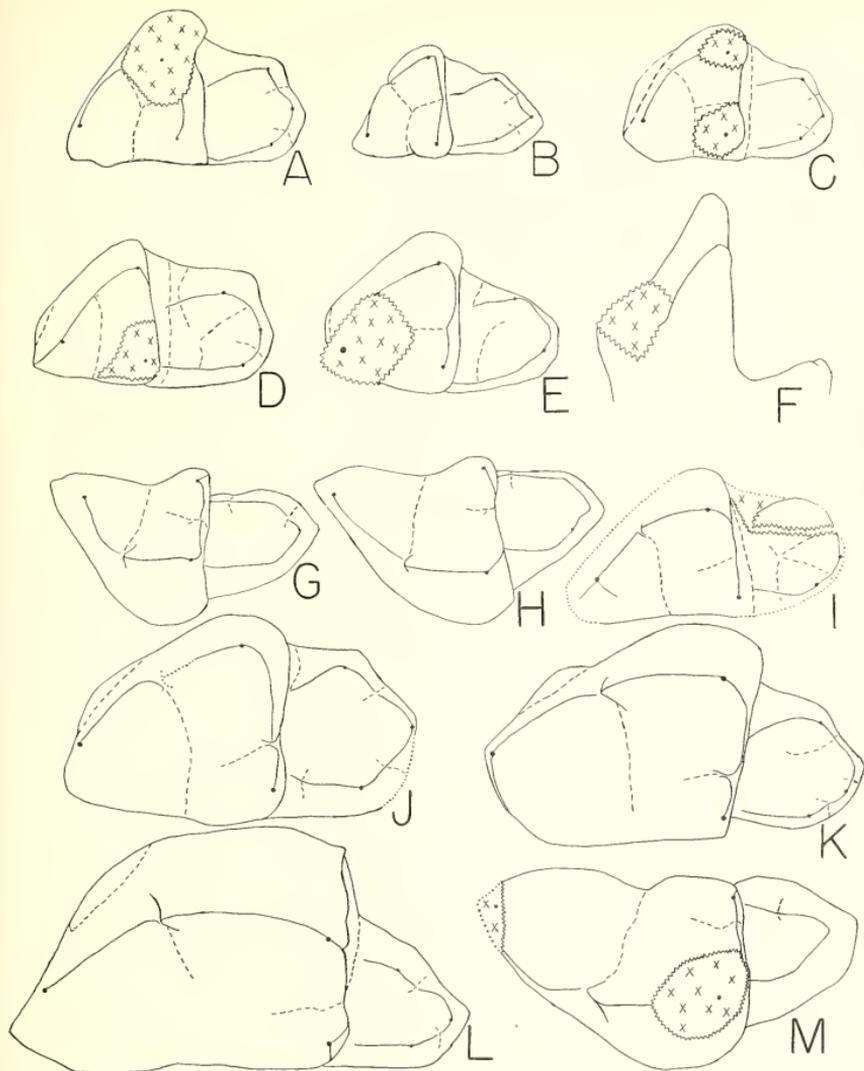
Prototomus torvidus sp. nov.

Text-figs. 1A, 4B

Type. NMB No. Eh. 522, partial right maxilla. See text-fig. 4B.

Type locality. Egerkingen γ .

Diagnosis and discussion. *P. torvidus* is slightly more carnassial than *Proviverra typica*, but the two species may nevertheless be congeneric. *Prototomus torvidus* is somewhat larger. In the upper molars the main differences are that the protocone of *Prototomus torvidus* is lower and the metacrista is taller than in *Proviverra typica*; the paracone and metacone are also closer together and taller. M³ is moderately reduced in *Prototomus torvidus* but not in *Proviverra*. The protocone lobe of the P⁴ of *Prototomus torvidus* is distinctly shorter anteroposteriorly than that of *Proviverra typica*, and lacks or nearly lacks cuspules on its lingual rim except for the protocone; in *Proviverra typica* there are usually rather prominent cuspules there. The metacrista of P⁴ is cut off from



TEXT-FIG. 1. Lower molars of proviverrines, mainly in occlusal view. A, *Prototomus torvidus*, NMB unnumbered, right M_3 , $\times 6.8$. B, *Proviverra typica*, NMB unnumbered, right M_3 , $\times 6.8$. C, *Proviverra minor* (Filhol), NMB No. Q.C. 1028, right M_3 , $\times 6.8$. D-F, *Proviverra gracilis*, MME No. 343, $\times 6.0$ D, occlusal view right M_2 ; E, occlusal view right M_3 ; F, lingual view right M_3 . G, *Cynohyaenodon trux*, NMB unnumbered, left M_3 , $\times 6.8$. H, *Cynohyaenodon ruetimeyeri*, NMB unnumbered, left M_3 , $\times 6.8$. I, cf. *Prodissoapsalis* sp., MME No. 3987, unerupted right M_2 , $\times 6.0$. J-K, *Paracynohyaenodon schlosseri*, type, NMB No. Qu. B. 393, $\times 6.8$. J, right M_2 ; K, right M_3 . L, *Prodissoapsalis theriodis*, NMB No. Em. 14, right M_3 , $\times 6.8$. M, *Prodissoapsalis phonax*, NMB unnumbered, left M_3 , $\times 6.8$. In all text-figures dotted lines are inferred, dotted regions are wear surfaces, dashed lines are valleys, large dots are cusp apices, and jagged lines and regions with X's are broken.

the paracone by a sharp carnassial notch; they do not more or less merge as in *Proviverra typica*. The parastyle of P⁴ is somewhat wider also, causing the deep notch in the anterior border of the tooth to be about central rather than distinctly on the labial half of the tooth as in *Proviverra typica*. In the lower molars the talonid and metaconid of *Prototomus torvidus* are relatively slightly smaller than in *Proviverra typica*, but the metaconid is still larger than the paraconid in lingual view. There is a reasonable possibility that *Prototomus torvidus* belongs to *Proviverra* even if *Prototomus* is generically distinct from *Proviverra*, but it is placed in *Prototomus* pending clarification of the early Eocene proviverrines of Europe.

The specific name is a Latin word meaning savage or wild, in allusion to the presumably predaceous habits of the species and also with reference to the work of R. J. G. Savage on the Old World Hyaenodontidae and that of D. E. Savage on the European Eocene.

Cynohyaenodon trux sp. nov.

Text-figs. 1G, 2B, 3B

Type. Unnumbered fragment of rostrum in Naturhistorische Museum, Basel. See text-fig. 3B.

Type locality. Egerkingen, quarry unknown.

Diagnosis and discussion. The paracone and metacone of the upper molars are much more separate than in *C. cayluxi* (the upper molars of *C. ? leenhardti* are unknown), being intermediate in this respect between those of *Prototomus torvidus* and *Proviverra typica*. The protocone lobe of the upper molars is slightly shorter anteroposteriorly than in *Proviverra typica*; the protocone is relatively low and the metacrista is relatively high and long, as in *Prototomus torvidus*. The protocone lobe of P⁴ is distinctly longer anteroposteriorly than that of *Prototomus torvidus*, being similar in this respect to that of *Proviverra typica*, but this lobe is narrow transversely and extends anteriorly nearly as far as does the parastyle. The notch in the anterior border of P⁴ is shallow and central; the nature of the metacrista is unknown. P³ has a third root in at least the type, unlike at least *Proviverra typica*. The metaconid of M₃ is moderately reduced and the paraconid is moderately anterior, and the cusps of the talonid are more or less merged into the talonid rim, unlike the situation in *Proviverra* and *Prototomus*. M₁ is not quite as tall as M₂. The paraconid of P₄ is relatively smaller than that of *Proviverra typica* but the talonid is relatively larger. The height of P₃ is much less than that of M₁. P₂ is taller than P₃; the apex of the protoconid of P₂ is about a third of the distance from the anterior end of the tooth. P₄ is widest at the talonid; P₃ is widest just anterior of the talonid. The alveolar length from the posterior end of the upper canine to the posterior end of P⁴ on the type of 25.2 mm.

The specific name is a Latin word meaning savage or fierce, given for the same reasons as *Prototomus torvidus*.

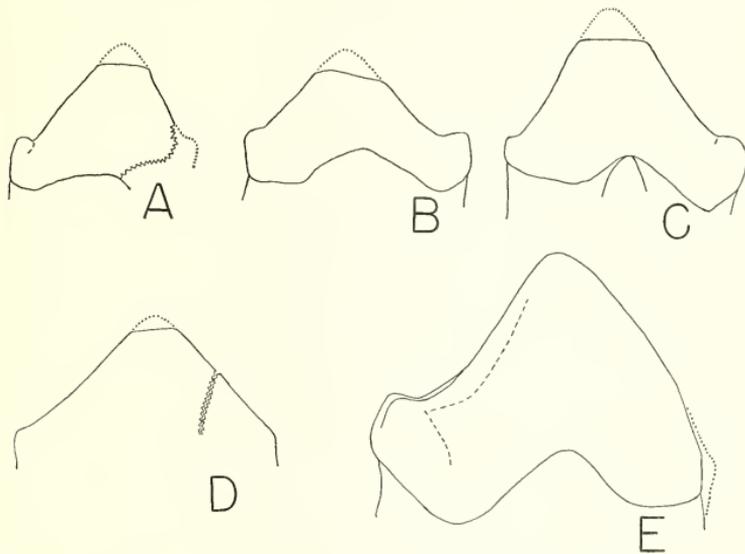
Cynohyaenodon ruetimeyeri (Depéret)

Text-figs. 1H, 2C, 4C

Type. The mandible figured by Ruetimeyer (1891) in his plate 7, fig. 10, is here designated as the type. It is in the Naturhistorische Museum, Basel.

Diagnosis and discussion. The upper molars of *C. ruetimeyeri* are rather similar to those

of *C. trux*, but are somewhat larger and the protocone lobe is slightly smaller. The protocone lobe of P^4 is more transverse than in the three Egerkingen species described above, and also slightly more transverse than in *C. cayluxi*. It does not extend far anteriorly. The notch in the anterior border of P^4 is moderately deep and distinctly on the labial half of the tooth. As in *C. cayluxi*, there is a distinct carnassial notch between the metacrista and the paracone. The embrasure pit (a pit in the maxilla in the embrasure

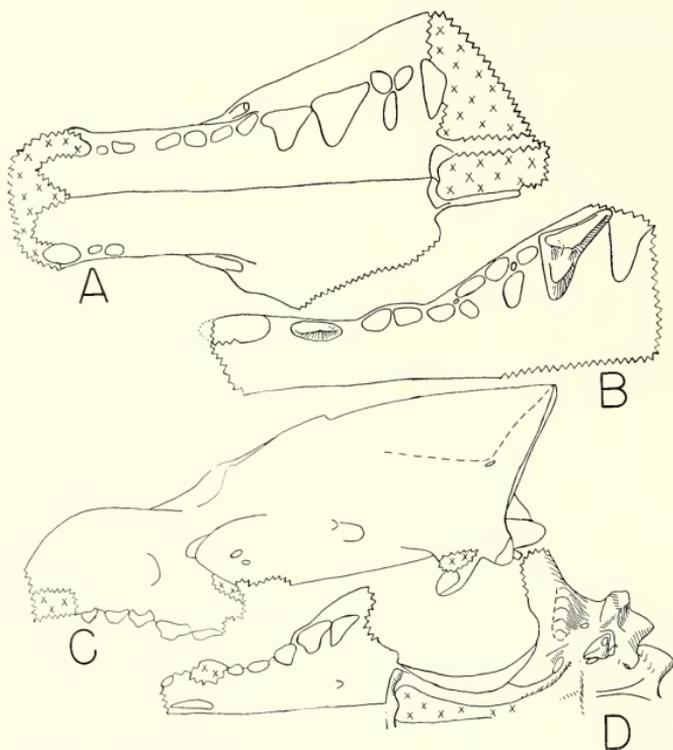


TEXT-FIG. 2. P_3 of proviverrines, labial view. A, *Proviverra typica*, NMB unnumbered, right P_3 , $\times 6.8$. B, *Cynohyaenodon trux*, NMB unnumbered, left P_3 , $\times 6.8$. C, *Cynohyaenodon ruetimeyeri*, NMB unnumbered, $\times 6.8$. D, *Proviverra gracilis*, MME No. 343, left P_3 , $\times 6.0$. E, *Prodissopsalis theriodis*, NMB unnumbered, $\times 6.8$. Symbols as in text-fig. 1.

between two cheek teeth) between M^2 and M^3 is about the same size as that between M^1 and M^2 , which is concordant with the fact that the trigonid of M_3 is not much larger than that of M_2 . The paraconid of the lower molars is somewhat more anterior than in *C. trux*, the metaconid is somewhat smaller, and M_1 is somewhat more reduced. The paraconid is somewhat further forward and the metaconid slightly smaller than in *C. cayluxi*. The lower premolars are considerably wider and more robust than in *C. trux*. P_4 is of about equal width at the middle and the talonid; P_3 is widest in the middle or just posterior of the middle. P_3 is considerably larger relative to P_4 than in *C. trux*; the height of P_3 is almost equal to that of M_1 . As in *C. trux*, the height of P_4 is greater than that of M_1 but less than that of M_2 .

Dépéret (1917, p. 172) casually established the genus and species *Pseudosinopa ruetimeyeri*, relying on Rütimeyer's figures. The two jaws mentioned as belonging to this

species are those figured by Rüttimeyer (1891) in his plate 7, figs. 10 and 11. Both specimens figured there are reversed as to the side of the mouth. On comparison of these jaws with the other specimens of Egerkingen proviverrines, it became evident that



TEXT-FIG. 3. Proviverrine skulls, not drawn with reticule. A, *Proviverra typica*, type, ventral view of rostrum with outlines of some alveoli and left P^1 , M^1 , and M^2 ; $\times 2.0$. B, *Cynohaenodon trux*, type, ventral view of rostrum with P^1 , M^1 , and outline of M^2 , $\times 2.0$. C-D, *Prodissozalis theriodis*, type, NMB No. Em. 12, $\times 0.5$. Left side and ventral view of left half of skull, with outlines of P^1 - M^1 ; additional orbital foramina may also be present. Symbols as in text-fig. 1.

the specimen of Rüttimeyer's fig. 10 is specifically and even generically different from that of his fig. 11, which belongs to *Prodissozalis phonax*. As both the names *Prodissozalis* and *Cynohaenodon* are in current use while *Pseudosinopa* is not, I have restricted the type of *P. rüttimeyeri* to the specimen of the older genus to preserve the current names. The spelling of the specific name is altered because the species was named after Rüttimeyer.

Prodissoptalis phonax sp. nov.

Text-figs. 1M, 4D

Type. NMB No. Em. 16, partial skull. See text-fig. 4D.

Type locality. Egerkingen, quarry unknown.

Diagnosis and discussion. The protocone of the upper molars is slightly smaller than that of *Prototomus torvidus* and *Cynohyaenodon trux*. The paracone and metacone are only moderately connate. The protocone of P⁴ and the upper molars is somewhat more anterior and lower and relatively slightly smaller than that of *Cynohyaenodon ruetimeyeri*. The paracone is slightly smaller relative to the metacone, and these cusps are usually slightly more connate than in *C. ruetimeyeri*. The embrasure pit between M² and M³ is distinctly deeper than that between M¹ and M², which corresponds with the fact that the trigonid of M₃ is considerably larger than that of M₂. M₁ is slightly more reduced in comparison to that of *C. ruetimeyeri*, and M₃ is somewhat taller relative to M₂. The paraconid is considerably more anterior, the metaconid is somewhat smaller, and the horizontal ramus is somewhat deeper and thicker than in *C. ruetimeyeri*.

In the type skull the postvallum of M² is almost entirely worn away; most of the metacone has been removed in the process. There is virtually no wear on the postvallum of P⁴ or M¹, although the cusps of these teeth are somewhat worn from the apices. This wear pattern emphasizes the importance that M²-M₃ shear had attained in *Prodissoptalis*. The skull is apparently somewhat deeper than that of *Proviverra*. The orbit extends only to the anterior part of M¹, not to the posterior part of P⁴ as in both American and European species of *Proviverra*.

The species *Cynodon helveticus* Rüttimeyer 1862, was founded on an isolated lower molar and has been variously referred to the Canidae and the Miacidae. The specimen in the Basel Museum now labelled as the type belongs to *Prodissoptalis phonax*. I do not regard the two species as necessarily synonymous, because the tooth mentioned is of a different size and morphology from the type of *C. helveticus* (or else, as is possible, the published measurement is ten per cent. off and the figure is quite unrecognizable). I have therefore proposed to the International Commission on Zoological Nomenclature that the name *Cynodon helveticus* be suppressed.

The specific name of *P. phonax* is a Greek word meaning bloodthirsty, given for the same reasons as *Prototomus torvidus*.

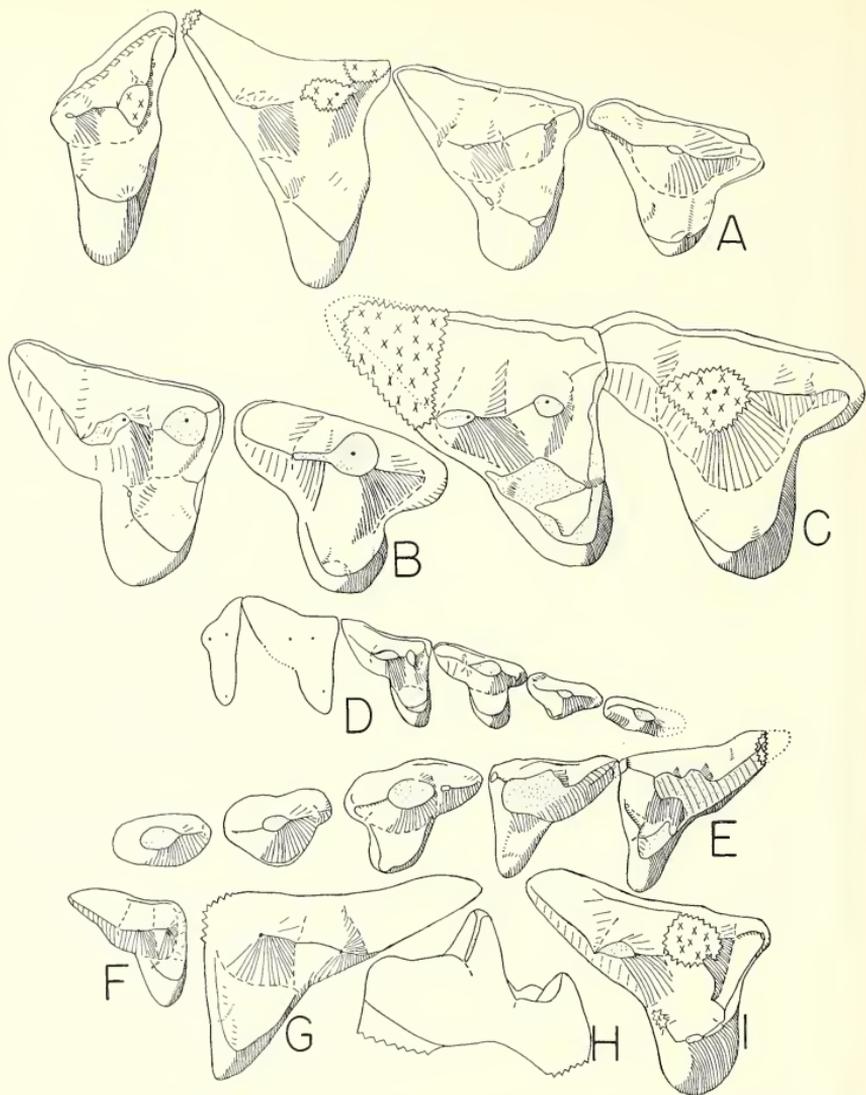
Prodissoptalis theriodis sp. nov.

Text-figs. 1L, 2E, 3C-D, 4E-G

Type. NMB No. Em. 12, nearly complete skull. See text-figs. 3C-D, 4E.

Type locality. Egerkingen, quarry unknown.

Diagnosis and discussion. The upper molars differ from those of *P. phonax*, aside from greater size, in having a somewhat longer metacrista. The upper and lower premolars are broader and more bulbous than those of *P. phonax*. The only structural difference in the lower molars is that in most specimens the talonid is relatively smaller in



TEXT-FIG. 4. Upper cheek teeth of proviverrines, mainly in occlusal view. A, *Proviverra typica*, right P⁴ (from type), M¹ (NMB, unnumbered isolated tooth), M² (NMB, unnumbered maxilla with P¹-M³), and M² (NMB No. Eh. 554), all $\times 6.8$. B, *Prototonus torvidus*, type, NMB No. Eh. 522, right P¹-M¹, $\times 6.8$; P⁴ is tilted slightly anteriorly. C, *Cynohyaenodon ruetimeyeri*, NMB unnumbered, right P¹-M¹, $\times 6.8$. D, *Prodissopsalis phonax*, type, NMB No. Em. 16, right P²-M¹ and outlines of M²⁻³, $\times 2.0$; not drawn with reticule. E-G, *Prodissopsalis theriodis*; not drawn with reticule. E, left P²-M¹ (type, NMB No. Em. 12) and M² (NMB unnumbered), all $\times 2.0$. F, right M¹ (NMB, unnumbered DP¹-M¹), $\times 2.0$. G, left M² (NMB, unnumbered), $\times 3.2$. H-I, *Prodissopsalis* sp., NMB No. Bchs. 266, right M¹, $\times 6.8$. H, direct posterior view; I, occlusal view. Symbols as in text-fig. 1.

P. theriodis; the horizontal ramus of the mandible is, however, relatively much deeper. The skull characters are as for *P. phonax*; it can be seen in *P. theriodis* that the infra-orbital foramen is rather high and the basicranium is short relative to these structures in *Proviverra*. The embrasure pit between M^2 and M^3 is very deep, in correspondence with the tall trigonid of M_3 . There is no evidence of a bulla.

Martin (1906) recognized that *P. theriodis* was generically distinct from all named forms, so he proposed the name *Propterodon* for it. Unfortunately he did not also propose a specific name, and by the vagaries of the rules of nomenclature *Propterodon iridinensis* is the type species of *Propterodon*. I believe that *Propterodon morrissi* (= *P. iridinensis*) is generically distinct from *Propterodon theriodis*, which thereby excludes *P. theriodis* from the genus originally based on it. The specimen figured by Rüttimeyer (1891, pl. 7, fig. 15a) on which *Propterodon* was largely based, is clearly referable to *Prodissopsalis theriodis* despite the inaccurate rendition of M_3 , the only tooth preserved. This inaccurate drawing led Matthew and Granger (1925) to believe that their *Propterodon iridinensis* was congeneric with *Prodissopsalis theriodis*. *P. theriodis* is different from '*Hyaenodon*' *schlosseri*, which is even more advanced. Stehlin (1940) mentions the presence in the late Ypresian Teredinasande (= sables à Unios) of Epernay, of a species related to *P. theriodis* but of greater size.

The name *theriodis* is a Greek word meaning savage, and is given for the same reasons as *Prototomus torvidus*.

GEISELTAL CARNIVORES

The geology and biota of the famous middle Eocene brown coal of Geiseltal have been well discussed by Krumbiegel (1959) and will not be repeated here. In 1952 Matthes described six genera and eight species of carnivores, all as new, from the Geiseltal. Two of the monotypic genera have elsewhere (Van Valen, in press, *b*) been transferred to the insectivore family Paroxyclaenidae and shown to represent only one species. I believe that only two genera and species are represented by the remaining named taxa, although as will be shown below there are also other carnivores present in the fauna.

The preservation of microscopic details in the Geiseltal material is justly famous but macroscopically the specimens of mammals are usually crushed so badly that, aside from the teeth, only the most obvious features of their anatomy can be determined. The photographs published by Matthes (1952) indicate most of what can be seen of the two species he discussed; the drawings in the present paper are meant only to supplement these photographs in regions which would otherwise be obscure. All the known specimens of Geiseltal carnivores are in the Museum für Mitteldeutsche Erdgeschichte, Halle/Saale.

The absence of any species of proviverrines in common between the faunas of Egerkingen and Geiseltal is somewhat surprising for neighbouring faunas supposedly of the same age. The ecology of a coal swamp is, however, presumably different from that of the Egerkingen fissures. No proviverrine species of either fauna is definitely more advanced than comparable species in the other fauna. The rarity of isolated teeth of small animals in the Geiseltal collection is perhaps due to the fact that the teeth are coloured shiny black like the matrix and are easily overlooked.

Proviverra gracilis (Matthes)

Text-fig. 2D

Leonhardtina gracilis Matthes 1952, p. 223.*Geiselotherium pilzi* Matthes 1952, p. 225.

Diagnosis and discussion. Only the lower dentition of *P. gracilis* is surely known (see below). It is the largest known European species of *Proviverra*; the length of M_2 of two specimens is 6.1 and 6.4 mm. The structure of the lower molars is, as far as determinable, the same as that of *Proviverra minor* Filhol, but the premolars are narrow and not robust as in the latter species. P_3 is unusual for European species of *Proviverra* in that it is relatively low; it lacks a paraconid and talonid. P_4 also lacks a paraconid. One upper tooth from Leonhardt Quarry, MME No. 2832, is probably referable to *P. gracilis*. Its labial length is about 6.8 mm.; the protocone lobe is missing, as is the junction between the metacone and the metacrista. The paracone and metacone are of about equal size, and are separated to about the same degree as in *P. typica*.

The diagnoses of *Leonhardtina* and *Geiselotherium* given by Matthes (1952) do not clearly distinguish between them. The only character in the diagnoses that is apparently different, the relative height of the paraconid and metaconid on the lower molars, is a result of breakage in the type of *L. gracilis*. I have compared the types with each other and find no reason to regard them as of distinct species.

Prodissopsalis eocaenicus Matthes

Text-figs. 5B-E

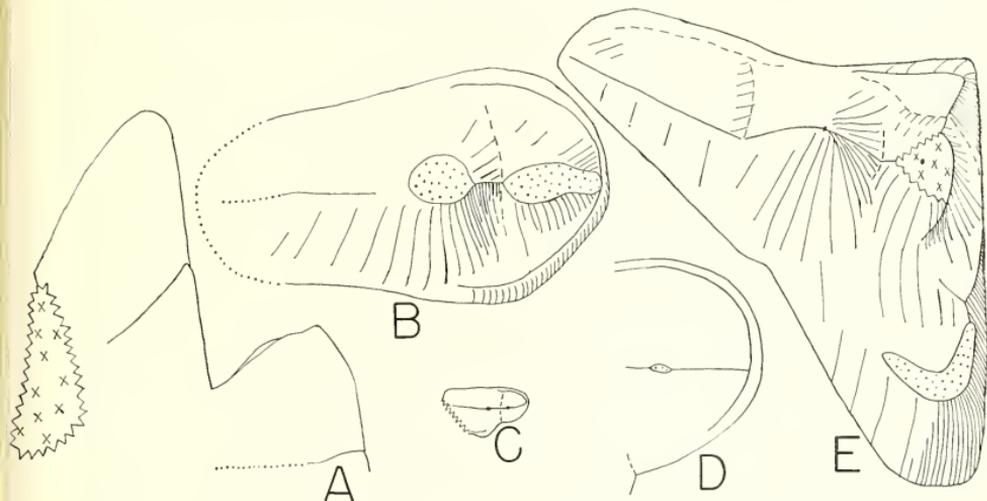
Prodissopsalis eocaenicus Matthes 1952, p. 206.*Imperatoria gallwiti* Matthes 1952, p. 214.*Imperatoria hageni* Matthes 1952, p. 220.*Geiselotherium robustum* Matthes 1952, p. 228.

Diagnosis and discussion. *P. eocaenicus* is most similar to *P. theriodis* but is considerably larger. In *P. eocaenicus* the metacrista of the upper molars is somewhat shorter, and the paracone and metacone are slightly more connate. The upper premolars are not clearly different when the total samples are considered except that the metastylar lobe of P^3 is somewhat larger in *P. eocaenicus*. The metaconid of the lower molars is slightly more posterior in *P. eocaenicus* and perhaps slightly smaller. The paraconid is also smaller and somewhat lower. A paraconid is present on the P_3 of *P. eocaenicus*; it is absent on the P_3 of *P. theriodis*.

The conspecificity of the upper dentitions (*P. eocaenicus* of Matthes) and the lower dentitions was determined by size, comparison with *P. theriodis*, morphological occlusal relations, and direct occlusal manipulation (allowing for crushing). The embrasure pit in the maxilla between M^2 and M^3 is larger than that between M^1 and M^2 , and these are of the relative size expected with the M_2 and M_3 of the lower dentitions. Almost all the differences between the mandibles and lower teeth mentioned by Matthes (1952) are due to crushing, and the few remaining differences are of the magnitude expected in a relatively invariable species. Metrically, only two measurements could be taken on as many as six specimens: the diameter of the trigonid of M_3 from the anterolingual base of the paraconid to the posterolabial base of the protoconid, and the length of P^3 .

The coefficients of variation (and the mean in parentheses) for these measurements are 2.8 (11.8) and 7.4 (12.6) respectively, both based on six specimens from two or three quarries. The upper jaws in fact differ more (in the structure of P^3 and in size) than do the lower jaws, but Matthes placed them in a single species and in this I follow him.

The degree of molarization of P^3 is somewhat variable in *P. eocaenicus*. In the type (MME No. 94) there is no trace of a protocone, while in MME No. 93 a distinct protocone lobe bearing a separate cingulum is present (text-fig. 5c). A third specimen, MME



TEXT-FIG. 5. A, cf. *Oxyaena* sp., BM No. M13778, lingual view right M_2 $\times 5.0$; not drawn with reticule. B-E, *Prodissopsalis eocaenicus*, not drawn with reticule. B, left P^3 , type, occlusal view, $\times 5.0$. C, left P^3 , MME No. 93, occlusal view, $\times 1.1$. D, metastylar lobe of left P^3 , type, occlusal view, $\times 5.0$. E, right M^2 , paratype, occlusal view, $\times 5.0$. Symbols as in text-fig. 1.

No. 3980, is intermediate. Presumably P^3 is about at the anterior limit of possible expression of the protocone prepattern.

The name *Prodissopsalis* has been chosen over *Imperatoria* by Savage (in press). I would have preferred the latter name to avoid phylogenetic commitments, and had in fact chosen it (Van Valen, in press), but Savage's choice may stand. The Egerkingen species *P. theriodis* is in fact somewhat more similar to *Dissopsalis* than is *P. eocaenicus*.

cf. *Prodissopsalis* sp.

Text-fig. 11

One mandible, described by Heller (1930) as an oxyaenid and not mentioned by Matthes (1952), is not referable to either of the species described above. This specimen is MME No. 3987; no information is available as to which individual quarry yielded it. The specimen is one of the two specimens of proviverrines I can recall that have deciduous teeth; the other is the type of '*Paracynohyaenodon*' *morrissi*. DP_3 and DP_4 are

present, as is the unerupted and broken M_2 . No evidence is available as to the presence or absence of M_3 . The paraconid of M_2 is slightly lower than the metaconid. The trigonid is relatively higher than that of the M_2 of *Proviverra gracilis*, the protoconid is much longer, and the talonid is somewhat shorter. The paraconid is more anterior and relatively longer. The talonid cusps are more prominent than in *P. gracilis*, and the basin and grooves there are deeper. The prefossid (the depression in the trigonid) is a deep pit, whose bottom slopes only gradually down lingually.

There is a possibility that this specimen belongs to the Limocyonini, but such a placement is not made here. The ancestors of *Thereutherium*, the only known European limocyonine, are as yet unknown, but it seems improbable that the species to which the present specimen belonged was ancestral because of its considerably greater size. Because it fits readily into *Prodissopsalis*, although not into any described species, this specimen is tentatively referred to *Prodissopsalis*. It is somewhat the smallest known species of that genus if correctly allocated; the length of M_2 is 7.2 ± 0.2 (approximate 95 per cent. confidence interval) mm., and the trigonid width of M_2 is 4.2 ± 0.1 mm.

Miacis? macintyri sp. nov.

Text-figs. 6A-C

Type. MME No. 3849.

Type locality. Geiseltal, quarry uncertain.

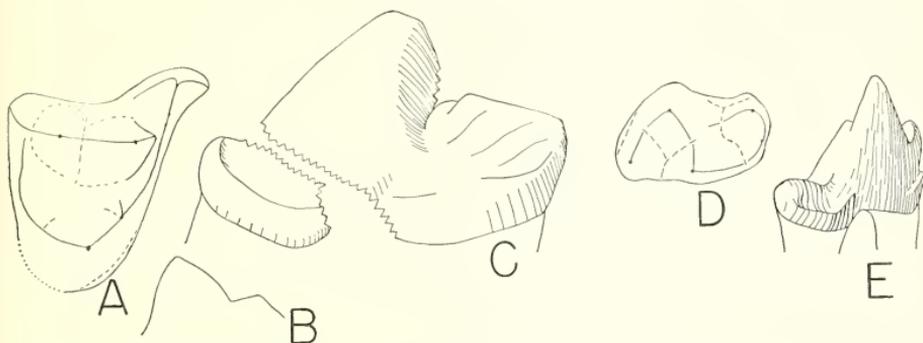
Diagnosis and discussion. A true miacid, not previously mentioned, occurs at Geiseltal. The type is a compressed skull with the upper and lower jaws nearly in occlusion, together with much of the skeleton. Without further preparation many diagnostic features are obscure, but enough is visible to show that an undescribed and interesting species is present.

The number of molars cannot yet be determined, but analogy with other species suggests that three will be found in each jaw. The full complement of four premolars is present. There is no parastyle on P^4 ; P^4 has a strongly tilted paracone. The labial cingulum of P^4 is incomplete, and the metacrista is highest anteriorly. The parastyle lobe of M^1 is moderately strong and projects anteriorly as well as labially. At least a precingulum is present on M^1 ; the presence of a postcingulum is uncertain. The paracone of M^1 is much larger than the metacone, and overhangs the anterior part of the tooth or nearly does so. The paracone and metacone are rather sharp, as is the centrocrista. The styler shelf is relatively narrow, and there is no distinct metaconule. M^1 is relatively narrow transversely. The length of P^4 is 9.8 ± 0.1 (approximate 95 per cent. confidence interval) mm., the length of the labial border of M^1 is 7.8 ± 0.2 mm., and the slant height of the paracone of P^4 from the base of the enamel is 6.3 ± 0.2 mm.

I have compared my notes and drawings of *M. ? macintyri* with the type of '*Viverra hastingsiae*' (probably the same as '*Viverravus angustidens*', fide Teilhard 1915), BM No. 30203. The M^1 of the latter is more transverse than in *M. ? macintyri*, the metacone is larger, the styler shelf is wider, the parastyle projects more labially but less anteriorly, and lingual cingula are nearly absent. In labial view, the angle at the top of the paracone of M^1 is larger than in *M. ? macintyri*. A definite parastyle is present on P^4 , although it is weak; the paracone and metacrista are lower relative to the length of P^4 ; and there is a rather large cusplule in the position of a mesostyle, low and posterolabial of the

paracone. *Miacis invictus* Matthew and Granger (1925), from the Irdin Manha, is smaller and structurally different in several respects.

As far as I can determine, the species most similar to *M.?* *macintyri* is *M.?* *exilis* from the French Phosphorites. On this species see Teilhard (1915). For the upper dentition of *M.?* *exilis* only a poor photograph of the lateral view of the skull has been published. Teilhard's comments, however, refer to the two features that are the most striking in the upper dentition of *M.?* *macintyri*, namely the much reduced metacone and the beak-like parastyle. These points are of course only suggestive without further knowledge of both species. *M.?* *macintyri* is much larger than *M.?* *exilis*.



TEXT-FIG. 6. A-C, *Miacis?* *macintyri*, MME No. 3849. A, occlusal view right M_1^1 , $\times 4.2$, not drawn with reticule. B, labial view paracone and metacone of right M_1^1 , $\times 4.2$, not drawn with reticule. C, labial view right P_4^1 , $\times 6.0$. D-E, *Eutheria* incertae sedis, MME No. 2833, $\times 6.0$. D, occlusal view; E, directly labial view. Symbols as in text-fig. 1.

It is quite possible that *M.?* *macintyri* will not prove to belong to the genus *Miacis* when better known. It may be noted that the M_1 of *M.?* *exilis* differs from that of the American species in having a lower trigonid and a broader talonid. The M_1 of at least *M.?* *macintyri* is squat and is small in comparison to P_4 . Probably relevant miacid material from Egerkingen is preserved in quantity at Basel. The species name is after G. T. MacIntyre, who is revising the Miacidae.

cf. *Miacidae*, incertae sedis

A single upper tooth figured by Heller (1930, pl. 1, fig. 6) appears to be the P_4 of a miacid, but it is not closely similar to any P_4 known to me. I could not find this tooth when I was in Halle in 1963.

Eutheria incertae sedis

Text-figs. 6D-E

One isolated tooth, MME No. 2833, from Cecilie Quarry, is of peculiar morphology and is not closely similar to any other mammal with which I have compared it. It could be a P_4 , a DP_4 , or a molar. The talonid is relatively small and very low; its top is at the

same level as the base of the enamel on the lingual side of the trigonid. Talonid cusps are nearly absent. The posterior wall of the trigonid slopes far posteriorly, especially on the lingual side. A strong labial cingulum is present by the talonid. The length of the tooth is 4.2 mm., the trigonid width is 2.7 mm., and the slant height of the protoconid from the base of the enamel on the anterior root is 3.7 mm.

When in Halle I regarded this tooth as the molar of a proviverrine descended from *Protomus palaeonictides*, but this allocation seems rather improbable. Its least unlikely affinities seem to be as the DP₄ of an erinaceoid or the M₂ of a miacine. The P₄ or DP₄ of a paroxyclaenid (Van Valen, in press, *b*) is also a possibility.

REMARKS ON OTHER OXYAENIDS

Proviverra minor (Filhol)

Text-fig. 1c

As noted above, the species described by Filhol (1877) as *Cynhyaendon minor* is referable to *Proviverra*. It is easily distinguishable from *P. typica* by the more bulbous premolars, but the molars are very similar. I could detect no consistent difference whatever in the upper molars. The lower molars of *P. minor* are slightly wider than those of *P. typica*, the talonid of M₃ (only) is slightly shorter, the paraconid of P₄ is relatively smaller, and the talonid of P₄ is slightly less developed lingually.

Prodissopsalis sp.

One upper molar (NMB No. Bchs. 266) from the Lutetian of Bouxwiller (Buchswiler), Alsace, is apparently referable to *Prodissopsalis*. It is probably a right M¹ and represents an undescribed species, being considerably smaller than *P. phonax* and structurally different as well. The parastyle is larger than in *P. phonax*, but the most important structural difference from the named species of the genus is in the relatively large size of the protocone, particularly its height. This is a primitive character, as is presumably the small size, and suggests that the Bouxwiller species is the most primitive of its genus. The protocone region is rather similar to that of *Oxyaena*. The wear pattern is, however, markedly different (cf. Van Valen, in press) and reference to the Proviverrini seems necessary. The relatively small protocone lobe and the moderate separation of the paracone and metacone indicate reference to *Prodissopsalis* rather than to *Protomus* or *Cynhyaenodon*. The length of the labial border is 5.8 mm., of the anterior border 4.5±0.1 (approximate 95 per cent. confidence limits) mm., and of the posterior border 6.8±0.1 mm.

cf. *Oxyaena* sp.

Text-fig. 5A

Three specimens possibly referable to *Oxyaena* are now known from the Blackheath Beds, probably of earliest Eocene age, at Abbey Wood, England. White (1931) has discussed the geology. The most diagnostic specimen is BM No. M13778, an unworn isolated M₂, from which the paraconid is missing. This tooth was figured inaccurately by Cooper (1932), who compared it especially with '*Sinopa*'. It differs from Wasatchian proviverrines especially by the fact that the hypoconid is slightly lower than the ento-

conid (cf. Van Valen, in press). The metaconid is about a third of the width of the protoconid. The width of the trigonid is 8.5 mm., the width of the talonid is 6.2 mm., the labial slant height of the protoconid from the base of the enamel on the anterior root is 13.9 mm., and the length (parallel to the base of the enamel) from the carnassial notch of the parolophid to the posterior end of the tooth is 11.0 mm. The second specimen, BM No. M15128, is the unworn protocone lobe of an upper molar, probably the M^1 of an oxyaenid. It differs from American species of *Oxyaena*, however, in having the lingual cingula, which are weak but joined lingually, definitely less than half the height of the protocone. Its anteroposterior length at the conules is 5.8 mm. A third specimen, BM No. M15125, is a (D) P^3 or (D) P^4 which is worn nearly to the roots. The protocone is weak and slightly anterior of the midline; there are weak lingual cingula, which are not joined on the lingual side of the protocone.

The only known specimen of *Argillotherium toliapicum*, from the London Clay, has recently been identified (Van Valen, in press) as very probably an immature oxyaenine, cf. *Oxyaena*. No additional specimens referable to the Oxyaeninae have been reported from Europe (Van Valen, in press). The lower molar of cf. *Oxyaena* from Abbey Wood is of an appropriate size for the skull of 'Argillotherium', and is very possibly conspecific with it. BM No. M15125 could be the last permanent or deciduous premolar of this species. BM No. M15128 is, however, considerably too small to fit into the single molar alveolus in the type of 'Argillotherium', and is probably at least specifically distinct. It is moreover not excluded that all three teeth from Abbey Wood are conspecific with each other and different from 'Argillotherium'.

cf. *Prototomus* sp.

The presence of the Proviverrini in England is shown by a fragment of mandible with M_3 , BM No. M20212, from the Blackheath Beds at Abbey Wood. The tooth is that of a primitive proviverrine. The lingual length is 4.7 mm., the trigonid width is 2.8 mm., the talonid width is 1.9 mm., and the labial slant height of the protoconid from the base of the enamel on the anterior root is 4.6 mm. It is probable that *Didelphis? colchesteri* Owen (1846) from Kyson (probably equivalent to or a facies of the Pebble-beds) is also a proviverrine and may represent the same species, although the type of *D.? colchesteri* may not be adequate for identification at the species level. On *D.? colchesteri* see also Charlesworth (1839), Lyell (1840), and Owen (1840); on the geology of Kyson see Prestwich (1850), Whitaker (1885), and White (1931). Prestwich (1850) and others ascribe the name *D.? colchesteri* to Charlesworth, but I have been unable to find a paper in which he uses this name.

Arfia gen. nov.

Type species. *Sinopa opisthotoma* Matthew 1901, p. 28.

Referred species. *Sinopa shoshoniensis* Matthew 1915, p. 73 (possibly a synonym of *A. opisthotoma*).

Diagnosis and discussion. *Arfia* differs from other proviverrines by the following characters: M_1 and M_2 unspecialized, metaconid of M_3 moderately reduced and paraconid of M_3 shifted anteriorly, M_3 enlarged, metaacrista of P^4 much reduced. Further differences have been given above with the comparison of genera. The name is onomatopoeic. *Arfia* represents a distinct specialization among the Proviverrini and, although possibly

ancestral to *Paracynhyaenodon* or even *Quercitherium*, is sufficiently different from these and from *Prototomus* to necessitate a separate genus.

Metasinopa fraasi Osborn 1909

When describing this species, based on one mandible, Osborn (1909) figured a maxilla as possibly conspecific and stated that M^3 was absent. That this was probably true in life is indicated by an apparently unbroken vertical surface of bone just posterior to M^2 . The presence of an M^3 in *M. fraasi* is, however, proved by a strong shear facet on the postvallid (the posterior wall of the trigonid) of M_3 . Furthermore, the postvallid wear is markedly stronger than the prevallid wear in *M. fraasi*, while the reverse is true of the maxilla. Therefore the maxilla is not conspecific with the mandible; the maxilla belongs to a small species of '*Hyaenodon*' as this genus is now defined, despite the presence of a nubbin on M^1 in the place of a protocone.

Propterodon morrisi (Matthew and Granger)

Paracynhyaenodon morrisi Matthew and Granger 1924, p. 1.

Propterodon iridinensis Matthew and Granger 1925, p. 4.

It is clear that the two species of proviverrines described by Matthew and Granger from the Irdin Manha Formation of Mongolia are conspecific. In the type description of *P. morrisi* the two preserved molariform teeth were identified as M_1 and M_3 , the latter incompletely erupted. Comparison with the specimens referred to *P. iridinensis* shows, however, that the ' M_3 ' of *P. morrisi* would be a perfect M_2 in size and morphology for *P. iridinensis* (M_1 and M_3 are known in specimens referred to the latter species) and that the morphology of the mandible is comparable; in particular the posterior mental foramen is under P_3 in both species when the present tooth identifications are used. There is space in the type specimen of *P. morrisi* for an unerupted M_3 , and the tooth here identified as DP_4 is low-crowned and narrow and has divergent roots and an anteriorly placed paraconid, all features that are characteristic of the DP_4 s of most primitive placentals.

TABLE 1. Measurements of upper teeth, in millimetres. With three or more specimens the standard deviation of the sample (not of the mean) is given, and the number of specimens is in parentheses.

	<i>Anterior margin</i>	<i>Posterior margin</i>	<i>Labial margin*</i>	<i>Mid-width</i>	<i>Posterior height metacone</i>	<i>Labial height paracone</i>
<i>Prototomus torvidus</i>						
P ³	—	—	5.5	2.1	—	—
P ⁴	4.4, 4.3	6.0, 5.2	5.6, 5.6	4.5, 4.0	—	4.2
M ¹	4.6, 4.8	6.7, 6.6	5.5, 5.4	—	4.6	—
M ²	5.9±0.2 (3)	8.1, 6.9	5.4, 5.2	—	4.1, 4.4	—
M ³	5.4	3.2	2.4, 2.0	—	1.7	—
<i>Proviverra typica</i>						
P ⁴	3.8±0.3 (3)	4.3±0.1 (3)	4.5±0.4 (4)	3.3±0.2 (6)	—	3.4±0.3 (3)
M ¹	4.8±0.4 (6)	6.3±0.6 (7)	4.6±0.2 (6)	—	3.7, 3.0	—
M ²	5.7, 5.9	7.6, 6.8	5.2, 4.5	—	3.6	—
M ³	5.9±0.6 (3)	4.1, 3.8	2.4, 2.4	—	—	—
<i>Proviverra minor</i>						
M ¹	4.6	5.9	4.3	—	—	—
M ²	5.4	6.8	4.5	—	3.2	—
M ³	6.1†	—	—	—	—	—
<i>Cynhyaenodon trux</i>						
M ¹	5.9	8.6	6.3	—	5.1	—
M ²	6.8	8.9, 8.9	5.8	—	4.1, 5.1	—
<i>Cynhyaenodon ruetimeyeri</i>						
P ⁴	5.7	7.4, 7.3	6.8	5.6, 5.6	—	—
M ¹	6.0±0.1 (4)	9.1, 9.7	6.9, 7.7	—	—	—
M ²	6.5, 7.5	10.1, 10.1	6.4, 7.4	—	5.7	—
M ³	7.8	4.9	3.0	—	—	—
<i>Prodissopsalis phonax</i>						
P ²	—	—	7.2	2.5	—	—
P ³	—	—	6.6, 6.7	3.8, 3.4	—	—
P ⁴	6.1	8.7	7.2, 8.1	6.1	—	—
M ¹	6.9±0.2 (3)	10.1, 10.9	7.8±0.1 (3)	—	5.7	—
M ²	8.7, 8.3	12.0, 11.6	7.4±0.2 (3)	—	—	—
M ³	8.8, 8.4	5.7, 6.0	3.0±0.2 (3)	—	2.6	—
<i>Prodissopsalis theriodis</i>						
P ²	—	—	8.0	8.7	—	—
P ³	—	—	4.2	5.8	—	—
P ⁴	8.5	11.5	11.3	8.5	—	—
M ¹	9.6, 8.7	13.0, 12.1	10.8, 9.7	—	—	—
M ²	11.2, 9.7	16.4	14.1	—	—	—

* for M³, length at metacone.

† approximate 95 per cent. confidence interval: ±0.4.

TABLE 2. Measurements of lower teeth, in millimetres.

	Lingual length	Trigonid width	Talonid width	Mandible depth below <i>M</i> ₂ protoconid
<i>Prototomus torvidus</i>				
				7.2*
<i>M</i> ₂	4.9†, 5.3	3.5	3.1	
<i>M</i> ₃	5.0†, 5.8	3.7	2.8	
<i>Proviverra typica</i>				
				6.2
<i>P</i> ₄	3.6	1.7	—	
<i>M</i> ₁	4.3, 4.2	2.3, 2.6	2.3, 2.1	
<i>M</i> ₂	4.5, 4.5	2.8, 2.9	2.5, 2.3	
<i>M</i> ₃	4.5, 4.7	2.8, 2.7	2.2, 1.9	
<i>Proviverra minor</i>				
				8.4
<i>P</i> ₄	4.6	2.4	—	
<i>M</i> ₁	4.7	3.0	2.8	
<i>M</i> ₂	5.0	3.4	2.9	
<i>M</i> ₃	5.0	3.2	2.2	
<i>Paracynhyaenodon schlosseri</i>				
				12.5
<i>M</i> ₁	7.4	4.3	4.0	
<i>M</i> ₂	8.4	4.9	4.2	
<i>M</i> ₃	9.0	5.2	3.4	
<i>Cynhyaenodon trux</i>				
				10.6
<i>P</i> ₂	5.4	2.1	—	
<i>P</i> ₃	5.4	2.4	—	
<i>P</i> ₄	5.8	2.6	—	
<i>M</i> ₁	5.7	3.2	2.7	
<i>M</i> ₂	6.1	3.7	2.8	
<i>M</i> ₃	6.5	3.6	2.2	
<i>Cynhyaenodon ruetimeyeri</i>				
				14.4, 11.5
<i>P</i> ₃	6.2, 5.5	3.2, 2.3	—	
<i>P</i> ₄	7.2	3.6	—	
<i>M</i> ₁	6.3, 6.3	3.5, 3.4	2.9	
<i>M</i> ₂	7.2, 7.0	4.2, 4.2	3.6, 2.8	
<i>M</i> ₃	7.0	3.8	2.4	
<i>Prodissopsalis plonax</i>				
				14.5
<i>M</i> ₁	7.1	3.8	3.6	
<i>M</i> ₂	8.1	4.4	3.7	
<i>M</i> ₃	8.8	4.6	3.6	
<i>Prodissopsalis theriodis</i>				
				—
<i>P</i> ₂	8.3	4.1	—	
<i>P</i> ₃	7.8	4.1	—	
<i>P</i> ₄	9.4	4.8	—	
<i>M</i> ₁	8.8	4.9	4.8	
<i>M</i> ₂	9.6, 9.7	5.3, 5.6	5.1, 5.5	
<i>M</i> ₃	11.4, 10.7	6.4, 5.7	3.8, 3.3	

* Approximate 95 per cent. confidence interval: ± 0.4 .† From Egerkingen β .

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APICAL DEVELOPMENT IN TURRITELLID
CLASSIFICATION WITH A DESCRIPTION
OF *CRISTISPIRA PUGETENSIS*
GEN. ET SP. NOV.

by RICHARD C. ALLISON

ABSTRACT. The nature of primary spiral ribs on apical whorls of *Turritella* (s.l.) is utilized for subdivision of the genus. However, variation causes some doubt as to the actual value of this criterion. Recognized variation is of two kinds: (1) 'variation' within a stock or group arising from improper grouping of species due to inadequate descriptive notation, and (2) actual variation displayed by various specimens of single species. Inadequate application of the terms 'unicarinate', 'mesocostate', 'unicostate', 'bicarinate', 'bicostate', &c. has confused efforts to arrange six Gulf Coast Eocene taxa in homogeneous groups. Notational systems proposed by Marwick (1957a, b) and Kotaka (1959) permit uniform description of apical developmental characters, and provide a firm base for taxonomic differentiation. The six taxa discussed belong to three separate apical types.

Some species are constant in apical development, while others show considerable variation. A given spiral rib may appear at various distances from the apex, but always seems to appear in a constant order relative to other spiral ribs. As long as this sequential order of appearance remains constant, Kotaka's notation allows continued use of apical ontogenetic features for taxonomy. This constancy of sequential appearance of primary spirals is not yet demonstrated for all apically variable turritellas; further investigation is needed to confirm apical developmental characters as reliable tools for all turritellids.

A new turritellid from the Eocene of Washington, *Cristispira pugetensis* gen. et sp. nov., illustrating orderly apical variation, is described and represents a new stock seemingly unrelated to presently known species from the north Pacific.

RECENTLY, a new turritellid was collected from the Raging River Formation (Eocene) of Washington by James D. Vine of the U.S. Geological Survey. The specimens were submitted to me by F. Stearns MacNeil for study and description. The material consists of approximately eighty external moulds which have been studied by means of latex casts.

The fossils are from a locality in the centre of the NE. $\frac{1}{4}$ of the SW. $\frac{1}{4}$ of section 15, Township 23 North, Range 7 East, Willamette Survey, in the Tiger Mountain-Taylor Mountain upland area, King County, Washington, U.S. Geological Survey locality M-648 (see USGS $7\frac{1}{2}$ -minute Hobart Quadrangle, 1953). The fossil locality is about 1,600 feet below the top of the Raging River Formation, and currently stands as the stratigraphically lowest recorded fossil occurrence in that formation. The subjacent sedimentary rocks of the Raging River Formation are approximately 1,000 feet thick but no fossil material is known from them. Vine (1962a, pp. 7-11) named the Raging River Formation and discussed its stratigraphic relationships and age. Lists of marine fossils identified by F. Stearns MacNeil and Welden W. Rau were included. *Turritella* n. sp. aff. *T. yabei* Kotaka of MacNeil's checklist is the *Cristispira pugetensis* gen. et sp. nov. of this paper. MacNeil concluded that the Raging River Formation is of middle Eocene to early late Eocene (late Ulatisian to early Narizian) age.

In view of the present trend towards subdivision of the genus *Turritella* Lamarck, it seems advisable to present at least a limited discussion of turritellid classification in connection with the description of the new genus. It is hoped that this discussion will emphasize the value of taxonomic subdivision of turritellids to palaeontologists.

The types and figured specimens of *Cristispira* are deposited in the U.S. National Museum. The hypotypes of *Turritella temblorensis* Wiedey and *Turritella arenicola* (Conrad) are in the Museum of Paleontology, University of California, Berkeley.

TURRITELLID CLASSIFICATION

Familial subdivision. The generic assignment of turritellas has been, and remains, difficult. Systematists have attempted to subdivide the inclusive genus *Turritella* (*sensu lato*) with varying degrees of success, and several investigators have closely examined the morphologic criteria used to subdivide the family. Notable have been the works of Palmer (1937), Bowles (1939), Merriam (1941), Palmer *in* Harris and Palmer (1947), Marwick (1957*a, b*), and Kotaka (1959). Each of these papers contains a history of previous efforts, so it is not repeated here. Merriam (1941, p. 35) has clearly stated the need for subdividing *Turritella* Lamarck. He states (*loc. cit.*):

The major desideratum with regard to the establishment of a universal classification of Turritellidae is information concerning the apical development of those subdivisions, mostly European and austral, to which taxonomic designation has already been given. Figures, descriptions, and available material are not satisfactory for this purpose.

It appears evident that if there is justification for subdivision of Lamarck's genus—and there undoubtedly is—a large number of units of at least subgeneric standing must ultimately be erected and adequately defined. In this manner alone can the classification be placed on a basis of actual genetic relationship.

There is still much to be done before the existing taxonomic units are thoroughly understood and described, but studies such as those of Marwick (1957*a*) have laid a firm foundation for further elaboration of turritellid classification.

Collectively these previously mentioned workers have given increasingly careful attention to the shape of the growth-line on the whorl sides and base, to the nature of the ontogeny of the primary spirals, to the type of protoconch, and to the details of the aperture. Such studies have shown an amazing diversity within the Turritellidae. One of the most significant advances has been the recognition of various groups or stocks of turritellids which have evolved along quite different lines. These groups are restricted in their zoogeographic distribution. Seemingly, no world-wide classification based on simple growth-line similarities (e.g. Guillaume's *Groupes*) can adequately express phylogenetic relationships. Convergences in adult appearance are rather common even though apical developmental characters may be quite divergent.

The morphologic criteria previously enumerated form the best basis for classification yet proposed, but some difficulties are still apparent, and the absolute significance of each of these characters in classification of all turritellids has not yet been demonstrated. Perhaps the most useful character has been the apical ontogeny. Many recognized groups, such as Merriam's stocks, have been found to be amazingly consistent in their ontogenetic development. This constancy seems to indicate that the youthful development is a valuable criterion which may be applied to turritellid classification.

Notation of apical whorls. The terminology applied to the apical whorls of gastropods is far from standardized. Cox (1955, pp. 195–8) and Cox *in* Moore *et al.* (1960, pp. I 111–14) has reviewed these terms and pointed out some of the limitations in their usage. The early whorls which immediately follow the protoconch in turritellids have been

variously referred to as the 'nuclear whorls', the 'nepionic whorls', and the 'neanic whorls'. Table 1 summarizes several authors' usages of the terminology applied to the protoconch and early portion of the teleoconch as used herein. For several reasons none of the terms enumerated above is satisfactory. 'Nuclear whorls' neither agrees with Dall's (1890-8) usage of 'nucleus' nor with Cox's (1955 and 1960) use of the same term. In addition, as Cox (1955, pp. 196-7) has pointed out, 'nucleus' is not an appropriate term for a series of whorls. The terms 'nepionic' and 'neanic' are equally objectionable as applications of life-cycle terminology to the hard parts of an organism, the precise

TABLE 1. Comparison of terminology applied to apical whorls of gastropods

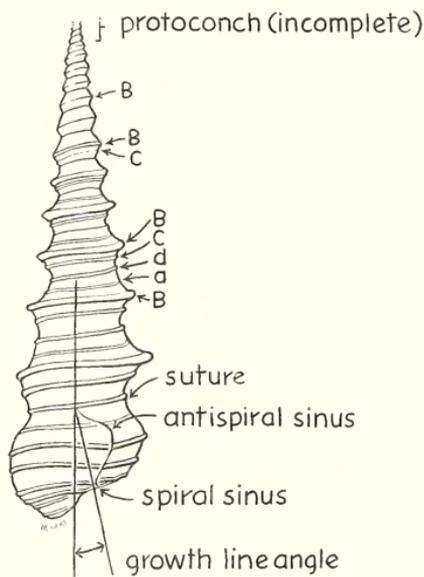
Dall (1890-1898)	Palmer (1937, 1947)	Merriam (1941)	Cox (1955, 1960)	Marwick (1957a, b)	Kotaka (1959)	This Paper
Protoconch = earliest caplike shell	Nucleus	Protoconch	Protoconch (nucleus = point of origin)	Nucleus = semi-globular initial part	Protoconch (nucleus = point of origin)	Protoconch (nucleus = point of origin)
				Protoconch		
	Nepionic whorls (first 3 or 4) or post-nuclear whorls		Early part of teleoconch	Neanic whorls	Neanic whorls	Early part of teleoconch

life history of which is unknown. Usage of 'nepionic' depends on correlation of the protoconch with the embryonic stage, an assumption that is clearly not warranted. If modern usage of 'embryo' is to be followed, the embryonic stage must be that part of the ontogeny before the animal becomes self-supporting. While some turritellids (e.g. *Gazameda gunnii* (Reeve) and others) have been shown to be ovoviviparous, developing the protoconch and the early whorls of the teleoconch within the embryo, other species (e.g. *T. communis* Risso) seem to be oviparous, though remaining only a short time in the plankton (Merriam 1941, pp. 12-13). The usage of 'neanic whorls' for the early part of the teleoconch implies that the protoconch represents the 'nepionic' stage. This implication would clearly not be true for ovoviviparous turritellids. Cox (1955, p. 195) has also pointed out that ornamentation may appear before the termination of the planktonic larval stage in many gastropods. For this reason, the implication that the protoconch and the 'nepionic' stage are correlative may also be incorrect for oviparous species; this latter usage would be correct only when the protoconch is terminated at the end of the planktonic larval stage. The usage of 'neanic whorls' also contradicts the usual application of this term in cephalopod literature where most authors have followed Hyatt. It seems clear that unless the life cycle of the gastropod in question is understood, there is no firm basis for application of these life-

cycle terms to the hard parts of gastropods. It is best to use the definition of 'protoconch' given by Cox (1955, p. 197) and to apply the term 'teleoconch' to the remainder of the shell, wholly avoiding the life-cycle terms. The protoconch and the early whorls in which the principal developmental stages are observed may be referred to collectively as the 'apical whorls', though it must be remembered that spiral rib development often continues throughout life in the Turritellidae.

Palmer (1937), Merriam (1941), Bowles (1939), and Palmer *in* Harris and Palmer (1947) have grouped species into unicarinate, mesocostate, unicastate, bicarinate, bicostate, cingulate, tricarinate, tricostate, and multicostate groups or stocks. Palmer *in* Harris and Palmer (1947, p. 280) has pointed out that her terms 'bicarinate', &c. have priority over Bowles's and Merriam's 'bicostate', &c., and that the former terms are more appropriate (see p. 670). Finlay (1930), Ida (1952), Marwick (1957*a, b*), and Kotaka (1959) have described these same relationships using several systems of notation with capital or capital and lower-case letters and numerals (see Marwick 1957*a*, p. 148; 1957*b*, pp. 12-14; and Kotaka 1959, p. 59). These latter systems describe the actual ontogeny more precisely, thus providing a more accurate basis for comparison.

The notation of Kotaka is here used to designate the major elements of the spiral sculpture (see text-fig. 1). B is the medial primary, D the peribasal one involved with the anterior suture; A is the first to appear adapical to B, and C is the first to appear abapical to B (between B and D). The conventions used by Kotaka (*loc. cit.*) and Marwick (*loc. cit.*) for secondary and tertiary spirals are not used in the present study because of their limited significance for generic differentiation, although they may be used advantageously in specific diagnoses. When the primaries are weakly developed, they are noted by a lower-case letter (e.g. b) instead of the capital. Numerical subscripts indicate order of appearance (e.g. B₁ indicates primary B appears first). D has been included in the formula when present, but no numerical subscript is given due to the difficulty in determining its point of origination. It should be capitalized when it forms a prominent element of the ornamentation visible on the whorl side, and designated by the lower-case d when it simply forms the angulation between the whorl base and side, remaining level or nearly level with the suture. In the present study 'unicarinate', 'mesocostate', 'bicarinate', 'unicastate', 'bicostate', &c. are used only to delimit the condition of the earliest



TEXT-FIG. 1. Diagrammatic representation of *Cristispira pugetensis* gen. et sp. nov. showing notational usage. The formula is $a_3 B_1 C_2 d$. The antispiral and spiral sinuses of the growth-line are indicated on the body whorl. The suture is immediately abapical to d.

post-protoconch whorls. Weak primaries are not neglected (e.g. a species with $a_1 B_1 c_1$ is considered tricostate, not unicastate or mesocostate). These terms should not be applied to whorls other than those showing the first ornamental stage.

Notation and progressive ontogenetic change. Palmer (1937, pp. 188–9) and Palmer in Harris and Palmer (1947, pp. 280–1) has classified her Gulf Coast Eocene species according to the sculpture of (1) the ‘nepionic’ whorls (first 3 or 4) and (2) the first ‘post-nepionic’ whorls, with each of these stages furnishing a basis for subdivision into unicarinate, bicarinate, and tricarinate species groups. As a consequence, the same species may be considered unicarinate on the basis of the ‘nepionic’ whorls, or bicarinate on the basis of the first ‘postnepionic’ whorls. This classification was an early attempt to provide a framework which describes the normal ontogenetic change in turritellids, and yet one which could accommodate certain unusual ontogenetic reversals (see discussion of *T. arenicola danvillensis*). This progressive change during ontogeny has been emphasized by Palmer (1947, p. 279):

Fragments taken from different parts in the length of the shell, unless fitted into the total pattern [of ontogeny], may seem to belong to different species. The change of ornamentation in the ontogeny of gastropods is universal but such a process is particularly accelerated and profusely developed in the Turritellidae.

She also states (op. cit., p. 280)

The factor of change enumerated in the first paragraph of this discussion [see above] is not accounted for in the Bowles–Merriam grouping. A species may be unicarinate on the nepionic or postnepionic whorls, becoming bicarinate and later multicarinate on the mature whorls. . . . There is no rigidity in their carination over the entire length of their shell. Therefore a qualifying statement must accompany any outline as to what part of the shell the ‘type carination’ may occur.

From this data, one may easily visualize the results of tachygenesis and bradygenesis. A unicastate form might be ‘accelerated’ in ontogenetic development to the point of being apically tricostate, or a tricostate form might be ‘retarded’ to a unicastate condition.

This progressive ontogenetic change may take three forms: (1) simple addition of spiral ribs, (2) changes in relative strength of ribs, either weakening or strengthening, and (3) loss of ribs present in earlier stages. All three features may occur independently of gerontism.

Inconsistent notation and variation. While the recognition of the basic type carination has proved useful in arranging many species, difficulties have been encountered with others. This difficulty stems from two major causes: (1) inadequate or inconsistent application of the terms ‘unicarinate’, ‘mesocostate’, ‘unicastate’, ‘bicarinate’, ‘bicostate’, &c., and (2) actual apical variation. For example, Palmer has not considered weak primaries in her assignment of the terms ‘unicarinate’, &c. (i.e. ‘unicarinate’ may signify only one primary present, or one primary which is stronger than its adjacent cohorts). Bowles and Merriam generally have followed the practice of recognizing in their terminology all primaries present. This difference between Palmer’s scheme and that of Merriam and of Bowles results from a difference in emphasis. Palmer has emphasized the enlarged ribs and applied the term ‘carinate’, while Merriam and Bowles have emphasized all the ribs and have applied the term ‘costate’ (‘carinae’ referring to strong keeled ribs and ‘costae’ referring to any rib). Therefore a form with $a_1 B_1 c_1$ might be considered uni-

carinate in Palmer's scheme and tricostate in Merriam's and Bowles's schemes (Palmer, personal communication, 6 April 1964). Where these terms are used, care should be taken to apply the proper termination, though usage of Kotaka's notation is less apt to result in confusion. As a result of the differing emphasis of these schemes, and of the inconsistent application of these terms by various investigators, a variety of apical developmental types may bear a single descriptive term. In addition, different primary ribs may appear first in separate unicarinate or unicostate genera [e.g. *Acutospira* with C_1 (unicostate) and *Cristispira* with B_1 (mesocostate)]. Note that mesocostate implies the B_1 condition; unicostate means a single primary (A, B, or C) appears first; unicarinate means a single primary rib which is keeled (A, B, or C) appears first, but may or may not be the only rib present. Merriam and Bowles have partially accounted for this problem by recognizing a 'cingulate' division for those species which have $A_1 C_1$, although the $B_1 C_1$ and $A_1 B_1$ conditions would both receive a 'bicostate' designation. This lack of precision in definition and usage of the terms 'unicarinate', 'mesocostate', 'unicostate', 'bicarinate', 'bicostate', &c. and the resultant improper grouping of species creates the impression that there is apical variation in otherwise consistent stocks. While the costate or carinate terms are useful in classification, they do not provide a sufficiently refined basis for comparison of species. Because of its greater precision and simplicity, the notational system of Kotaka should be more generally adopted as a tool in turritellid classification.

An example of the utility of this notation is provided by consideration of six Gulf Coast taxa; all have been wholly or partially referred to as 'unicarinate' or 'unicostate' at some stage during their life cycle and therefore warrant comparison to *Cristispira pugetensis*. Three separate apical developmental types may be recognized among these species; one, *T. arenicola* (Conrad), illustrates actual variation in the apical characters of different individuals. It is hoped that this view will explain some anomalies in classification based on apical development. The features of these six taxa are summarized in the following discussion (note the inadequacy of simple 'carinate' and 'costate' classification).

Turritella alveata Conrad 1855

Development. Data are from Palmer in Harris and Palmer (1947, pp. 288-90, pl. 36, figs. 7-12). The earliest post-protoconch whorls show $a_1 B_1 c_1$ with a_1 very fine and much weaker than C_1 at first, shortly progressing to $a_1 B_1 C_1$, and finally to $A_1 B_1 C_1 d$. c_1 is stronger than a_1 initially. The protoconch consists of one to one and a half whorls.

Remarks. Palmer has considered this species apically unicarinate (op. cit., p. 281): 'Obscure unicarinate stage, followed by a short bicarinate stage, succeeded by a tricarinate stage.' The weak primaries, a and c, are neglected in the 'nepionic' whorl designation. Bowles's (1939, p. 271) tricostate diagnosis of the form is in agreement with the classification adopted here. The apical development apparently remains constant. *T. creola* and *T. alveata* appear to be closely allied species.

Turritella creola Palmer in Harris and Palmer 1947

Development. Data are from Palmer in Harris and Palmer (1947, p. 286, pl. 35, figs. 2, 4, 5, 11). The development is $a_1 B_1 c_1$, i.e. the species is truly tricostate initially, soon

showing a stronger C, or $a_1 B_1 C_1 d$. c_1 is much stronger than the very weak a_1 initially. The protoconch consists of one whorl.

Remarks. Palmer (loc. cit.) has classified this species as a unicarinate-bicarinate form, these statements applying to the $a_1 B_1 c_1$ stage and the $a_1 B_1 C_1$ stage respectively. The species should be considered tricostate. Palmer (ibid.) states:

This species [*T. creola*] may be differentiated from *T. arenicola* in that the bicarinate feature has been formed as a definite character by the stage of the fifth whorl and the unicarinate phase is shortened and limited to the first four postnuclear whorls. In this respect *T. creola* seems to be more of a derivative of *T. dutexata* and allies of the lower Claiborne, than directly related to *T. arenicola*.

She states again (op. cit., p. 287):

T. creola is apparently the Jackson representative of the *T. dutexata* stock of the lower Claiborne.

While tachygenic development of *T. dutexata* ($a_2 B_1 C_1 d$) or *T. arenicola* ($a_3 B_1 c_2 d$) could develop a species such as *T. creola*, the latter is better classified along with those species included in Bowles's 'tricostate group' (Bowles 1939, pp. 270-1). Application of the terms 'carinate' and 'costate' therefore seems to have obscured the relationships of this species.

T. creola has not been cited for apical variability.

Turritella apita de Gregorio 1890

Development. Data taken from Palmer (1937, pl. 24, figs. 1, 3, 7, 10). The development is $a_2 B_1 C_1 d$, soon becoming $a_2 B_1 c_1 d$. In other words, the species is actually bicostate apically; a_2 is always weak, and C_1 (never as strong as B_1) becomes reduced in strength relative to B_1 . The latter spiral remains strong and gives the whorls an angulate appearance. The protoconch consists of about two whorls.

Remarks. Bowles (1939, p. 275) has classed *T. apita* as a unicosate species, although his illustration (pl. 31, fig. 4) does not show the earliest whorls. The text implies an $a_3 B_1 c_2$ development. Palmer in Harris and Palmer (1947, p. 285, no fig.) classes *T. apita* as a bi-unicarinate species (referring to the 'nepionic' and first 'postnepionic' whorls respectively). She states (loc. cit.):

It and *T. arenicola danvillensis* are the only two *Turritellas* [*sic*] of the Claiborne-Jackson Eocene which belong in such a group [bi-unicarinate]. *T. apita* passes into the unicarinate stage and retains it throughout life, while in *T. arenicola*, the unicarinate stage is a transitional phase, developing five and more spiral ribs, depending on the locality of its occurrence.

The discrepancies in assignment seem to be the result of inadequate material and insufficiently precise terminology. The treatment of Palmer in Harris and Palmer ignores the adult $a_2 c_1$ and utilizes only the young $B_1 C_1$ and the adult B_1 characters.

Turritella arenicola danvillensis Stenzel and Turner 1940

Development. Data taken from Stenzel and Turner (1942, card 58), and K. V. W. Palmer (personal communication). $B_1 C_1$ appear on the third whorl. By the seventh or eighth whorl C_1 weakens (but does not disappear) and the species is 'unicarinate' though still 'biscostate' at this stage; C_1 strengthens on the ninth or tenth whorl; a_2 then appears along with several other secondaries on the posterior slope. d angulates the whorl at the

suture. The protoconch consists of about two whorls (see Palmer *in* Harris and Palmer 1947, pl. 34, fig. 4).

Remarks. Palmer *in* Harris and Palmer (1947, pp. 284–5, pl. 34, figs. 1, 4, 5; pl. 35, fig. 1) reports examination of over one thousand fragments with abundant apical material from the type locality at Danville Landing, Louisiana. She mentions no disagreement with Stenzel and Turner's description of the apical ontogeny. Dr. Palmer has informed me (personal communication, 6 April 1964) that the double carination of the third whorl is sharp, after which the lower rib weakens until the whorls are 'unicarinate', and that the lower rib then increases in size until the whorls again become 'bicarinate'. However, C_1 does not actually disappear. The species should be considered apically bicarinate, but such a simple statement seems to be insufficient for evaluation of its relationships. *T. apita* and *T. arenicola danvillensis* are both classified as bicarinate-unicarinate by Palmer; on *T. arenicola danvillensis* C_1 is weakened temporarily on the early whorls, while it is weakened throughout adult whorls in *T. apita*. This seems to be evidence of close relationship, differing in degree rather than in kind. *T. arenicola danvillensis* could be sufficiently bradygenic to show an ancestral bicarinate condition, followed by a descendent unicarinate stage with a 'normal' $a_3 B_1 C_2 d$ development.

It is interesting to note that the apical development of *T. arenicola danvillensis* is different from that of *T. arenicola*. *T. arenicola* is apically unicastate, but some specimens (Pl. 92, fig. 10) very closely approach the bicostate condition; such convergence may very well attest to the close relationship of the two taxa. However, it seems likely that *T. arenicola danvillensis* should be given independent specific and generic rank. Even if the two species are closely related, attainment of the unicastate condition in *T. arenicola* could form a convenient arbitrary boundary for discrimination of separate generic entities. Careful study of the apical stages from various demes of *T. arenicola* and *T. arenicola danvillensis*, coupled with a similar analysis of their stratigraphic relationships, should aid in the interpretation of the phyletic relationships and the dependent taxonomy.

T. arenicola danvillensis apparently is consistent in its early development, for Palmer records no individual variation in her study of the abundant specimens from Danville Landing.

Turritella arenicola (Conrad) 1865

Development. Data taken from Bowles (1939, pp. 275–6, pl. 31, figs. 5–7). The development is $a_3 B_1 c_2 d$ plus several more secondaries posteriorly. One or both secondaries posterior to a_3 seem to appear concurrently with it. This is a truly unicarinate and mesocostate species. B is slightly anterior of the whorl midline apically, later migrating to a more central position on the adult whorls. The protoconch consists of about two whorls (figured for comparison on Pl. 92, fig. 10).

Remarks. Palmer (1937, pp. 197–8), Bowles (loc. cit.) and Palmer *in* Harris and Palmer (1947, pp. 281–3) have concurred in classifying *T. arenicola* as a unicarinate or unicastate species. However, Bowles has remarked on the individual variation seen on the apical whorls. He states (op. cit., p. 276):

There is a certain amount of individual variation in the persistence of the unicarinate sculpture on the apical whorls. On some specimens the second prominent revolving rib appears as early as the third

whorl, while in others it is still absent on the eighth or ninth whorls. It invariably does appear, however, and it always appears anterior to the original carination.

c_2 appears as a fine thread almost immediately after B_1 on the specimen figured for comparison. The point of initiation of a given spiral element (number of whorls from the protoconch) is quite variable in other species as well (e.g. *Cristispira pugetensis*), even in specimens from a single locality. Bowles does not clearly specify whether variants are common among specimens from a single locality or if the variation is more commonly between individuals from separate localities. However, the order of rib appearance, and therefore the notation used here, remains constant in *T. arenicola* and in all other variable species with which the writer is acquainted.

Bowles (1939, p. 276) notes the close resemblance of *T. arenicola* (Conrad) to *T. dutexata* Harris, which seems to be a bicostate ($a_2 B_1 C_1 d$) form. Palmer (1937, p. 199) classifies *T. dutexata* as tricarinate-bicarinate. Her illustration of an incomplete specimen (pl. 26, fig. 1) shows a tricarinate (tricostate) individual, which remains so, but the specimen of fig. 4 on the same plate is clearly bicarinate (bicostate). Harris originally described the species as bicarinate to the very apex, mentioning no tricarinate stage. If *T. dutexata* or its relatives are ancestral to the *T. arenicola* group, we might think of the a_3 and c_2 of *T. arenicola* as having been retarded in their point of insertion (bradygenesis).

Turritella arenicola branneri Harris 1894

Development. Data from Palmer in Harris and Palmer (1947, pl. 34, figs. 2, 3, 6, 7). The primary spirals develop in the order $a_3 B_1 c_2 d$, plus several other secondaries posteriorly. This is a truly unicarinate and mesocostate subspecies. The protoconch consists of about two whorls.

Remarks. Palmer (1937, p. 197, pl. 23, figs. 1, 2) and Palmer in Harris and Palmer (loc. cit.) has considered *T. arenicola branneri* unicarinate. Bowles (1939, p. 275) considers it a junior synonym of *T. arenicola* (Conrad), and Palmer (1947, p. 282) considers that it has been synonymized with good reason. Nevertheless, she lists it separately 'to tabulate the characters of extreme forms so that such may be used as criteria for judging other variations and the value of named units.' *T. arenicola branneri* seems properly considered as a junior synonym.

T. arenicola branneri has not been specifically cited for apical variation.

Summary

Careful study of these species suggests that the apical variation previously implied is in part real and in part the result of inadequate terminology. *T. alveata* Conrad and *T. creola* Palmer in Harris and Palmer are better considered as members of Bowles's 'tricostate group'. *T. apita* de Gregorio and *T. arenicola danvillensis* Stenzel and Turner seem to be related and should either be placed in a group by themselves (bicarinate-unicarinate group of Palmer) or in Bowles's 'bicostate group'. *T. arenicola* (Conrad) and *T. arenicola branneri* Harris belong to Bowles's 'unicostate group'. Thus constituted, three separate groups are recognized, each group apparently warranting taxonomic recognition. Formal designation of these taxa should await review and inclusion of other Gulf Coast species.

While these six taxa have not been classified as members of a single group, all have had the term 'unicarinate' or 'unicostate' applied to some part of their ontogenetic cycle. Classification of these six species in one group would necessitate inconsistent application of the criteria used to designate the class; i.e. the variation in such a group would be unnatural and in part the result of insufficiently refined descriptive notation for the comparison of apical stages. This 'variation' actually constitutes valid differences which we may recognize in taxonomy.

Among these six taxa, only *T. arenicola* (Conrad) has been specifically cited for its individual apical variation. As I have previously emphasized, the various spirals appear at different distances from the protoconch in different individuals of the species, but the order of appearance remains constant. *Cristispira pugetensis* also is markedly variable in this same fashion, but again the sequential order of spiral rib appearance remains constant. Instances in which the sequential order of insertion of the primary spirals is reversed in individual variants are unknown to the writer; such cases would create considerable difficulty for the uniform application of the sequential order of apical spirals to taxonomy, but in their absence such criteria seem to be of considerable value.

Variable species may not be well adapted with respect to their apical shell characters, hence showing a wider phenotypic expression in the absence of direct selection pressure. Constant species may be more thoroughly adapted with a lesser range of phenotypic expression. Conversely, environmental influences may be more important than genetic factors in producing apical variation. Studies on living turritellids should be undertaken in order to evaluate these factors. Variation between separate demes (stratigraphic and geographic separation) of the same species should also be investigated. If comparisons show the position of primary rib appearance to differ consistently between separate demes, we may find tachygenesis and bradygenesis to be significant mechanisms of evolution in the Turritellidae. Interpretation of such processes may provide a usable tool in reconstructing the broad outlines of phyletic history.

The diversity of the many Gulf Coast turritellid species does not militate against use of apical ontogeny as a taxonomic key, but presents various examples of rather rapid diversification (radiation). In all likelihood, taxonomy based on these apical characters as well as growth-line characteristics, &c., would closely approach a true phyletic classification. Instances will be found in which arbitrary 'cut-offs' will be necessary, but this is a natural result of well-documented phyletic relationships being expressed in taxonomy.

It is impossible in this brief study to give a thorough review of all cases which may have bearing on the validity of using apical ontogeny in classification. The six taxa discussed have been chosen for examination because of their bearing on the new material from the Washington Eocene and because they illustrate the applicability of more refined notation in comparing apical stages of turritellids.

SYSTEMATIC DESCRIPTION

Phylum MOLLUSCA
 Class GASTROPODA
 Subclass PROSOBRANCHIA
 Order CAENOGASTROPODA

Family TURRITELLIDAE Woodward 1851
 Subfamily TURRITELLINAE Woodward 1851
 Genus CRISTISPIRA gen. nov.

Type species. Here designated *Cristispira pugetensis* sp. nov.

Diagnosis. Shell turritelliform; protoconch of three or four (?) smooth whorls; primary spirals appearing in order $a_3 B_1 C_2 d$; adult growth-line with double sinus, deepest part of antispiral sinus usually above whorl midline and substantially embayed; spiral sinus shallower and broader with deepest part of embayment on d or slightly above; growth-line angle variable, ranging from about 15° to 25° ; base of whorl with prominent revolving spirals; aperture subovate with heavy parietal wash.

Name. Latin *crista*, f. = crest; *spira*, f. = coil, twist.

Discussion. The very slightly effuse basal and columellar lips and the subovate aperture of *Cristispira* are vaguely reminiscent of *Mesalia* and other genera assigned to the Pareorinae Finlay and Marwick 1937. However, the concave basal growth-line and lack of a ridge on the adapical columellar lip show that it is a member of the Turritellinae (see Marwick 1957a, p. 164, under 'Zaria').

Cristispira pugetensis sp. nov.

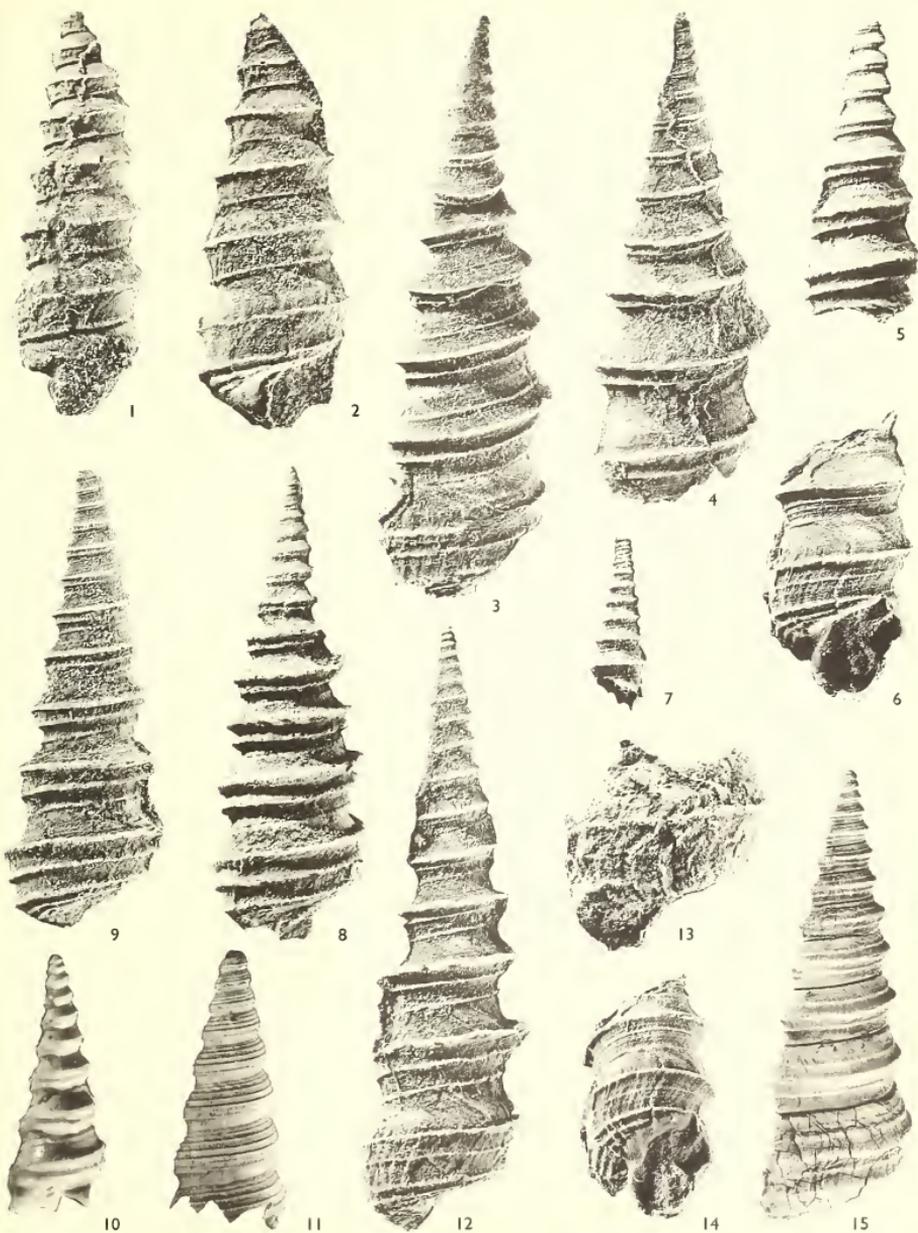
Plate 92, figs. 1-9, 12-14

1962a *Turritella* n. sp. aff. *T. yabei* Kotaka, MacNeil in Vine, p. 9.

Description. Shell of medium size; maximum observed length 56 mm.; maximum observed diameter 16 mm. Pleural angle averages about 19° , ranges from about 15° to 30° ; apical angle usually about same as pleural angle, but on some specimens much wider than pleural angle. Spire profile normally conical to concave conical, but specimens with wider apical angle obconical adapically. Primary spirals develop in order $a_3 B_1 C_2 d$; d forms angulation between side and base exactly at suture nearly throughout ontogeny, only rarely becoming raised on whorl side adjacent to anterior suture. Protoconch of about three or four (?) sharply convex smooth whorls (multispiral); about

EXPLANATION OF PLATE 92

- Figs. 1-9, 12-14. *Cristispira pugetensis* gen. et sp. nov. USGS locality M-648, Raging River Formation, Washington. Rubber casts. USNM Cat. No. 132. Fig. 3, holotype; remainder, paratypes. 1, specimen with $B_1 d$ alone ($\times 1.7$), 648626. 2, specimen with $B_1 d$ alone ($\times 1.6$), 648627. 3, specimen with $a_3 B_1 C_2 d$ ($\times 1.7$), 648628, holotype. 4, specimen with $B_1 C_2 d$ ($\times 1.7$), 648629. 5, specimen with $a_3 B_1 C_2 d$ ($\times 1.5$), 648630. 6, specimen with $B_1 C_2 d$ showing slightly effuse columellar lip and parietal wash ($\times 1.6$), same as fig. 14, 648631. 7, specimen with $B_1 d$ alone showing protoconch partially decorticated ($\times 2.6$), 648632. 8, specimen with $B_1 C_2 d$ ($\times 1.7$), 648633. 9, specimen with $B_1 C_2 d$ ($\times 1.7$), 648636. 12, specimen with $B_1 C_2 d$ ($\times 1.7$), 648634. 13, gerontic whorl showing heavy growth-lines ($\times 2$), 648635. 14, same as fig. 6, showing parietal wash ($\times 1.3$), 648631.
- Figs. 10, 11. *Turritella arenicola* (Conrad). UCMP locality A-1043, Jackson Group, Louisiana. 10, specimen with $a_3 B_1 C_2 d$ plus posterior secondary; accelerated specimen with c_2 as a fine thread almost immediately after B_1 ($\times 9.3$), UCMP 36491. 11, specimen showing growth-line ($\times 1.9$), UCMP 36492.
- Fig. 15. *Turritella temblorensis* Wiedey. UCMP locality B-7853, Topanga Formation, California. Specimen showing double sinused growth-line with ? $a_3 B_1 C_2 d$ ($\times 0.95$), UCMP 36493.



fifth whorl a strong medial angulation (B_1) appears, increasing in strength and angulating whorls throughout ontogeny until last one or two, when it may decrease in strength slightly with onset of gerontism; normally with five or six unicarinate apical whorls before appearance of C_2 on lower third of whorl, though point of insertion of C_2 is quite variable, C_2 failing to appear at all on some smaller specimens; C_2 variable in strength from coarse thread to slightly subordinate to B_1 ; a_3 even more variable, making its appearance in only about one-third of specimens, apparently never earlier than in young adult whorls; a_3 variable from coarse thread, when discernible, to weak primary, but always subordinate to B_1 and C_2 . Whorl profile variable with diverse development of primaries, from strongly angulate medially on specimens with no a_3 or C_2 to 'pagoda-form' on specimens with strong, subequal B_1 and C_2 with no a_3 , subrounded with slight medial angulation on specimens with $a_3 B_1 C_2 d$ all developed. Well-preserved specimens with many fine spiral threads. Body whorls of occasional large specimens with gerontic features such as slight obsolescence of primaries, heavy strengthening of growth-lines, and a slight tendency toward looser clasping of preceding whorl causing d to be weakly exposed and suture more deeply impressed. Suture normally moderately impressed and clearly discernible. Base flattened and ornamented with four or five coarse secondary spirals. Aperture subovate with heavy parietal wash; basal and columellar lips very slightly effuse, continuing to parietal wash; peristome incomplete. Growth-line moderately variable; antispiral sinus moderately deep with deepest part of embayment usually between a_3 and B_1 ; growth-line usually spirally convex just below posterior suture; spiral sinus shallower and broader than antispiral sinus with maximum at d or slightly above; growth-line with broad shallow antispiral concavity on base; growth-line angle moderate and variable, ranging between 15° and 25° .

Name. The species name refers to the Puget Sound region and Puget Lowlands of western Washington.

Holotype. USNM 648628. *Paratypes,* USNM 648626-7, 648629-35. All material is from U.S. Geological Survey locality M-648.

Discussion. Only three primary spiral developmental combinations occur: $B_1 d$, $B_1 C_2 d$, or $a_3 B_1 C_2 d$ (i.e. $a_3 B_1 d$ or $a_3 C_2 d$ are never found in this species) in spite of the variation in point of insertion of a_3 and C_2 . Specimens lacking C_2 invariably lack a_3 , although C_2 may be present without a_3 . a_3 is therefore always retarded first, and C_2 next; the primary spirals are both inserted and retarded in an orderly manner. This sequential order of rib appearance has also been described in *T. arenicola* (Conrad) (Bowles 1939, p. 276, also quoted on page 673 of this paper). A fundamental order of this nature seems to be usual in turritellids; the apical ontogeny may be variously retarded or accelerated, but the sequence of spiral appearance in different groups remains constant and is therefore a useful criterion in classification.

MacNeil *in* Vine (1962a) has classified *C. pugetensis* as '*Turritella* n. sp. aff. *T. yabei* Kotaka' and Kotaka has included *T. yabei* under *Acutospira*. In 1959 Kotaka (pp. 101-2) proposed *Acutospira* as a new subgenus of *Colpospira* Donald 1900, and referred three Japanese Tertiary species to it. The type species, *A. okadai* Nagao 1928, develops the primaries in the order $A_2 b_3 C_1 d$, with C_1 appearing just slightly before A_2 . Therefore the apical ontogeny differs markedly from that of *Cristispira*. The type species of *Colpospira* Donald is multicostate apically with a deep antispiral sinus and a very shallow or negative growth-line angle (see Marwick 1957a, pp. 151-3). The growth-line of

Acutospira Kotaka is similar, but in view of the differences in apical development, the subgeneric relationship of *Acutospira* to *Colpospira* seems questionable.

A. tashiroi Kotaka has a growth-line with a strongly negative angle; apparently it is tricostate, but the apical development is not known. Adult whorls have a very heavily developed A. *A. yabei* Kotaka seems to be bicostate, developing B and C at about the same point apically with A appearing later (d also present). This differs considerably from the development of typical *Acutospira*. The growth-line is sharply and deeply embayed and the deepest part lies on A; the growth-line angle is very small or negative. In general appearance 'A.' *yabei* resembles *C. pugetensis*, but the latter has a prolonged early development of B. In *Cristispira*, the maximum depth of the growth-line is usually between a_3 and B_1 and the growth-line angle is wider, never becoming negative.

MacNeil (1964, pp. B-2, 3, pl. 1, figs. 5-8, 12-18) has described a bicostate turritellid, *Turritella kotakai*, with a strong B on the adult whorls, from the Miyara Formation (middle or late Eocene) of Ishigaki-shima, Ryūkyū Islands. This new species seems to be related to 'A.' *yabei* Kotaka. Its apical development is $B_1 C_1 d$ with no A appearing.

While some of the early Tertiary Japanese turritellids are similar in gross aspect to *C. pugetensis*, the refined generic concepts used here preclude congeneric assignment.

C. pugetensis seems to have no definite relatives among described species from the Pacific Coast Tertiary. Various subspecies assigned to the *T. variata* and *T. diversilineata* branches of the *T. uvasana* stock of Merriam (1941) are similar in general appearance and have the coarsely ornamented whorl base, but they are bicostate on the apical whorls. Among other Pacific Coast species, those referable to the *T. broderipiana* stock of Merriam (1941) are uncostate, but these have a broad, shallow growth-line with a single sinus. This latter group seems to be referable to *Archimediella* (*Torculoidella*) Sacco 1895 (see Marwick 1957a, pp. 159-60).

One species, *T. temblorensis* Wiedey, from the Californian Miocene, warrants comparison. It is apparently a uncostate form which may develop the primary spirals in the order $a_3 B_1 C_2 d$ as in *Cristispira*, but the very earliest apical whorls are not known. Merriam has considered the growth-line to be single sinused (1941, p. 116), but better material from the Topanga Formation shows it to be double sinused and concave on the base (see Pl. 92, fig. 15). Loel and Corey (1932, p. 265) have called attention to the similarity in appearance of *T. temblorensis* and *Zaria duplicata* (Linnaeus), but the latter bears the characteristic convex basal growth-line of the Pareorinae, while the former belongs to the Turritellinae. As Merriam has suggested (op. cit., p. 117), the similarity is one of homeomorphy. In general appearance *T. temblorensis* is very similar to *Cristispira*. The whorl base bears the coarse revolving ribs, the growth-line angle is about the same, and a small parietal wash seems to be present. However, the growth-line has a much broader and shallower antispinal sinus with its deepest part falling near B. The segment of the growth-line above the maximum flexure is spirally concave rather than convex as in *Cristispira*. C apparently develops very soon after B and follows after several whorls, along with a secondary just below the posterior suture (concurrently?). A uncostate stage does not seem to be prolonged as in *C. pugetensis*. In spite of the several similarities between these two species, I am inclined to judge the difference in growth-line as of supraspecific importance. Discovery of more complete apical material of *T. temblorensis* and stratigraphically and geographically intermediate forms may further elucidate their relationship.

The developmental patterns of several Gulf Coast Eocene species have been reviewed in the preceding pages. *T. apita* de Gregorio differs from *Cristispira* in its apical development ($a_2 B_1 C_1$ becoming $a_2 B_1 c_1 d$) although the adult shell is reminiscent of some variants of the Washington species. *T. arenicola danwillensis* Stenzel and Turner also differs markedly in the early development ($B_1 C_1$ with C_1 weakening for a few whorls, then strengthening and followed by a_2) and has more evenly convex and regularly ornamented adult whorls. *T. creola* Palmer and *T. alveata* Conrad are apically tricostrate ($a_1 B_1 c_1 d$) and therefore not closely related.

T. arenicola (Conrad) and *T. arenicola branneri* Harris are the only Gulf Coast taxa which warrant careful comparison with *C. pugetensis*. Apically their development is $a_3 B_1 c_2 d$; a_3 and a secondary just posterior to it seem to appear concurrently. The protoconch consists of about two whorls and a parietal wash is present. The growth-lines have their maximum flexure near the midline of the whorl above B_1 and below a_3 . The antispiral sinus is deeply embayed, though not so sharply as in *Cristispira*. The growth-line, as in *Cristispira*, has a very slight spiral convexity just below the suture, and the growth-line angle measures about 10° . The base of the whorl bears revolving ribs of moderate strength (Palmer 1937, pl. 23, fig. 2) but the complete apertural details are not known.

Conrad originally assigned *T. arenicola* to *Mesalia*?, but this assignment seems to have been based on the rather shallow whorl height and broad pleural angle rather than apertural characteristics. *T. arenicola branneri* Harris differs from *T. arenicola* only in the number of secondaries on the adult whorls and in the pleural angle. Bowles (1939, p. 275) has properly considered it a junior synonym of *T. arenicola* (Conrad).

While *T. arenicola* (Conrad) and *T. arenicola branneri* Harris are similar to *Cristispira* in many aspects, I am somewhat hesitant to assign them to the latter genus. The Gulf Coast taxa have a much rounder whorl profile and more numerous revolving spirals, with one of the posterior secondaries appearing concurrently with a_3 ; the basal spirals are not so well developed as in *Cristispira*. Perhaps the most significant difference is the more broadly rounded antispiral sinus with the narrower growth-line angle. As Marwick (1957a, pp. 156, 158) has emphasized in his discussions of *Kurosioia* Ida, *Maoricolpus* Finlay, and *Stiracolpus* Finlay, geographic and stratigraphic factors should not be ignored for purposes of classification. Convergences are quite common in the Turritellidae. Marwick (1957a, p. 158) states: 'Close agreements in outer lip characters and in primary spiral ontogeny are essential for generic grouping, and even then the possibility of convergences of distant stocks with simple characters must be considered.'

Unfortunately, the phyletic relationships of *Cristispira* remain obscure. No certain ancestor or congener is yet known from the Tertiary deposits of the Americas and the western Pacific. While *T. temblorensis* Wiedey and *T. arenicola* (Conrad) are similar morphologically, both differ in the details of the growth-line. Wide geographic or stratigraphic separation, or both, in the absence of intermediate forms, contributes additionally to the speculative nature of congeneric assignments. In all probability relatives of *Cristispira* will be found in as yet unknown north Pacific fossil faunas.

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A NEW CALAMITALEAN CONE FROM THE MIDDLE PENNSYLVANIAN OF SOUTHERN ILLINOIS

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ABSTRACT. A new species of the calamitalean cone genus *Paracalamostachys* Weiss, *P. cartervillei*, is described. The holotype consists of a group of cones found in an 'ironstone' nodule of Middle Pennsylvanian age. The cones are small, ranging from 11 to 17 mm. in length, and 4.0 to 4.5 mm. in diameter. Several cones are present at a node on the cone-bearing stem, they lack peduncles, and consist of whorls of bracts and sporangiophores arranged alternately, the fertile whorls being superposed. Approximately six sporangiophores are present in the fertile whorl and twelve bracts in the sterile whorl. Each sporangiophore bears four horizontally elongate sporangia arranged in the form of a Maltese cross around a central stalk. The sporangiophores are enclosed by the upturned ends of the subtending bracts. Spores ranging in size from 40 to 100 μ were isolated from sporangia and are referable to the form genus *Calamospora* Schopf, Wilson, and Bentall, being comparable to the dispersed spore species, *C. breviradiata* Kosanke. The cone is apparently homosporous and is compared with previously described species of the genus *Paracalamostachys* Weiss and related genera.

THE holotype of a new species of the genus *Paracalamostachys* Weiss (Weiss 1884) was recently discovered at an abandoned mine site about half a mile West of Carterville, Illinois. It consists of a compressed axis bearing cones at three nodes preserved in an 'ironstone' nodule. At this Middle Pennsylvanian plant locality in Williamson County (Sec. 4, T 9 S, R 1 E), Herrin Quadrangle, nodules containing plant material are found in place in shales above the Herrin (Illinois No. 6) coal, and in weathered shales forming the upper part of the overburden material removed from above the coal during mining. The horizon from which the holotype is derived is in the Carbondale Formation of the Kewanee Group (Kosanke *et al.* 1960).

The original appearance of the specimen is shown in Plate 93, figs. 1 and 2. The fossil was more fully exposed by etching with a 10 per cent. solution of phosphoric acid which removed the nodular matrix. This etching action of the acid was allowed to proceed for varying lengths of time, while being observed under a binocular dissecting microscope. Periodic flushings with distilled water were applied to halt the action of the acid so that critical examination of the progress of the etching could be determined. The above technique revealed that the cones were preserved in some depth in the matrix and that they were not so compressed as the original appearance of the specimen suggested. This method of study has yielded a considerable amount of information concerning the structure of the cones and may prove to be particularly useful with reproductive structures found in comparable nodules. In some cases a fine white material, apparently consisting of phosphates produced in the treatment, may form on the nodular surface. Application of a dilute solution of ammonium hydroxide followed by thorough washing with distilled water removes most of this unwanted by-product of the acid treatment.

Spore samples were taken from sporangia in various positions along the axis of the cone. These were picked off, as spore masses, as the phosphoric acid etching proceeded. Extremely short oxidation (2 to 3 minutes) with concentrated HNO_3 followed by a washing with 10 per cent. potassium hydroxide solution released the individual spores

from the spore mass and made them more readily examined, without affecting their structure.

Genus *PARACALAMOSTACHYS* Weiss

Paracalamostachys cartervillei sp. nov.

Plate 93, figs. 1-5; text-fig. 1

Diagnosis. Small cone composed of alternating whorls of bracts and sporangiophores with sporangiophores of successive whorls superposed. Approximately six sporangiophores and twelve bracts in each of the two types of whorls. Each sporangiophore having a central stalk bearing four horizontally elongate sporangia. Cones homosporous, having spores of the *Calamospora breviradiata* Kosanke type. Position of attachment of sporangiophore stalk to cone axis not known.

Stratigraphic occurrence. Shales above the Herrin (Illinois No. 6) coal, Carbondale Formation, Kewanee Group, Middle Pennsylvanian.

Holotype. Specimen No. 563 and slide preparations in the Paleobotanical Collections, Botany Department, Southern Illinois University.

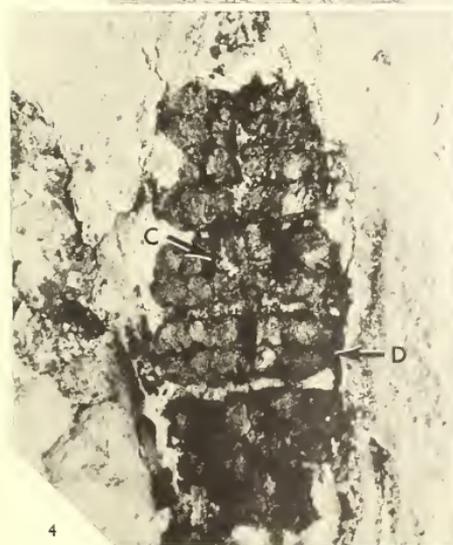
Description of cone. The overall length of the entire specimen (Pl. 93, figs. 1, 2) is 3.8 cm., the diameter of the axis bearing the cones ranging from 2.5 mm. just above a node, to about 3.0 mm. immediately below a node. The length of the cones, which are present at three nodes along the axis, varies from 11 to 17 mm. while their maximum diameters range from 4.0 to 4.5 mm. Three cones are present at each of the two upper nodes and two cones are present at the lowest node. The type of foliage borne by the fertile stem cannot be determined; however, a few elongate structures suggestive of *Asterophyllites* type foliage are present in the nodule (Pl. 93, fig. 1, B) and have an orientation consistent with their having been leaves of the stem.

Prior to treatment with phosphoric acid, each cone showed several horizontal rows of brown, somewhat spherical structures which subsequent study showed to be sporangia and spore masses. Numerous bracts, present in whorls, alternate with the whorls of fertile parts and have broad basal portions and acute tips. The exact number of bracts in each whorl is estimated at being twelve on the proportion of the diameter of the cone which one bract occupies. Except where the bracts are obviously displaced due to crushing, they turn abruptly upward immediately to the outside of the sporangia and cover the fertile parts, giving the cone a compact appearance.

Selective etching of the matrix has made it possible to determine some features of the sporangiophores. The part and counterpart of the cone indicated by the letters A in Plate 93, figs. 1 and 2 respectively were chosen for this purpose since they appeared to be the most complete. Fig. 3 shows this cone (Pl. 93, fig. 1, at A) at the same magnification after

EXPLANATION OF PLATE 93

Figs. 1-5. *Paracalamostachys cartervillei* sp. nov. 1, 2, Part and counterpart of holotype showing appearance before treatment to expose material. Cone which was more fully exposed by acid treatment indicated by A; possible foliar structures indicated by B. $\times 3$. 3, Cone indicated by A in fig. 1 after acid treatment. $\times 3$. 4, Enlarged view of exposed cone showing details of sporangiophores. Indications explained in text. $\times 9$. 5, Isolated spore of *Calamospora breviradiata* type from holotype specimen. $\times 500$.



removal of the matrix. Portions of six whorls of sporangiophores have been uncovered. The upper and lower whorls are very incomplete, but the four central whorls are exposed in a fair degree of completeness (Pl. 93, fig. 4). Each sporangiophore bears four sporangia which are circular in outline, except for flattened areas where they are in mutual contact, when viewed in the tangential aspect (Pl. 93, fig. 4, at c). The horizontally elongate form of the sporangia can be seen in views that are more radial (Pl. 93, fig. 4, at d). The sporangiophore stalks are generally poorly preserved and their positions are marked by hole-like depressions in most cases. No distal expansion or head was found on the stalks of the sporangiophores, but the preservation does not preclude their having been present originally. In the centrally located sporangiophore of the third whorl from the top of the cone (Pl. 93, fig. 4, at c) the tissue of the sporangiophore stalk is preserved and consists of a slightly raised area having a circular outline. The sporangia of each sporangiophore occur in two superposed pairs. Superposition is also evident between the sporangiophores of the second and third whorls from the top of the cone, while those of the fourth whorl are less clearly superposed with the members of the higher whorls (Pl. 93, fig. 4). This is due to vertical separation of the sporangia in the centre of the whorl, which occurred during the acid treatment. Although it is difficult to delimit some of the members of the whorls of sporangiophores, it is most likely that they were superposed throughout the cone. In cases where the sporangiophore stalk (or the depression marking its position) is viewed in radial aspect this structure has an essentially horizontal orientation (Pl. 93, fig. 4, at d). The form and orientation of the parts of the sporangiophores suggest that the sporangiophore stalks were attached to the cone axis approximately midway between bract whorls. Unfortunately, no clear instance of the attachment of a sporangiophore stalk to the cone axis was found.

Parts of the cone which were uncovered most completely suggest that the number of sporangiophores was probably six per whorl. These sporangiophores are closely enveloped by the bracts which appear as fine lines of dark material in the nodular matrix in side view (Pl. 93, fig. 4, above the arrow at d).

Poor preservation of cuticular remains present in the specimen does not allow a determination of the structure of the epidermis.

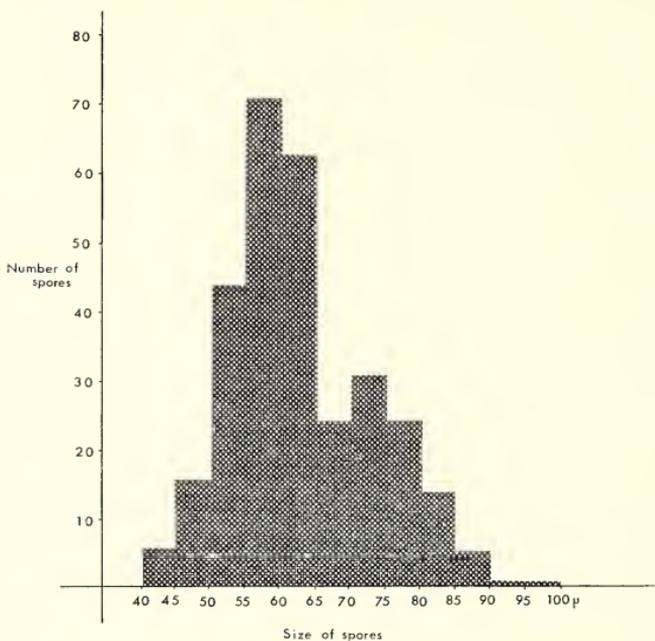
Description of spores. Spores isolated from the cones are radial, trilete, and were probably spherical prior to compression. The size range is from 40 to 100 μ with a peak at 55–60 μ . The trilete rays are short and vary in length from 11 to 16 μ . The exine is uniformly thin (less than 2 μ) and the area contagionis is present in most spores. The spores are referable to the form genus *Calamospora* S.W. and B. (Pl. 93, fig. 5).

The trilete mark is distinct, the lips slightly to more prominently elevated and the commissure is thin and attenuate. In most specimens the spore coat shows numerous folds, which may be due to the thinness of the spore wall. The spore coat is laevigate and translucent.

Spores within sporangia from all parts of the cones exhibit a similar size range. Of three hundred spores, the size ranged from 40 to 100 μ as shown in the histogram (text-fig. 1). The largest spores generally show little or no folding even though their wall thickness is the same as that of the smaller spores. It is likely that *P. cartervillei* was homosporous since the cones exhibit a similar range in spore size throughout their lengths.

Kosanke (1950) has previously described spores of *Calamospora* from Illinois. Two

species, *C. breviradiata* Kosanke and *C. hartungiana* S.W. and B. occur at the horizon from which our cones were taken. In many specimens isolated from the cones the structure of the trilete was similar in every respect to that of *C. breviradiata* (e.g. the specimen in Kosanke 1950, pl. 9, fig. 4). In other spores isolated from the cones the lips of the trilete were lower, but definite, and extended from 1 to 2 μ on either side of the suture



TEXT-FIG. 1. Histogram of spore size distribution in the holotype of *Paracalamostachys cartervillei*.

(Pl. 93, fig. 5). In wall structure and mean size the spores are similar to *C. breviradiata* as described by Kosanke but exhibit a greater size range than that reported by him for this species. The difference in structure of the trilete, present in spores from the same sporangium, may be due to varying degrees of compression, or of spore maturity. For the present we are assigning the spores of *P. cartervillei* to the dispersed spore species *Calamospora breviradiata* Kosanke.

Discussion. Information obtained from the cones and their included spores clearly indicates a botanical affinity with the order Calamitales. The cones from Carterville are similar to several species of the genera *Paracalamostachys* and *Calamostachys* described by Weiss (1876, pl. 16, figs. 1, 2; 1884, pl. 21, fig. 6 and pl. 22, figs. 1, 2, 5, 10-14). The former genus is maintained as distinct from *Calamostachys* on the grounds that the exact position of sporangiophore attachment is not known. In *Calamostachys* the sporangio-

phore stalk is attached to the cone axis approximately midway between successive bract whorls. As the new material did not allow the position of sporangiophore attachment to be determined, appropriate comparison can best be made with species of *Paracalamostachys*. Among the various species of this genus, the new form is somewhat similar to *P. minor* Weiss (1884) but differs from that species in that the spores of the new cone are distinguishable from those of *P. minor* as described by Hartung (1933). *P. striata* Weiss is distinguished from the Illinois cones in part by being heterosporous (Hartung 1933), while *P. polystachya* (Sternberg) Weiss has elongate peduncles and exposed sporangia. *P. rigida* Weiss is a smaller cone, but little is known concerning this form and it cannot, therefore, be adequately compared with the cones from Illinois. The species *P. heterospora* recently described by R. and W. Remy (1958) is a very large cone, about 15 cm. long, and is heterosporous. It seems most likely that the new species, *P. cartervillei*, may have been of the *Calamostachys* type since compression specimens of *Palaeostachya* often show some indication of the axillary attachment of the sporangiophores in the form and orientation of the sporangia even when the sporangiophore stalk is not visible (e.g. figures in Weiss 1884, pl. 21, figs. 3, 4). The new cone is also distinct in numerous ways from the recently described genus *Calamocarpon* (Baxter 1963).

The more than twenty-five species of *Calamostachys* currently recognized encompass a very wide range in form, size, and mode of preservation. The only feature common to all of these forms is the mid-internodal attachment of the sporangiophore stalks to the cone axis between successive bract whorls. The structural details of some species, primarily petrified forms, such as *C. binneyana*, *C. ludwigi*, *C. casheana*, and *C. americana* are known. In the case of most of the compression forms much less is known and comparison among the various supposed species is limited to obvious features such as cone length, diameter, and the spacing of fertile and sterile whorls. In a few instances the number of bracts and sporangiophores present in the whorls can be estimated and has been used in distinguishing some of the compression species.

Paracalamostachys cartervillei resembles *Calamostachys binneyana* in the approximate number of bracts and sporangiophores present in the cone whorls, but it is smaller in length and diameter. The spores of *C. binneyana* persisted in tetrads which often contained aborted spores and were enclosed in a perisporial membrane. There is no evidence that these features were present in *P. cartervillei*. On the basis of measurements presented by Hartung (1933) for the spores of *C. binneyana*, it appears that *P. cartervillei* produced spores of greater diameter and with a greater size range than did *C. binneyana*. Of the remaining forms of *Calamostachys* which may be compared with the Carterville cones, *C. ludwigi* should be noted for its similarity. *C. ludwigi* differs from the Carterville cones in the same features which set them apart from *C. binneyana*. All the remaining species of *Calamostachys* are clearly distinct from *P. cartervillei* on the basis of numerous features.

Inability to determine the exact position of sporangiophore stalk attachment to the cone axis makes it necessary to refer the Carterville cone for the present to the genus *Paracalamostachys* in which this structural feature is not known.

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LOWER AND MIDDLE DEVONIAN SPORES OF NORTH AND CENTRAL VESTSPITSBERGEN

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ABSTRACT. From the Devonian succession in North and Central Vestspitsbergen, seven hundred rock-specimens collected by the author and over three hundred collected by previous Expeditions have been examined macroscopically; two hundred and fifty of these were prepared for microscopic investigation. These included specimens from every Spitsbergen formation, and consisted typically of medium to fine-grained clastic sediments. Eighty-two dispersed spore species are recorded, of which forty-eight new species are systematically described. Five new genera (*Bullatisporites*, *Craspedispora*, *Cymbosporites*, *Aulicosporites*, and *Chelinospora*) are proposed, and another genus (*Archaeozonotriteles*) is emended. Twenty-five morphologically complex species were sectioned, in order to elucidate and interpret their structure. Consideration is given to corrosion and preservation of the spore exine.

THIS paper describes only the preparation and systematics of the dispersed spores from the Devonian succession of North and Central Vestspitsbergen. In a later paper the microfloral assemblages and their stratigraphical applications will be discussed.

The study of the dispersed spores from the Devonian succession of Spitsbergen was undertaken at the joint suggestion of Mr. N. F. Hughes and Mr. W. B. Harland. An initial study by Dr. P. F. Friend and Mrs. M. Mortimer had shown the presence of spores from horizons in the Mimer Valley Series.

All the samples studied were collected by members of various Spitsbergen Expeditions organized from the Sedgwick Museum, although prior to 1959 few samples were collected for this purpose; samples for palynological preparation and examination were collected by Dr. P. F. Friend and Dr. D. J. Gobbett in 1959, and by the author in 1961.

The spore genera and species are based solely on morphological criteria, their botanical affinities are for the most part unknown.

The Devonian succession in Spitsbergen is confined to the island of Vestspitsbergen, where the Devonian outcrops over a large area (Friend 1961, p. 79, fig. 1). It consists of about six thousand metres of predominantly Old Red Sandstone facies. Numerous sections were collected for palynological study throughout the area by the author, in the hope of producing a stratigraphical succession based on dispersed spores. Well-localized samples collected by previous Cambridge Spitsbergen Expeditions were also used. For general stratigraphy and stratigraphical nomenclature, I have followed Friend (1961) throughout.

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PREPARATION AND EXAMINATION OF SAMPLES

Specimens were examined macroscopically, and information on colour, grain-size, calcareous and micaceous content, plant fragments, and any weathering was recorded. A representative selection of two hundred and fifty specimens, comprising a variety of lithological types ranging from coals to coarse-grained sandstones, and all of probable continental origin, were prepared for microscopic examination. Red oxidized shales and sandstones failed to produce any spores, but all other lithological types, though not all other samples, produced spores; the grey and green siltstones yielded the best preserved and most diverse assemblages.

Although the same basic technique was used throughout, with such a variety of lithologies every sample required individual attention and timing at each stage of its preparation. The macroscopic record of each sample prepared was studied, so that any constant reaction might perhaps be related to some visible feature, thus helping to improve the selection of suitable samples. Each specimen for microscopic investigation was scrubbed in distilled water to remove any Recent contamination. About 3 gm. of sediment were broken up with a hammer into approximately 3–5 mm. fragments. To avoid any contamination, the specimen was crushed within sheets of newspaper on an anvil, both the hammer and anvil surfaces being washed after each crushing. If the specimen was superficially weathered, care was taken to use only the central part.

Calcareous samples were treated with 20–30 per cent. hydrochloric acid, and left for at least 2 hours (and frequently overnight). All clastic samples were then treated with cold 50–60 per cent. hydrofluoric acid for 2–14 days; the remaining sediment was then transferred to a nickel crucible to which fresh hydrofluoric acid was added and boiled for 30–40 minutes.

Insoluble fluorides resulting from the previous treatment were removed in warm 10–30 per cent. hydrochloric acid in a water-bath. Frequently as many as ten of these 5-minute treatments were needed to remove all the fluorides.

To the washed residue in 10 cc. of distilled water were added 2–3 drops of 50 per cent. Stergene (or other non-ionic detergent). This was then subjected to a 5–20 second treatment with an ultrasonic disintegrator (1:1 end ratio steel probe vibrating at 20 kilocycles per second). This disaggregated clumps of organic and mineral matter. The residue was then washed in distilled water until the top fluid remained clear.

Oxidation of the humic material was then carried out in Schulze solution. Maceration time varied from 10 minutes to 5 hours, with different samples.

Frequently, further clearing and concentration with an alkali was necessary, and a few drops of 5 per cent. potassium hydroxide, sodium hydroxide, or ammonium hydroxide were used, the latter seemingly gave the best results. The residue was left in alkali for about 15 seconds.

Often minerals which survived the HF treatments were in such concentration that they required removal by a heavy liquid separation. Acidified zinc bromide (S.G. 2.2) was used, the preparation being centrifuged for 20 minutes at 1,800 revolutions per minute.

Only two coals are present in the Spitsbergen Devonian succession; these were crushed and then macerated in Schulze solution for 24–48 hours, thereafter following the preparation technique for clastic sediments.

From these residues at least two strew-slides were prepared for each productive sample, the residue being mounted in unstained glycerine jelly on standard glass slides, and covered with No. 0 coverslips. The slide was tapped lightly, to encourage the residue to settle in one plane, and after allowing the glycerine jelly at least three days to set, the coverslips were sealed with gold size. Single megaspore and microspore mounts were made of several species. Single spores were also separated from residues for serial sectioning, following the embedding and sectioning techniques of Wigglesworth (1959) and Hughes, Dettmann, and Playford (1962). From one to four specimens of twenty-three species were sectioned at 2–3 μ intervals, perpendicular to the equatorial plane, mounted in glycerine jelly and sealed as before. From unproductive samples, one slide was usually prepared as a negative record of the sample. Surplus residue was stored in polythene-stoppered glass tubes, in 50 per cent. glycerine containing a few drops of phenol to prevent fungal growth.

All the strew-slides were first surveyed at $\times 125$ magnification. However, after all productive samples had been studied, the interpretation of morphological features and specific identification was completed at magnifications of $\times 500$ and $\times 1250$, using as many well-preserved specimens as possible and the sections where available. After the specific descriptions were complete, a quantitative estimation was made of the species present, by counting under high power 200 specimens from each sample yielding a sufficient number of well-preserved spores.

DISPERSED SPORE SYSTEMATICS

Nomenclature and Classification. The nomenclature of the described Spitsbergen Devonian spores follows the rules of priority and typification of the International Code of Botanical Nomenclature (1961, Montreal). No botanical affinities are implied with generic designations, which relate to form genera based solely on their morphological features. The nomenclature of suprageneric categories is the artificial classification proposed by Potonié and Kremp (1954), later amplified by them (1955, 1956a) and by Potonié (1956, 1958, 1960), and subsequently revised in part by Dettmann (1963).

Terminology. In the systematic section, the descriptive terms used are for the most part those which have been well defined, clearly understood, and widely accepted by previous authors. An effort has been made to keep the number of terms to a minimum.

The author uses the terms intexine and exoexine (Potonié and Kremp 1955) to denote respectively the inner and outer layers of a two-layered spore wall (exine). Where the exoexine is stratified (occasionally separate, but never truly cavate), for example in *Cirratirradites avius* sp. nov. (Pl. 99, fig. 11), the terms outer exoexine and inner exoexine are used. In Spitsbergen Devonian species referred to the genus *Perotrilites* (Erdtman)

ex Couper 1953, the exact nature of the outermost layer is unknown; it may be a true perine, or it may be an outer exoexine, and the non-committal term outer sculptine is used.

The term cavate (Dettmann 1961) is used for asaccate spores in which the spore wall layers are separated from each other by a cavity, the width of which is at least 20 per cent. of the total spore radius, or if less, then the outer layer is thinner and loosely enveloping, as for example in *Perotriletes pannosus* sp. nov. (Pl. 102, fig. 14). This excludes *Densosporites* and *Anulatisporites* which, as demonstrated by Smith (1960, pl. 20, figs. 1-8), occasionally have a small cavity between the intexine and exoexine, and *Geminosporea* in which the intexine sometimes separates wholly or partially from the exoexine.

Equatorial flange is used for what appears in proximo-distal aspect to be a membranous zona, but proves from sections to be a sharply tapering cingulum.

Granulate pseudosculpture is used where corrosion of the infra-granulate structure of a spore wall has resulted in an upstanding 'ornament' of granules.

A crumina is defined as a separation and extension of the outer part of the exine (or exoexine). This may occur primarily in the distal region, as for example in *Hystri-cosporites monosaccus* (Archangelskaya) comb. nov. (Pl. 96, figs. 1, 2), where it is a separation of the outer exoexine; or in the equatorial region as in *Labiadensites fimbriatus* (Waltz) Hacquebard and Barss 1957, see Dettmann and Playford 1963 (pl. 96, figs. 1, 2), where the outer part of the exine is separated and extended.

Miospore is used for dispersed spore species, in which the mean diameter is less than 200 μ , and megaspores for dispersed spore species in which the mean diameter is more than 200 μ .

New species have been erected only where fifteen or more adequately preserved specimens were available for study. Assignment to previously described species is made only when there is reasonable evidence for identity from published illustrations and descriptions. Frequently, however, descriptions are short and illustrations poor, and although the Spitsbergen specimens may appear similar, I cannot be certain that their construction is identical. In most of these cases I have erected new species, recording in my comparisons where conspecificity may occur; in the event of a re-examination of poorly described species, any conspecificity may be easily located. All type and other figured specimens here described, are housed in the Sedgwick Museum, Cambridge, and referred to by a preparation slide number, followed by the 'east-west' and 'north-south' mechanical stage readings, and then by the Sedgwick Museum Spitsbergen Specimen number and a Sedgwick Museum number. In single mount preparations, the slide number is prefixed 'M', with sections the slide number is prefixed 'S'. The stage readings are from the Leitz Dialux microscope No. 3 (serial no. 526724) in the Sedgwick Museum, Cambridge.

Anteturma SPORITES H. Potonié 1893

Turma TRILETES (Reinsch) Dettmann 1963

Supersubturma ACAVATITRILETES Dettmann 1963

Subturma AZONOTRILETES (Luber) Dettmann 1963

Infraturma LAEVIGATI (Bennie and Kidston) H. Potonié 1956

Genus LEIOTRILETES (Naumova) Potonié and Kremp 1954

Type species. *Leiotriletes sphaerotriangulus* (Loose) Potonié and Kremp 1954.

Leiotriletes parvus Naumova 1953

Dimensions. (Twenty specimens) Equatorial diameter 16–24 μ (mean 19 μ).

Occurrence. Fraenkelryggen Division, and Lower Reuterskiöldfjellet Sandstone; Gedinnian and Siegenian.

Leiotriletes pyramidalis (Luber) comb. nov.

1941 *Azonotriletes pyramidalis* Luber, in Luber and Waltz, p. 54, pl. 12, fig. 182.

1955 *Filictriletes pyramidalis* Luber, p. 60, pl. 3, fig. 70.

Dimensions. (Eighteen specimens) Equatorial diameter 54–95 μ (mean 70 μ). Elevated lips, individually 2–3 μ wide, 4–9 μ high.

Remarks. *Filictriletes* lacks type species designation, and embraces within it spores of several previously well-established genera (Potonié 1958, p. 35).

Occurrence. Reuterskiöldfjellet Sandstone and Mimer Valley Series; Siegenian to Eifellian.

Comparison. *Leiotriletes pulvereus* Balme and Hassell 1962 (p. 5, pl. 1, fig. 182) has a larger size range, weaker lip development, and is punctate. *L. tumidus* Butterworth and Williams 1958 (p. 359, pl. 1, figs. 5, 6) has a smaller size range and is tumid. *L. ornatus* Ishchenko 1956 (p. 22, pl. 2, figs. 18–21) is smaller and has thicker lips.

Leiotriletes pagius sp. nov.

Plate 94, figs. 1, 2

Diagnosis. Miospores trilete; amb convexly triangular with broadly rounded apices. Laesurae distinct, simple, straight, almost reaching the equatorial margin. Exine 2.5–4 μ thick, homogeneous, laevigate.

Dimensions. (Twenty-two specimens) Equatorial diameter 46–63 μ (mean 54 μ).

Holotype. Preparation KA 251/9, 21.5 94.8, K905, N231.

Locus typicus. South Mimerdalen, Central Dicksonland, Spitsbergen; Reuterskiöldfjellet Sandstone, Siegenian.

Description. Holotype diameter 58 μ . Exine 4 μ thick.

Comparison. *Leiotriletes dissimilis* McGregor 1960 (p. 27, pl. 11, fig. 1) has punctate contact areas, low distinct lips and a thinner exine. *Leiotriletes confertus* McGregor 1960 (p. 27, pl. 11, fig. 2) also has distinct lips and a thinner exine, and the only difference between these two McGregor species is the punctate contact area and open commissure in *L. dissimilis*, which might be the result of preservation. *Leiotriletes devonicus* Naumova 1953 (p. 22, pl. 1, fig. 5) and *L. trivialis* Naumova 1953 (p. 45, pl. 5, fig. 14) are both considerably smaller. Naumova (1953) in describing *L. devonicus* states 'exine dense, thick, spore margin thickened'. This thick wall might be misinterpreted as a cingulum, unless seen in broken specimens or in oblique aspect, and many form species included within *Stenozonotriletes*, may in fact be thick-walled representatives of *Leiotriletes* or *Punctatisporites*. If *Stenozonotriletes simplex* Naumova 1953 (p. 36, pl. 3, fig. 17; p. 69, pl. 10, fig. 3; and p. 130, pl. 19, figs. 16, 17) should prove to have a thick wall and not a cingulum, then *Leiotriletes pagius* sp. nov. would be synonymous with it.

Occurrence. Lower Reuterskiöldfjellet Sandstone; Siegenian.

Genus PUNCTATISPORITES (Ibrahim) Potonié and Kremp 1954

Type species. *Punctatisporites punctatus* Ibrahim 1933.

Punctatisporites glaber (Naumova) Playford 1962

Dimensions. (Twenty specimens) Equatorial diameter 29–44 μ (mean 38 μ).

Occurrence. Throughout the Lower and Middle Devonian succession.

Punctatisporites laevigatus (Naumova) comb. nov.

1953 *Stenozonotriletes laevigatus* Naumova, p. 70, pl. 10, figs. 9, 10.

Dimensions. (Twenty specimens) Equatorial diameter 51–71 μ (mean 61 μ). Exine 3.5–6 μ thick.

Remarks. Variation in length of laesurae frequently occurs within a single specimen. Naumova (1953, p. 70) in her description, records 'a thick exine', and the narrow border to which she refers (which is approximately 4 μ thick in her illustration) is probably an optical section through this thick exine, rather than a cingulum as suggested by her generic placing; the species is therefore more appropriately placed within *Punctatisporites*.

Comparison. *Punctatisporites aerarius* Butterworth and Williams 1958 (p. 360, pl. 1, figs. 10, 11) is larger and has a thinner exine. *Stenozonotriletes facilis* Ishchenko 1956 var. *facilis* (p. 73, pl. 14, figs. 162–4) may be conspecific, but it is not clear from the description whether the otorochka (5 μ wide) is a cingulum or the optical section of a thick wall.

Occurrence. Fraenkelryggen Division, Dicksonfjorden Sandstone, Reuterskiöldfjellet Sandstone, and Mimer Valley Series; Gedinnian to Givetian.

Punctatisporites flavus (Kosanke) Potonié and Kremp 1955

1950 *Calamospora flava* Kosanke, p. 41, pl. 9, fig. 2.

1955 *Punctatisporites flavus* (Kosanke) Potonié and Kremp, p. 42.

Dimensions. (Twenty-two specimens) Equatorial diameter 95–152 μ (mean 120 μ).

Occurrence. Lower Mimer Valley Series and probable Upper Reuterskiöldfjellet Sandstone, Emsian and Eifelian.

Genus CALAMOSPORA Schopf, Wilson, and Bentall 1944

Type species. *Calamospora hartungiana* Schopf, in Schopf, Wilson and Bentall 1944.

Calamospora microrugosa (Ibrahim) Schopf, Wilson, and Bentall 1944

Synonymy. See Playford 1962, p. 579.

Dimensions. (Twenty specimens) Equatorial diameter 50–110 μ (mean 86 μ). Exine 2 μ or less thick.

Occurrence. Kapp Kjeldsen Division, Dicksonfjorden Sandstone, Reuterskiöldfjellet Sandstone, and Mimer Valley Series; Siegenian to Givetian, more common in the Givetian.

Calamospora nigrata (Naumova) comb. nov.1953 *Leiotriletes nigratus* Naumova, p. 23, pl. 1, fig. 9.1958 *Leiotriletes nigratus* Ishchenko, p. 35, pl. 1, fig. 5; non Naumova 1953.

Dimensions. (Twenty-six specimens) Equatorial diameter 60–80 μ (mean 76 μ). Exine 1 μ or less thick.

Remarks. The short laesurae, and thin folded exine suggest correct inclusion within *Calamospora*. Naumova (1953) quotes dimensions of 60–70 μ , and Ishchenko (1958) 90–110 μ . Neither author states the number of spores measured. Naumova's readings are probably two equatorial axes of the same spore. The Spitsbergen spores are of intermediate size. In some specimens there is a tetrad impression of narrow arcuate folds (the *curvaturae* and *curvaturae imperfectae* of Potonié and Kremp 1955).

Comparison. *Leiotriletes atavus* Naumova 1953 (p. 23, pl. 1, fig. 8) is smaller and lacks folding. *Calamospora saariana* Bhardwaj 1957 (p. 81, pl. 22, figs. 13–15) is also smaller and possesses lips.

Occurrence. Present in the majority of well-preserved samples; Gedinnian to Givetian, most common in the Emsian.

Calamospora witneyana Chaloner 1963

Dimensions. (Fifteen specimens) Equatorial diameter 116–212 μ (mean 151 μ).

Occurrence. Reuterskiöldfjellet Sandstone and Lower Mimer Valley Series; Siegenian and Emsian.

Genus TRILEITES (Erdtman 1945, 1947) ex Potonié 1956

Type species. *Trileites* (al. *Triletes*) *spurius* (Dijkstra) Potonié 1956.

Trileites oxfordiensis Chaloner 1963

Dimensions. (Twenty specimens) Equatorial diameter 186–530 μ (mean 290 μ).

Occurrence. Dicksonfjorden Sandstone, Reuterskiöldfjellet Sandstone and Mimer Valley Series; Siegenian to Givetian.

Infraturma APICULATI (Bennie and Kidston) R. Potonié 1956

Genus GRANULATISPORITES (Ibrahim) Potonié and Kremp 1954

Type species. *Granulatisporites granulatus* Ibrahim 1933.

Granulatisporites muninensis sp. nov.

Plate 94, figs. 3–5

Diagnosis. Miospores trilete; amb triangular with straight to slightly convex sides and rounded apices. Laesurae straight, length two-thirds to full spore radius, accompanied by smooth, raised lips, individually up to 2 μ wide. Exine 1 μ thick, homogeneous to infragranulate, contact areas laevigate, proximo-equatorial and distal surfaces sculptured with evenly spaced granules.

Dimensions. (Twenty specimens) Equatorial diameter 24–30 μ (mean 27 μ).

Holotype. Preparation KA 293/1, 56-7 105-1, K556, N233.

Lucus typicus. East Munindalen, Central Dicksonland, Vestspitsbergen; Plantekløfta Conglomerate, probable Givetian.

Description. Holotype triangular with straight sides, diameter 25 μ . Laesurae four-fifths spore radius, accompanied by lips individually 1 μ wide, slightly separating equatorially. Slight curvatural ridges in radial regions.

Remarks. The lips are frequently inaperturate, and are sometimes separated equatorially. Slight curvaturae are occasionally present in the radial regions.

Comparison. *Granulatisporites triconvexus* Staplin 1960 (p. 15, pl. 3, figs. 11, 12) is larger, more finely granulose, the lips are less prominent and there is no suggestion of laevigate contact areas. *Granulatisporites planiusculus* (Luber) Playford 1962 (p. 533, pl. 79, fig. 18) is larger, has a thinner exine and lacks the laevigate contact areas. *Archaeozonotrites parvibasilaris* Naumova var. *triangulatus* Chibrikova 1959 (p. 71, pl. 11, fig. 5) has a thicker exine and sculptured contact areas. *Anapiculatisporites devonicus* var. *azonatus* (Chibrikova) Vigran 1964 (p. 13; pl. 1, figs. 21–23) differs only in having a sculpture of coni.

Occurrence. Present in most productive samples; Gedinnian to Givetian, most common in the Givetian.

Genus CYCLOGRANISPORITES Potonié and Kremp 1954

Type species. *Cyclogranisporites leopoldi* (Kremp) Potonié and Kremp 1954.

Cyclogranisporites rotundus (Naumova) comb. nov.

1953 *Lophotrites rotundus* Naumova, p. 58, pl. 7, fig. 19; p. 108, pl. 16, fig. 34.

1953 *Lophotrites rotundus* Naumova var. *minor*, p. 96, pl. 15, fig. 10; p. 108, pl. 16, figs. 29, 30. No type designated.

Dimensions. (Twenty-five specimens) Equatorial diameter 29–45 μ (mean 35 μ).

Remarks. *Lophotrites rotundus* Naumova var. *minor*, lacks both holotypic designation and description. Its separation from *L. rotundus* Naumova is made on its slightly smaller

EXPLANATION OF PLATE 94

All figures $\times 500$ unless otherwise stated; from unretouched negatives.

Figs. 1, 2. *Leiotrites pagius* sp. nov. 1, Holotype, sectional focus; KA 251/9, 21.5 94.8, K905, N231.

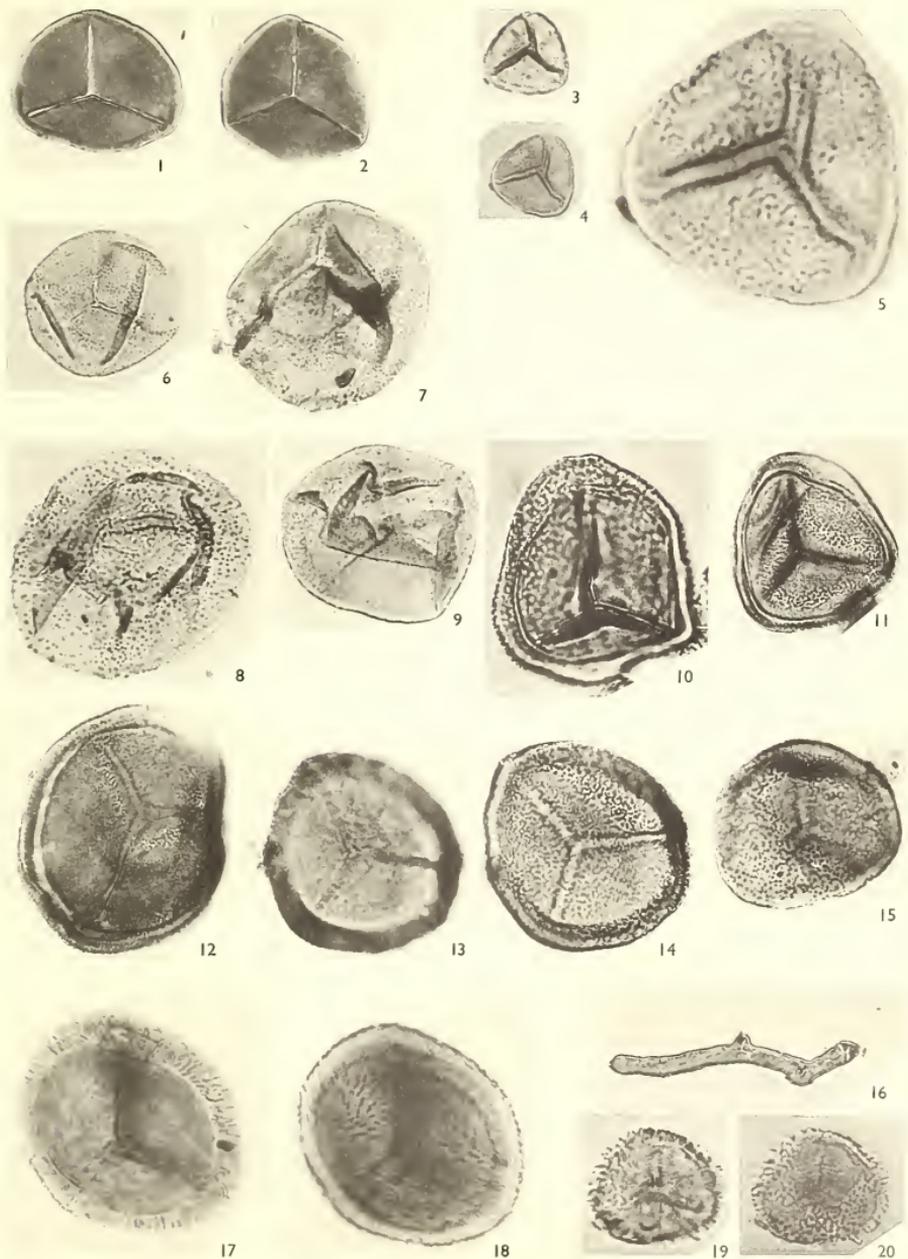
2, Proximal surface; KA 251/7, 40.2 97.5, K905, N232.

Figs. 3–5. *Granulatisporites muninensis* sp. nov. 3, 4, Holotype, proximal and distal surfaces respectively; KA 293/1, 56.7 105.1, K556, N233. 5, Holotype, $\times 1000$; distal surface, showing granules.

Figs. 6–9. *Cyclogranisporites plicatus* sp. nov. 6, Holotype, KA 258/3, 50.4 100.1, K922, N234. 7, Showing curvaturae; KA 258/2, 49.4 91.4, K922, N235. 8–9, Specimens showing variation in size of granules. 8, KA 258/4, 35.1 91.2, K922, N236. 9, KA 258/2, 49.1 91.6, K922, N237.

Figs. 10–18. *Geminospora* spp. 10–11, *G. tuberculata* (Kedo) comb. nov. 10, Proximal surface; KA 229/3, 22.1 89.4, K550, N238. 11, Distal surface; KA 255/2, 41.3 87.5, K760, N239. 12–16. *G. svalbardiae* (Vigran) comb. nov. 12, Distal surface, showing intexine; KA 255/2, 48.2 93.5, K760, N240. 13, 14, Proximal and distal surfaces respectively; KA 243/2, 35.8 91.5, K767, N241. 15, Distal surface; KA 243/2, 47.0 97.2, K767, N242. 16, Section, showing lips and uniformly thick exine; KA 286/S2, 52.5 94.9, K773, N243. 17–18. *G. spinosa* sp. nov. Holotype, proximal and distal surfaces respectively; KA 243/1, 30.4 107.3, K767, N244.

Figs. 19–20. *Acanthotrites raptus* sp. nov. Holotype, proximal and distal surfaces respectively; KA 258/3, 47.0 108.7, K922, N245.



size. However, as only two specimens of *L. rotundus* var. *minor* were measured and as the Spitsbergen specimens span the size range of both, the variety is included within the synonymy. Its circular amb and granulose sculpture indicate more appropriate inclusion within *Cyclogranisporites*.

Occurrence. Upper Mimer Valley and Wijde Bay Series; Givetian.

Cyclogranisporites plicatus sp. nov.

Plate 94, figs. 6-9

Diagnosis. Miospores trilete, originally spherical; amb circular to subcircular. Laesurae distinct to discernible, straight, length $\frac{1}{2}$ – $\frac{2}{3}$ spore radius, simple, or accompanied by smooth often sinuous lips, individually 0.5–2 μ wide. Exine thin, 1 μ or less, homogeneous, supporting a granulose ornament of variable density. Low, narrow curvaturae or curvaturae imperfectae are present in approximately one-third specimens. Major compressional folds always present.

Dimensions. (Forty-five specimens) Equatorial diameter 51–82 μ (mean 66 μ).

Holotype. Preparation KA 258/3, 50-4 100-1, K922, N234.

Locus typicus. Mimerdalen, Central Dicksonland, Spitsbergen; ? Reuterskiøldfjellet Sandstone, Emsian.

Description. Holotype subcircular, diameter 53 μ . Laesurae simple, length two-thirds spore radius. Exine less than 1 μ thick, densely sculptured. Three compressional folds.

Remarks. Variation in size and density of ornament is demonstrated in Plate 94, figs. 8, 9. Curvaturae imperfectae seen in Plate 94, fig. 7.

Comparison. *Lophotriletes rugosus* Naumova 1950 (pl. 2, fig. 6) var. *rugosus* Naumova 1953 (p. 27, pl. 2, fig. 1 and p. 54, pl. 7, fig. 1), is smaller, and may have a sculpture of cones. *Cyclogranisporites lasius* (Waltz) Playford 1962 (p. 585, pl. 79, figs. 19, 20) has more distinct laesurae and a thicker exine. *Retusotriletes verruculatus* Naumova 1953 (p. 29, pl. 2, fig. 10) is smaller, and is roundly triangular. *R. punctatus* Chibrikova 1959 (p. 52, pl. 5, fig. 7) is also smaller and roundly triangular. Miospores recorded from ?*Enigmophyton superbium* fructification Høeg 1942 (p. 118, pl. 49, figs. 9–11) appear to be very similar, but are probably laevigate.

Occurrence. Present in most well-preserved samples, but extremely common in the Reuterskiøldfjellet Sandstone and Lower Mimer Valley Series; Gedinnian to Givetian.

Genus GEMINOSPORA Balme 1962

Type species. *Geminospora lenurata* Balme 1962.

Discussion. Although the type species has a slightly thicker distal surface (a feature common to many Devonian spores), the difference is not appreciable and the genus cannot be regarded as truly patinate. Although the species described below do not show this feature, they are regarded as being of similar construction, and are included within this genus.

Geminospora tuberculata (Kedo) comb. nov.

Plate 94, figs. 10, 11

1955 *Archaeozonotriletes tuberculatus* Kedo, p. 35, pl. 5, figs. 6, 7.

Description of specimens. Miospores trilete; amb roundly triangular to subcircular. Laesurae straight, length two-thirds to full spore radius, simple, or rarely accompanied by narrow, sharp lips, individually 0.5–1 μ wide. Exine two-layered; intexine very thin, 1 μ or less, homogeneous, separated at least in part from the exoexine; exoexine 2–3 μ thick, finely infragranulate. Proximal surface laevigate, distal surface sculptured with granules and small cones 1 μ or less high. Major folding common, frequently the intexine is more strongly folded.

Dimensions. (Twenty specimens) Equatorial diameter 40–65 μ (mean 56 μ).

Remarks. Chibrikova (1959, p. 58), includes *Geminospora tuberculata* (Kedo) in synonymy with *Archaeozonotriletes meonacanthus* Naumova nom. nud. The latter, however, lacks both holotypic designation and description.

Comparison. *Archaeozonotriletes plicatus* Naumova nom. nud. in Chibrikova 1959 (p. 64, pl. 8, fig. 10) is very similar, and may prove to be conspecific.

Occurrence. Upper Mimer Valley Series; Givetian.

Geminospora svalbardiae (Vigran) comb. nov.

Plate 94, figs. 12–16

1964 *Lycospora svalbardiae* Vigran, p. 23, pl. 3, figs. 4, 5; pl. 4, figs. 1, 2.

Description of specimens. Miospores trilete; amb roundly triangular to subcircular. Laesurae usually straight, occasionally slightly sinuous, length three-quarters to full spore radius, frequently accompanied by low lips, individually 1–3 μ wide. Exine, at least in some specimens visibly two-layered; intexine thin, less than 1 μ thick, homogeneous, rarely folded, closely appressed to or slightly separate from the exoexine; exoexine 3–7 μ thick, finely infragranulate. Contact areas laevigate, occupying most of the proximal surface, proximo-equatorial (where the contact areas are short of the equatorial margin) and distal surfaces densely granulate. Exoexine frequently with tangential and acute folds.

Dimensions. (Thirty-four specimens) Equatorial diameter 50–88 μ (mean 72 μ).

Remarks. The arcuate folding (Pl. 94, fig. 13), often gives the impression of a cingulum under lower power, however, the section (Pl. 94, fig. 16) although very compressed, clearly demonstrates the constant exine thickness; also the exclusively distal ornament, and lips formed by an upturning of the exoexine; no intexine is visible in the sections. This constant exine thickness and exclusively distal sculpture indicate more appropriate inclusion in *Geminospora*.

Comparison. *Apiculatisporis* sp. Hoffmeister, Staplin, and Malloy 1955a (pl. 1, fig. 13) appears to be very similar. However, it is not possible to see from the photograph whether it is sculptured proximally. *Retusotriletes parvimammatus* Naumova 1953 var. *famenensis* Naumova 1953 (p. 124, pl. 18, fig. fig. 22) is clearly similar to some specimens, but there is no mention of a laevigate proximal surface, lips, or the presence of major

folds. *Geminospora lemurata* Balme 1962 (p. 5, pl. 1, figs. 5–10) is smaller, lacks lips, and has a slightly thicker distal surface. *Archaeozonotriletes atratus* Naumova 1953 (p. 99, pl. 15, fig. 25) has much wider and higher lips, and has an ornament of verrucae. *Archaeozonotriletes notatus* Naumova 1953 (p. 84, pl. 13, fig. 12) lacks lips, and there is no mention of a laevigate proximal surface.

Occurrence. Very common throughout the Upper Mimer Valley Series, but also occurs in the Wijde Bay Series, Lower Mimer Valley Series and Reuterskiöldfjellet Sandstone; Emsian to Givetian.

Geminospora spinosa sp. nov.

Plate 94, figs. 17–18

Diagnosis. Miospores trilete; amb roundly triangular to subcircular. Laesurae straight, length three-quarters to full spore radius, simple or more usually accompanied by narrow sharp lips, individually 0.5–2 μ wide, up to 5 μ high. Exine two-layered; intexine thin, 0.5–2 μ wide, homogeneous, usually slightly separate at least in part from the exoexine; exoexine 2–5 μ thick, coarsely infragranulate. Contact areas laevigate, frequently depressed, occupying from two-thirds to the whole of the proximal surface, proximo-equatorial (where the contact areas are short of the equatorial margin) and distal surfaces sparsely sculptured with spines, 0.5–1.5 μ wide, 3–6 μ long.

Dimensions. (Fifteen specimens) Equatorial diameter 59–91 μ (mean 70 μ).

Holotype. Preparation KA 243/1, 30.4 107-3, K767, N244.

Locus typicus. North ridge of Kinanderfjellet, Central Dicksonland, Spitsbergen; Upper Mimer Valley Series, probable Upper Givetian.

Description. Holotype subcircular, diameter 80 μ . Laesurae indistinct, masked by elevated lips totalling 4 μ wide. Intexine very thin, partly separate from exoexine; exoexine 5 μ thick, radial diameter of depressed contact area 30 μ . Proximo-equatorial and distal spines 1–2 μ wide, 3–5 μ long.

Remarks. The spines are usually appressed against the exoexine. Darkening at the equatorial end of the laesurae in some specimens is usually due to slight folding, and gives the spores an appearance similar to *Pulvinispora* Balme and Hassell. However, in this genus the darkened appearance is due to a thickening rather than a folding (Balme and Hassell 1962, p. 10).

Comparison. *Archaeozonotriletes comans* Chibrikova 1959 (p. 70, pl. 19, fig. 3) has shorter simple laesurae, and a denser ornament.

Occurrence. Mimer Valley Series; Eifelian and Givetian.

Genus ACANTHOTRILETES (Naumova) Potonié and Kremp 1954

Type species. *Acanthotriletes ciliatus* (Knox) Potonié and Kremp 1954.

Acanthotriletes raptus sp. nov.

Plate 94, figs. 19–20

Diagnosis. Miospores trilete; amb circular, subcircular to roundly triangular. Laesurae distinct to discernible, simple, straight, length $\frac{1}{2}$ – $\frac{2}{3}$ spore radius. Exine 1–2 μ thick, homo-

geneous to finely infragranulate; proximal surface laevigate, distal surface evenly crowded with spines and subordinate cones, 0.5–2.5 μ wide, 1.5–4 μ high, with polygonal bases, and often only tapering at their apices.

Dimensions. (Fifteen specimens) Equatorial diameter 34–42 μ (mean 38 μ).

Holotype. Preparation KA 258/3, 47.0 108.7, K922, N245.

Locus typicus. South Mimerdalen, Central Dicksonland, Vestspitsbergen; Reuterskiöldfjellet Sandstone, Eifelian.

Description. Holotype subtriangular with convex sides and broadly rounded apices, diameter 38 μ . Laesurae approximately half spore radius. Exine 1 μ thick, spines 0.5–1.5 μ wide, up to 4 μ high.

Remarks. This species is included within *Acanthotriletes* rather than *Apiculatisporis* on the basis of its dominant, albeit short, spinose ornament.

Comparison. All species which may be closely compared with *Acanthotriletes raptus* sp. nov. have no record of a laevigate proximal surface. This feature alone I regard as sufficient for specific separation. However, I am aware that unless studied under oil immersion, it is not always easy to identify this feature in small, proximo-distally compressed specimens, and an absence of proximal sculpture may have been overlooked by some authors. I have assumed that this might be the case, and therefore list below other differing features. *A. usitatus* Naumova 1953 (p. 24, pl. 1, fig. 15) is triangular and has longer laesurae. *Apiculatisporis pineatus* Hoffmeister, Staplin, and Malloy 1955b (p. 38, pl. 38, fig. 3) has a larger, more varied ornament. *Acanthotriletes parvispinosus* Naumova 1953 (p. 24, pl. 1, fig. 16) is smaller and has longer laesurae. *A. tenuispinosus* Naumova var. *tenuispinosus* has longer laesurae and narrower spines.

Occurrence. Reuterskiöldfjellet Sandstone; Eifelian.

Genus HYSTRICOSPORITES McGregor 1960

Type species. *Hystricosporites delectabilis* McGregor 1960.

Hystricosporites porrectus (Balme and Hassell) comb. nov.

Plate 95, figs. 1–3

1962 *Archaeotriletes porrectus* Balme and Hassell, p. 10, pl. 5, figs. 1–4.

Description of specimens. Miospores trilete; amb circular to subcircular. Laesurae obscured by membranous, often sinuous, elevated lips, 32–60 μ high, length equal to full spore radius. Exine three-layered; intexine approximately 1 μ thick, homogeneous, closely appressed to the exoexine and often indistinct; exoexine 4–9 μ thick, inner exoexine infragranulate, outer exoexine and sculptural elements homogeneous. Contact areas laevigate, proximo-equatorial and distal surfaces support a dense ornament of grapnel-tipped spines, typically 25–35 μ long (range 15–40 μ) rarely with a bulbous base, the shaft tapering gradually towards the apex. The majority are preserved in lateral compression.

Dimensions. (Twenty specimens) Equatorial diameter 90–184 μ (mean 118 μ), polar diameter (including apical processes) 102–170 μ (mean 141 μ).

Remarks. Since the submission for publication of the paper by Balme and Hassell (1962) there has been further generic subdivision of spores with grapnel-tipped appendages, and the Australian species may now more suitably be included within *Hystricosporites* McGregor. Sections (Pl. 95, figs. 2, 3) demonstrate clearly the homogeneous intexine, the infragranulate inner exoexine and the homogeneous outer exoexine and sculptural elements. The elevated lips are formed only from the outer layer of the exoexine.

Comparison. *Hystricosporites delectabilis* McGregor 1960 (p. 32, pl. 11, figs. 13, 14, text-fig. 2) is larger, and lacks the greatly elevated lips. *Hystricosporites corystus* Richardson 1962 (p. 173, pl. 25, figs. 1, 2) has a sparse ornament of spines, and a thinner exine.

Occurrence. Upper Mimer Valley Series; Givetian.

Hystricosporites porcatus (Winslow) comb. nov.

Plate 95, figs. 4-6

1962 *Dicrospora porcata* Winslow, p. 52; pl. 11, figs. 4, 5, 5a; pl. 12, fig. 5; pl. 22, fig. 15.

1964 *Hystrosporites costatus* Vigran, p. 14, pl. 5, figs. 3-5.

Description of specimens. Miospores trilete; amb circular to subcircular. Laesurae indistinct, obscured by sinuous, elevated lips, 10-34 μ high, 2-5 μ wide, length $\frac{2}{3}$ - $\frac{4}{5}$ spore radius. Exine three-layered; intexine 2 μ or less thick, homogeneous, usually closely appressed to the exoexine and often indistinct; exoexine 6-12 μ thick, inner exoexine infragranulate, outer exoexine and sculptural elements homogeneous. Contact areas, radial diameter $\frac{2}{3}$ - $\frac{3}{4}$ spore radius, each supporting 8-15 low, slightly sinuous muri, 2-8 μ wide, 3-6 μ high, 1-8 μ apart, bordered by low curvaturae 6-10 μ wide. Proximo-equatorial and distal surfaces support bulbous based grapnel-tipped spines, typically 15-30 μ long (range 10-45 μ), 17-23 round the equatorial margin.

Dimensions. (Twenty-six specimens) Equatorial diameter 84-164 μ (mean 111 μ); radial diameter of contact area 26-44 μ .

Remarks. In ill-preserved specimens, the intexine separates from the exoexine, and is often folded. Section (Pl. 95, fig. 6) demonstrates clearly the low, wide, proximal radial muri; but in this strongly compressed specimen the stratification of the exine is not seen. Dimensions recorded for the Spitsbergen specimens are somewhat smaller than those recorded by Winslow (1962, p. 52).

Comparisons. This is the only species recorded to date, which reports the presence of proximal, radial muri, though it would appear from the illustrated holotype that *Hystricosporites delectabilis* McGregor 1960 (pl. 11, fig. 13) may possess this feature.

Occurrence. Upper Mimer Valley Series; Givetian.

Hystricosporites mitratus sp. nov.

Plate 95, figs. 7, 8

Diagnosis. Miospores trilete; amb circular to subcircular. Laesurae indistinct, length approximately half of the spore radius, accompanied by smooth, narrow often sinuous, elevated lips, 2-4 μ wide, 16-27 μ high. Exine 5-12 μ thick, finely infragranulate; contact areas laevigate, small, radial diameter approximately half of the spore radius,

bounded by smooth, narrow elevated curvaturae, basally 3–7 μ wide, 12–20 μ high; proximo-equatorial and distal surfaces support an ornament of grapnel-tipped spines, typically 20–35 μ long (range 12–40 μ), with enlarged, often bulbous bases, 12–25 round the equatorial margin.

Dimensions. (Twenty-three specimens) Equatorial diameter 88–136 μ (mean 113 μ); radial diameter of contact area 23–40 μ (mean 32 μ).

Holotype. Preparation KA 148/5, 28·8 92·7, F1598, N252.

Locus typicus. Huginaspiskardet, Central Dicksonland, Vestspitsbergen; Lower Mimer Valley Series, Eifelian.

Description. Holotype subcircular, diameter 120 μ . Lips 18 μ high, each 2–3 μ thick. Curvaturae 18 μ high, radial diameter of contact area 30 μ . Grapnel-tipped spines 24–44 μ long.

Remarks. This species was not sectioned, and although no intexine was visible it seems very probable that the exinal stratification is similar to sectioned species of the genus *Hystricosporites* McGregor. The curvaturae are of the same dimensions as the lips, and probably formed during the same developmental stages within the tetrad, and formed only from the outer homogeneous layer of the exoexine.

Comparison. *Archaeotriletes honestus* Naumova 1953 (p. 124, pl. 18, figs. 24, 25) has a thicker exine, thicker, lower curvaturae, and lacks lips, a feature associated with the curvaturae in *H. mitratus* sp. nov.

Occurrence. Upper Reuterskiøldfjellet Sandstone; and Lower Mimer Valley Series; Emsian and Lower Eifelian.

Hystricosporites monosaccus (Archangelskaya) comb. nov.

Plate 96, figs. 1, 2

1963 *Archaeotriletes monosaccus* Archangelskaya, p. 19, pl. 2, figs. 1–5.

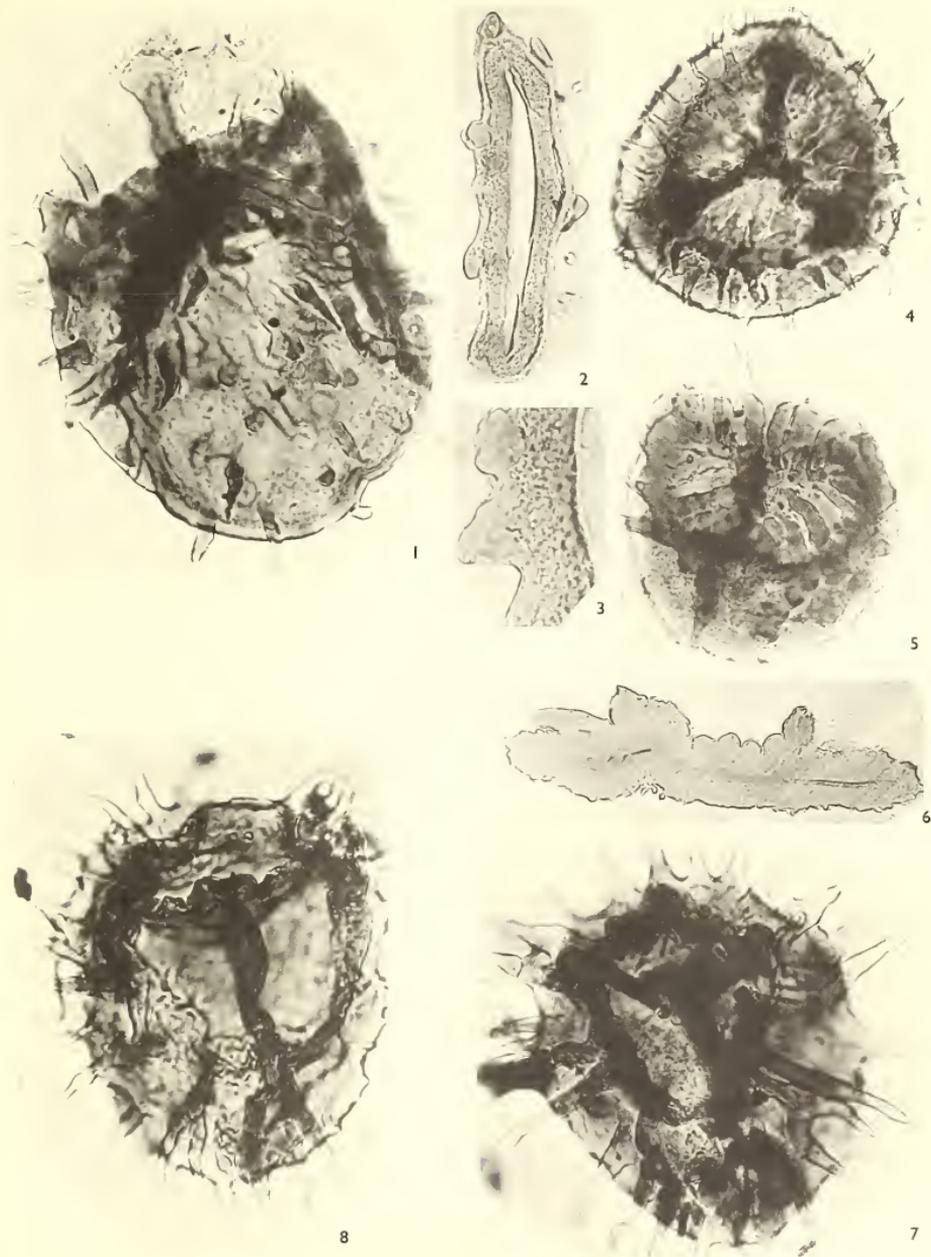
1964 *Hystricosporites coronatus* Vigran, p. 15, pl. 3, figs. 1–3.

Description of specimens. Miospores trilete; amb circular to subcircular. Laesurae obscured by high, membranous, sinuous lips, 20–72 μ high, individually 2–4 μ wide at their base, narrowing upwards, length three-quarters to full spore radius. Exine three-layered; intexine 1–3 μ thick, homogeneous, frequently partly separated from the exoexine; exoexine 8–18 μ thick, inner exoexine coarsely infragranulate, outer exoexine

EXPLANATION OF PLATE 95

All figures $\times 500$ unless otherwise stated; from unretouched negatives.

Figs. 1–8. *Hystricosporites* spp. 1–3. *H. porrectus* (Balme and Hassell) comb. nov. 1, Lateral view; KA 123/4, 35·6 94·0, G1358, N246. 2, Section showing the three-layered exine; KA 123/S9, 47·5 102·7, G1358, N247. 3, Section ($\times 1000$) showing the homogeneous outer exoexine forming the spines, and the infra-granulate inner exoexine; KA 123/S10, 52·2 105·5, G1358, N248. 4–6. *H. porcatus* (Winslow) comb. nov. 4, Proximal surface; KA 261/4, 49·4 89·3, K891, N249. 5, Proximal oblique aspect (most of the grapnel-tipped spines have been eroded); KA 133/1, 42·3 93·1, G1385, N250. 6, Section showing proximal radial muri; KA 123/S4, 42·3 93·8, G1358, N251. 7–8. *H. mitratus* sp. nov. 7, Holotype, central oblique focus; KA 148/5, 28·8 92·7, F1598, N252. 8, Proximal oblique aspect; KA 148/5, 25·0 98·4, F1598, N253.



homogeneous to infragranulate. Distally, the outer exoexine separates from the inner exoexine, and distends distally as a crumina, typically 70–90 μ long (range 23–109 μ). Proximal surface supports an ornament of radial muri, 6–10 μ wide, up to 8 μ high; distal surface with grapnel-tipped spines, 10–32 μ high, with enlarged and frequently bulbous bases, more sparsely disposed on the crumina.

Dimensions. (Twenty-two specimens) Overall equatorial diameter 63–143 μ (mean 99 μ), polar diameter (including apical processes and crumina), 77–248 μ (mean 172 μ).

Remarks. This species is included within *Hystricosporites* McGregor 1960, rather than *Archaeotriteles* Naumova 1953, because of the absence of an equatorial extension. The great difference between the equatorial and polar axial measurements, results in the spores lying parallel to the longer polar axis, and because the proximal surface is flat, details of the contact areas are rarely seen. Sections (Pl. 96, fig. 2) clearly demonstrate the construction of the distal crumina; this feature is not seen in other Spitsbergen Devonian species. Sections of *Labiadensites fimbriatus* (Waltz) Hacquebard and Barss 1957, in Dettmann and Playford 1962 (p. 679, pl. 96, figs. 1, 2) demonstrates the slight development of a cruminate cingulum.

Comparison. *H. monosaccus* (Archangelskaya) comb. nov. differs from all other grapnel-tipped species, in possessing a crumina.

Occurrence. Upper Mimer Valley Series; Givetian.

Hystricosporites corystus Richardson 1962

Description of specimens. Miospores trilete, amb subcircular to subtriangular. Laesurae straight, length approximately three-quarters to full spore radius, frequently obscured by membranous, often sinuous, elevated lips, 34–68 μ high, extending to the equatorial margin. Exine three-layered; intexine rarely seen, approximately 1 μ thick, homogeneous; exoexine 14–30 μ thick, inner exoexine infragranulate, outer exoexine and sculptural elements homogeneous. Contact areas laevigate, proximo-equatorial and distal surfaces support a sparse ornament of grapnel-tipped spines 30–60 μ long, 8–13 μ wide, 10–13 spines round the equatorial margin.

Dimensions. (Fifteen specimens) Equatorial diameter 64–210 μ (mean 141 μ), polar diameter (including apical processes) 96–214 μ (mean 151 μ).

Occurrence. Upper Mimer Valley Series; Givetian.

Genus *RAISTRICKIA* (Schopf, Wilson, and Bentall 1944) Potonié and Kremp 1954

Type species. *Raistrickia grovensis* Schopf in Schopf, Wilson, and Bentall 1944.

Raistrickia aratra sp. nov.

Plate 96, figs. 3, 4

Diagnosis. Miospores trilete; amb circular to subcircular. Laesurae indistinct, straight, length $\frac{1}{2}$ – $\frac{2}{3}$ spore radius, simple or rarely accompanied by low narrow lips. Exine 2–6 μ thick, homogeneous; supporting a very variable sculpture of predominantly high baculo-verrucae, 3–12 μ wide, 6–14 μ high, with occasional rugulae, 5–7 μ wide, 7–10 μ

high, up to 25 μ long, cones and spines 2–10 μ wide, 4–12 μ high, the cones often with papillate tips. Concentration of sculptural elements variable, but they are always sparser and more reduced proximally, where spines and cones are more frequent.

Dimensions. (Twenty specimens) Equatorial diameter 38–92 μ (mean 61 μ).

Holotype. Preparation KA 243/1, 27-0 92-3, K767, N256.

Locus typicus. East Munindalen, Central Dicksonland, Vestspitsbergen; Plantekløfta Conglomerate; probable Upper Givetian.

Description. Holotype circular, diameter 78 μ . Laesurae simple, straight, length two-thirds of spore radius. Exine 4 μ thick, variable ornament of baculo-verrucae 9–13 μ high, rugulae, up to 8 μ wide and 25 μ long, cones up to 9 μ high, often with papillate tips, and a few small spines. Sculpture reduced proximally.

Remarks. Although the specimens appear well preserved, evidence from occasional specimens suggests that many of the verrucae, spines and cones, are the result of corrosion of bacula and rugulae by a splitting and 'rounding off' of originally high, flat-topped sculptural elements. This species is included with the genus *Raistrickia* on the basis of predominant baculo-verrucae and variable sculptural elements.

Comparison. *Lophozonotrilletes macrogrumosus* Kedo 1957 (pl. 4, figs. 21, 22) has a thicker wall, and lower more rounded processes. *Raistrickia irregularis* Kosanke 1950 (p. 47, pl. 11, fig. 5) has longer laesurae accompanied by lips, and smaller sculptural elements. *Raistrickia? gibberosa* Hacquebard 1957 (p. 310, pl. 2, fig. 1) has longer laesurae and a more regular ornament. *R. cf. clavata* Vigran 1964, p. 16, pl. 2, fig. 10, is smaller, and never has sculptural elements over 9 μ high, but is otherwise similar.

Occurrence. Upper Mimer Valley Series; Givetian.

Genus BULLATISPORITES gen. nov.

Type species. *Bullatisporites bullatus* sp. nov.

Diagnosis. Miospores trilete; amb circular to subcircular. Exine sculptured with pila, the caput frequently supporting a small spine; sculpture somewhat reduced proximally. Contact areas occasionally depressed, and sometimes bounded by curvatural folds.

EXPLANATION OF PLATE 96

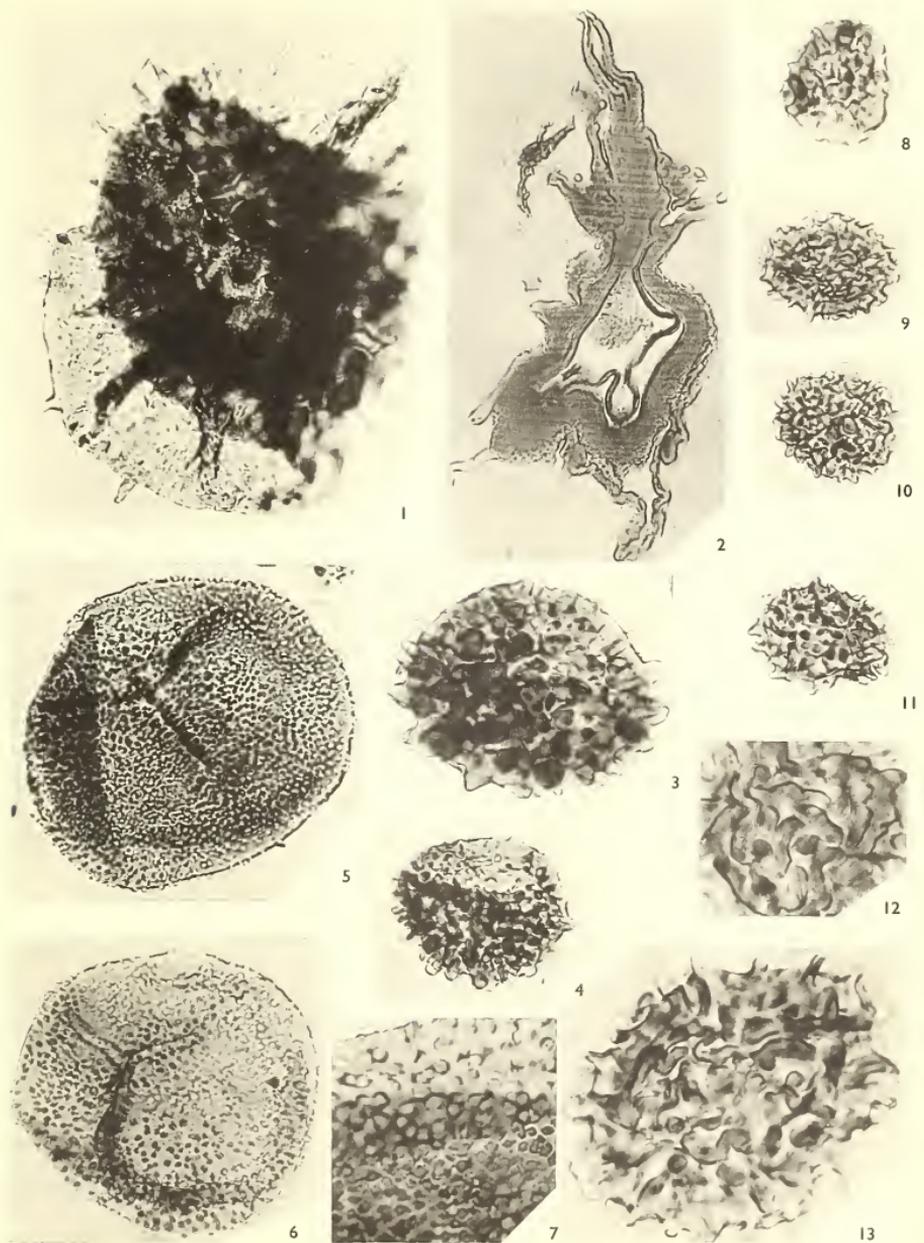
All figures $\times 500$ unless otherwise stated; from unretouched negatives.

Figs. 1–2. *Hystricosporites monosaccus* (Archangelskaya) comb. nov. 1, Lateral view; KA 255/M2, 28-6 108-0, K760, N254. 2, Section showing three-layered exine and crumina; KA 255/S3, 54-4 101-0, K760, N255.

Figs. 3–4. *Raistrickia aratra* sp. nov. 3, Holotype, proximal oblique aspect; KA 243/1, 27-0 92-3, K767, N256. 4, Lateral view; KA 243/1, 52-3 96-8, K767, N257.

Figs. 5–7. *Bullatisporites bullatus* gen. et sp. nov. 5, Holotype, proximal surface; KA 258/1, 55-7 101-8, K922, N258. 6, Proximal surface; KA 258/1, 27-8 88-3, K922, N259. 7, ($\times 1000$) Details of the pila on the holotype.

Figs. 8–13. *Convolutispora* spp. 8, *C. vermiformis* Hughes and Playford, Distal surface; KA 261/4, 49-0 98-2, K891, N260. 9–13. *C. disparalis* sp. nov. 9, Holotype, optical section; KA 243/2, 54-9 103-8, K767, N261. 10, Distal surface; KA 293/1, 48-9 93-4, K556, N262. 11, Proximal surface; KA 243/1, 41-8 105-9, K767, N263. 12, ($\times 1000$) Details of sculpture; KA 243/3, 54-4 88-9, K767, N264. 13, Holotype ($\times 1000$).



Comparison. Differs from other genera within the *Infraturma Apiculati*, in being both circular and pilate. *Dibolisporites* Richardson (1965) includes species with variable ornament which may possess pila, but the sculptural elements are predominantly biform.

Derivation of name. *L. bulla*—knob, boss.

Bullatisporites bullatus sp. nov.

Plate 96, figs. 5–7

Diagnosis. Miospores trilete; originally spherical, amb circular. Laesurae straight, length $\frac{1}{3}$ – $\frac{2}{3}$ spore radius, accompanied and frequently obscured by lips, 1–3 μ wide, up to 5 μ high. Exine 1–2 μ thick, infragranulate; proximo-equatorial and distal surfaces densely covered with pila, caput 1–2 μ wide, collum 0.5–1.5 μ wide, 1–3 μ high, the caput frequently supports at its apex a minute spine. The contact areas support a somewhat reduced sculpture of variable concentration and extent; curvaturae sometimes present in the radial regions. Major and minor folding common.

Dimensions. (Twenty-two specimens) Equatorial diameter 84–112 μ (mean 100 μ).

Holotype. Preparation KA 258/1, 55.7 101.8, K922, N258.

Locus typicus. South Mimerdalen, Central Dicksonland, Spitsbergen; Reuterskiøldfjellet Sandstone, Emsian.

Description. Holotype 98 μ . Laesurae just perceptible (under oil), length approximately half of the spore radius. Lips each 1.5 μ wide, slightly raised. Exine 1 μ thick, two major distal folds; proximo-equatorial and distal pila 1–2.5 μ high, caput 1–2 μ wide, collum 0.5–1.5 μ wide. In the contact areas, pila reduced only in the region adjacent to the lips.

Remarks. Lack of preferred orientation suggests a spherical shape. Curvaturae imperfectae are present in approximately one-quarter of the specimens. Only under oil immersion can the finer details of the pila be seen.

Comparison. *Retusotriletes gibberosus* Naumova nom. nud. 1953 (pl. 22, fig. 110) see Kedo 1955 (p. 21, pl. 1, fig. 16) lacks typification and description; however, the specimen illustrated by Kedo is clearly similar to *B. bullatus* sp. nov. and may be conspecific. Kedo states that the 'protuberances are round' but his illustration indicates that they may be pila.

Occurrence. Dicksonfjorden Sandstone, Reuterskiøldfjellet Sandstone, and Lower Mimer Valley Series; Siegenian to Eifelian.

Infraturma MURORNATH Potonié and Kremp 1954

Genus CONVOLUTISPORA Hoffmeister, Staplin, and Malloy 1955

Type species. *Convolutispora florida* Hoffmeister, Staplin, and Malloy 1955.

Convolutispora vermiformis Hughes and Playford 1961

Plate 96, fig. 8

1957 *Convolutispora flexuosa* forma *minor* Hacquebard, p. 312, pl. 2, fig. 10.

Dimensions. (Seventeen specimens) Equatorial diameter 37–52 μ (mean 46 μ).

Remarks. The Spitsbergen Devonian specimens are somewhat smaller than those described from other areas.

Occurrence. Upper Mimer Valley Series; Givetian.

Convolutispora disparalis sp. nov.

Plate 96, figs. 9–13

Diagnosis. Miospores trilete; amb circular to subcircular, equatorial margin undulating. Laesurae indistinct, simple, straight, length $\frac{1}{2}$ – $\frac{2}{3}$ spore radius. Exine excluding ornament 1–2 μ thick, homogeneous; distal and proximo-equatorial surfaces sculptured with a variable ornament of sinuous, narrow, frequently anastomosing rugulo-cristae, 1–3 μ wide, decreasing in width from their base, 2–5 μ high, usually with an undulating crest, often forming an imperfect reticulum, the intersections of which occasionally support a small papillum or spine. Lumina irregular, up to 6 μ in longest diameter. Contact areas support a reduced, sparse ornament, of low, smooth rugulae, small cones and granules.

Dimensions. (Sixty-one specimens) Equatorial diameter (excluding muri) 31–52 μ (mean 40 μ).

Holotype. Preparation KA 243/2, 54-9 103-8, K767, N261.

Locus typicus. East Munindalen, Central Dicksonland, Spitsbergen; Plantekløfta Conglomerate, probable Upper Givetian.

Description. Holotype subcircular, diameter 44 μ . Laesurae length $\frac{2}{3}$ spore radius. Exine approximately 1 μ thick; rugulo-cristae 1–2 μ wide, 1–3 μ high, the intersections often with papillate tips.

Comparison. The presence of a reduced proximal sculpture, and of papillae on many of the intersections, separates this species from *Convolutispora fromensis* Balme and Hassell 1962 (p. 8, pl. 1, figs. 14–16) which in addition has lower muri; and *Convolutispora venusta* Hoffmeister, Staplin, and Malloy 1955b (p. 385, pl. 38, fig. 11) which also has wider, lower ridges.

Occurrence. Common throughout the Upper Mimer Valley Series; Givetian.

Convolutispora mimerensis (Vigran) comb. nov.

Plate 97, figs. 1–3

1964 *Reticulatisporites mimerensis* Vigran, p. 17, pl. 2, figs. 16, 17.

Description of specimens. Miospores trilete; amb convexly subtriangular to circular. Laesurae simple, straight, length $\frac{1}{2}$ – $\frac{2}{3}$ spore radius, frequently obscured by sculptural elements. Exine 5–8 μ thick (including muri), supporting low, smooth, slightly sinuous muri, 2–5 μ broad, 1–3 μ high, most of which anastomose, forming an imperfect reticulum. Lumina irregular, 7 μ wide in longest diameter.

Dimensions. (Twenty specimens) Equatorial diameter 36–68 μ (mean 53 μ).

Remarks. Variation occurs in the orientation and spacing of the muri which are often radially directed and more widely spaced equatorially (Pl. 97, fig. 2). I have included this species in *Convolutispora* on the basis of its imperfect rather than perfect reticulum.

Comparison. *Convolutispora crassa* Playford 1962 (p. 594, pl. 81, figs. 10–12) is larger, has a thicker exine and flat-topped muri. *Camptotriletes simplex* Naumova nom. nud. in Kedo 1955 (p. 26, pl. 2, fig. 14) may be conspecific, but the illustration is too poor to see details of the sculpture, and the species lacks holotypic designation.

Occurrence. Upper Mimer Valley Series; Givetian.

Convolutispora tegula sp. nov.

Plate 97, figs. 4–8

Diagnosis. Miospores trilete; amb circular to subcircular, occasionally oval. Laesurae frequently indistinct, simple, straight, length $\frac{2}{3}$ – $\frac{3}{4}$ spore radius. Exine including ornament 5–9 μ thick, homogeneous, often punctate, with a crowded sculpture of short, broadly rounded, partly anastomosing muri, 2–7 μ wide, 2–4 μ high, the shorter muri often polygonal in outline, lumina subordinate, less than 1 μ wide.

Dimensions. (Thirty-five specimens) Equatorial diameter 41–70 μ (mean 53 μ).

Holotype. Preparation KA 286/2, 27·4 107·8, K773, N267.

Locus typicus. East Munindalen, Central Dicksonland, Spitsbergen; Plantekløfta Conglomerate, probable Upper Givetian.

Description. Holotype circular, diameter 68 μ . Laesurae indistinct, length approximately two-thirds spore radius. Exine punctate, 8 μ thick, muri 3–7 μ wide, 2–4 μ high.

Remarks. Plate 97, fig. 7, shows corrosion of the muri.

Comparison. *Convolutispora fromensis* Balme and Hassell 1962 (p. 8, pl. 1, figs. 14–16) closely resembles *C. tegula* sp. nov. in sculptural pattern, but has a much thinner exine and narrower muri. *Convolutispora florida* Hoffmeister, Staplin, and Malloy 1955b (p. 384, pl. 38, figs. 5, 6) has a more extensively anastomosing mureoid pattern, and wider lumina. *Convolutispora usitata* Playford 1962 (p. 595, pl. 82, figs. 4, 7, and 8) has similar sculpture, but is much larger.

Occurrence. Upper Mimer Valley Series; Givetian.

Genus RETICULATISPORITES (Ibrahim) Potonié and Kremp 1954

Type species. *Reticulatisporites reticulatus* Ibrahim 1933.

Reticulatisporites emsiensis sp. nov.

Plate 97, figs. 9–11

Diagnosis. Miospores trilete; amb circular to sub-circular. Laesurae distinct to discernible, length $\frac{1}{2}$ – $\frac{3}{4}$ spore radius, simple or more usually accompanied by low narrow folds. Exine 2–4 μ thick (excluding muri), infra-granulate; proximal surface laevigate or more frequently sparsely sculptured with small verrucae or granules, 2 μ or less in height and width, distally sculptured with strongly developed muri 1–4 μ wide, 3–8 μ high, enclosing more or less uniform lumina 8–20 μ in longest diameter, polygonal in outline centrally, more rounded equatorially.

Dimensions. (Twenty-three specimens) Equatorial diameter 49–82 μ (mean 65 μ). Number of equatorial muri 11–20, number of distal lumina 14–36.

Holotype. Preparation KA 240/2, 37.4 101.5, K582, N269.

Locus typicus. Manchesterbreen spur, Central Dicksonland, Spitsbergen; Lower Mimer Valley Series, Emsian.

Description. Holotype circular, diameter 72 μ . Laesurae simple, length two-thirds spore radius. Exine 4 μ thick, very sparse proximal ornament of granules, distal muri 2–3 μ wide basally, narrowing upwards, 5–8 μ high, lumina 12–20 μ wide.

Remarks. Both Naumova (1953) and Chibrikova (1959) include species assignable to *Reticulatisporites*, within *Archaeozonotriletes*.

Comparison. Small size and exclusively distal reticulate sculpture, separates *Reticulatisporites emsiensis* sp. nov. from the majority of other well-described species of Devonian and Carboniferous age. *Reticulatisporites speciosus* Hacquebard and Barss 1957 (p. 18, pl. 2, fig. 7) has an exclusively distal reticulum, but is larger, has longer laesurae, wider lips and a thicker exine. *Archaeozonotriletes retiformis* Naumova 1953 (p. 87, pl. 14, fig. 4) is very similar and may be conspecific, but no mention is made of a granulate proximal surface or a reticulum confined to the distal surface.

Occurrence. Reuterskiøldfjellet Sandstone, and Lower Mimer Valley Series; Emsian.

Reticulatisporites sp. cf. *Dictyotriletes minor* Naumova 1953

Plate 97, figs. 12, 13

Description of specimens. Miospores trilete; amb circular to subcircular. Laesurae simple, straight, length approximately two-thirds spore radius. Exine 1–2 μ thick, finely infra-

EXPLANATION OF PLATE 97

All figures $\times 500$ unless otherwise stated; from unretouched negatives.

Figs. 1–8. *Convolutispora* spp. 1–3. *C. mimerensis* (Vigran) comb nov. 1, Proximal surface; KA 286/3, 20.8 97.0, K773, N265. 2, Distal surface; KA 227/1, 38.0 98.9, K623, N266. 3, ($\times 1000$) Sculptural details (proximal). 4–8. *C. tegula* sp. nov. 4–6, Holotype, proximal, sectional and distal foci; KA 286/2, 27.4 107.8, K773, N267. 7, Poorly preserved specimen; KA 241/3, 28.5 95.0, K767, N268. 8, ($\times 1000$) Sculptural details of the holotype.

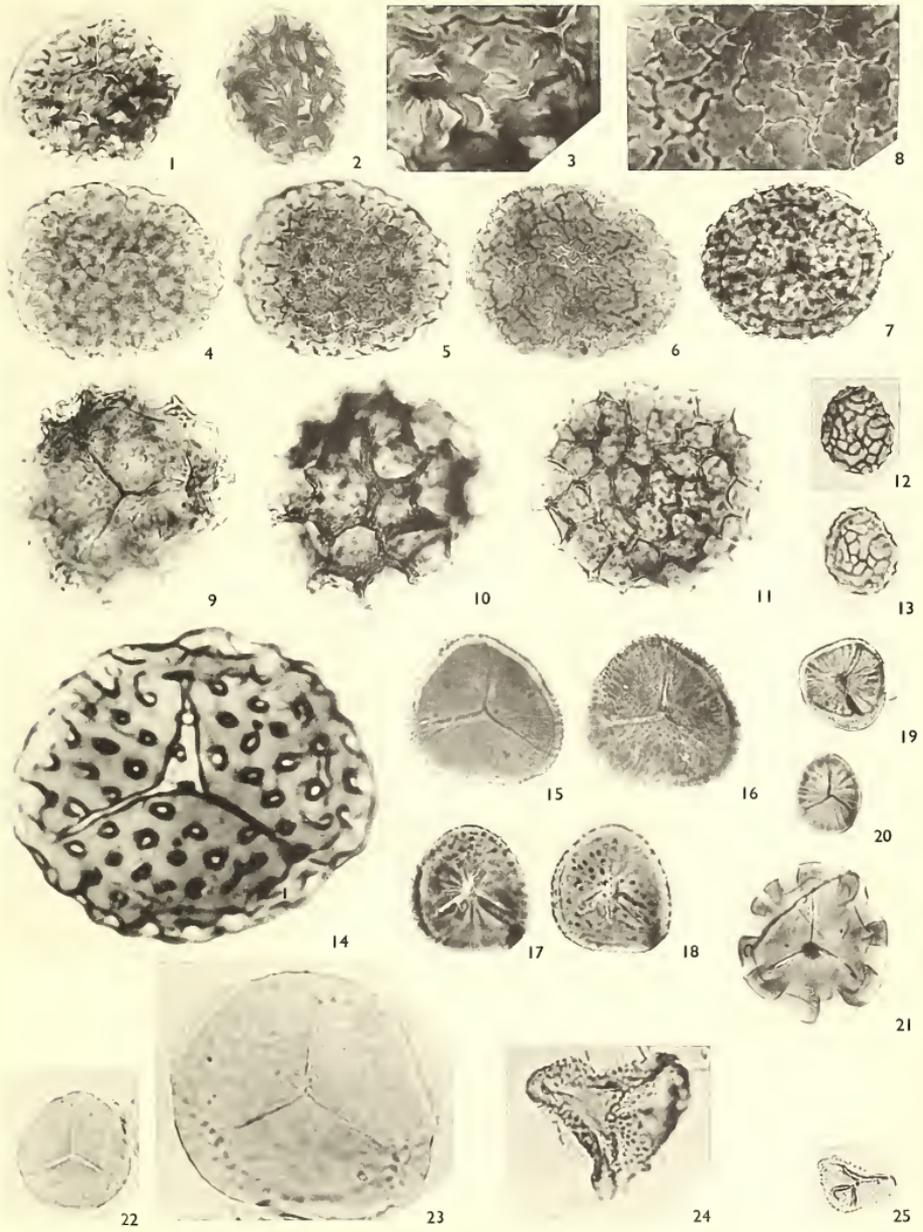
Figs. 9–13. *Reticulatisporites* spp. 9–11. *R. emsiensis* sp. nov. 9, 10, Holotype, proximal and distal surfaces respectively; KA 240/2, 37.4 101.5, K582, N269. 11, Distal surface; KA 281/6, 57.0 107.5, K850, N270. 12–13. *R. sp. cf. Dictyotriletes minor* Naumova, Proximal and distal surfaces respectively; KA 274/7, 36.0 107.3, K872, N271.

Fig. 14. *Perforosporites* sp. Proximal surface; KA 209/M2, 32.0 97.7, K519, N272.

Figs. 15–21. *Emphanisporites* spp. 15–18. *E. decoratus* sp. nov. 15, 16, Holotype, proximal and distal surfaces respectively; KA 251/3, 33.5 88.9, K905, N274. 17, 18, Proximal and distal surfaces respectively; KA 251/9, 20.6 96.5, K905, N275. 19. *E. neglectus* Vigran, Proximal surface; KA 162/1, 37.5 89.1, G1356, N273. 20. *E. minutus* sp. nov. Holotype, proximal surface; KA 262/4, 56.8 91.5, K908, N276. 21. *E. patagiatus* sp. nov. Holotype, proximal surface; KA 271/3, 38.1, 99.3, K897, N277.

Figs. 22–23. *Craspedispora craspeda* gen. et sp. nov. 22, Holotype, proximal surface; KA 258/3, 42.8 89.4, K922, N278. 23, Holotype ($\times 1000$).

Figs. 24–25. *Diatomozonotriletes* sp. 24, Distal surface ($\times 1000$); KA 243/2, 54.1 103.6, K767, N279. 25, Proximal surface; KA 229/1, 38.0 94.8, K550, N280.



ALLEN, Lower and Middle Devonian miospores

granulate, contact areas laevigate, proximo-equatorial and distal surfaces sculptured with narrow, low muri, basally $1\ \mu$ or less wide, narrowing upwards, approximately $1\ \mu$ high; lumina $3\text{--}7\ \mu$ in longest diameter.

Dimensions. (Five specimens) Equatorial diameter $18\text{--}32\ \mu$ (mean $27\ \mu$).

Comparison. Too few specimens are present for exact comparison: *Dictyotriletes minor* Naumova 1953 (p. 28, pl. 2, fig. 7) is clearly similar, but is triangular, and the muri are somewhat higher. However, the illustration of *D. minor* in Kedo 1955 (p. 2, pl. 2, fig. 13) has lower muri, is subcircular, and compares very closely with the Spitsbergen specimens.

Occurrence. Reuterskiøldfjellet Sandstone and Mimer Valley Series; Emsian to Givetian.

Genus PERFOROSPORITES Scott and Rouse 1961

Type species. *Perforosporites robustus* Scott and Rouse 1961.

Discussion. Separable from *Foveosporites* Balme 1957 on its regular distribution of fovea.

Perforosporites sp.

Plate 97, fig. 14

Descriptions of specimens. Miospores trilete; amb circular. Laesurae simple, straight, length $\frac{1}{2}\text{--}\frac{3}{4}$ spore radius. Exine $6\text{--}10\ \mu$ thick, infragranulate; contact areas laevigate, proximo-equatorial and distal surfaces with a sparse, regular ornament, of circular to oval fovea, $1\text{--}4\ \mu$ wide, $3\text{--}6\ \mu$ long, $3\text{--}24\ \mu$ apart. Distally the exine slightly 'overhangs' the fovea.

Dimensions. (Two specimens) Equatorial diameter $116\text{--}17\ \mu$.

Comparison. *Perforosporites robustius* Scott and Rouse 1961 (p. 978, pl. 113, figs. 1–6, pl. 114, figs. 1–5) the only species previously attributed to this genus, is roundly triangular, smaller, has less distinct and longer laesurae, and frequently has blunt, short papillae. *Reticulatisporites textilis* Balme and Hassell 1962 (p. 9, pl. 2, figs. 11, 12) has sculptured contact areas, indistinct laesurae, and more numerous fovea.

Occurrence. Top of the Reuterskiøldfjellet Sandstone, and bottom of the Lower Mimer Valley Series; Upper Emsian.

Genus EMPHANISPORITES McGregor 1961

Type species. *Emphanisporites rotatus* McGregor 1961.

Emphanisporites rotatus McGregor 1961

1962 *Radforthia radiata* Winslow, p. 72, pl. 16, figs. 15, 15a, pl. 22, fig. 17.

Dimensions. (Ten specimens) Equatorial diameter $34\text{--}47\ \mu$ (mean $39\ \mu$).

Comparison. *Stenozonotriletes ornattissimus* Naumova nom. nud. (pl. 22, fig. 11) lacks holotypic designation and description, but may have proximal muri, in which case it would be synonymous. *Radiaspora* sp. A Balme 1962 (p. 6, pl. 1, figs. 11, 12), may prove to have proximal rather than distal muri, and would then be conspecific with *E. rotatus*

McGregor. *Radforthia radiata* Winslow 1962 (p. 72, pl. 16, figs. 15, 15a, pl. 22, figs. 17) appears to differ only in its greater size range, and although neither McGregor (1961) nor Winslow (1962) give the mode of their measurements, *R. radiata* must be synonymous at least in part, with *E. rotatus*.

Occurrence. Reuterskiöldfjellet Sandstone and Lower Mimer Valley Series; Siegenian to Lower Eifelian.

Emphanisporites neglectus Vigran 1964

Plate 97, fig. 19

Description of specimens. Miospores trilete; amb circular to roundly triangular. Laesurae distinct, straight, length $\frac{2}{3}$ – $\frac{4}{5}$ spore radius, narrow, occasionally accompanied by slightly sinuous lips, each up to 1μ wide. Exine 0.5 – 2.5μ thick, infragranulate; depressed contact areas support a distinct to discernible ornament of low, narrow muroid folds, surrounded by low, sharp, curvaturae; proximo-equatorial and distal surfaces laevigate or very finely granulose.

Dimensions. (Twenty-six specimens) Equatorial diameter 30 – 47μ (mean 40μ). Radial diameter of contact area approximately four-fifths of total spore radius.

Comparison. *Emphanisporites obscurus* McGregor 1961 (p. 5, pl. 1, fig. 14), is larger and lacks curvaturae.

Occurrence. Dicksonfjorden Sandstone, Reuterskiöldfjellet Sandstone, and Lower Mimer Valley Series; Siegenian, Emsian.

Emphanisporites decoratus sp. nov.

Plate 97, figs. 15–18

Diagnosis. Miospores trilete; amb roundly triangular to subcircular and occasionally oval. Laesurae distinct, straight, length two-thirds to full spore radius, occasionally accompanied by low, smooth lips, individually less than 1μ wide. Exine 1 – 4μ thick, homogeneous to infragranulate; proximal surface with distinct to discernible radially disposed muroid folds of variable number, 2μ or less wide, distal surface supporting an ornament of cones and spines, 1.5 – 5μ high, 0.5 – 2μ wide.

Dimensions. (Twenty-nine specimens) Equatorial diameter 34 – 61μ (mean 49μ).

Holotype. Preparation KA 251/3, 33.5 88.9, K905, N274.

Locus typicus. South Mimerdalen, Central Dicksonland, Spitsbergen; Reuterskiöldfjellet Sandstone, Siegenian.

Description. Holotype roundly triangular, diameter 51μ . Laesurae simple, almost reaching equatorial margin. Exine 3μ thick; proximal muri indistinct, distal surface supporting a predominance of cones, 1μ wide, up to 1.5μ high.

Remarks. Although cones usually predominate, specimens with a dominance of spines exist.

Comparison. Differs from other species of *Emphanisporites* yet described in having a strongly sculptured distal surface. *Emphanisporites neglectus* Vigran (Pl. 97, fig. 19) is occasionally sculptured, but then, only with very fine granules.

Occurrence. Lower Reuterskiöldfjellet Sandstone, Siegenian.

Emphanisporites minutus sp. nov.

Plate 97, fig. 20

Diagnosis. Miospores trilete; amb roundly triangular to subcircular. Laesurae straight, length three-quarters to full spore radius, accompanied by smooth, narrow lips, individually less than $1\ \mu$ wide. Exine $2\text{--}3\ \mu$ thick, homogeneous to infragranulate; proximal surface with $15\text{--}30$ radially disposed muri, approximately $1\ \mu$ wide, distal surface laevigate.

Dimensions. (Twenty specimens) Equatorial diameter $16\text{--}27\ \mu$ (mean $24\ \mu$).

Holotype. Preparation KA 262/4 56·8 91·5, K908, N276.

Locus typicus. South Mimerdalen, Central Dicksonland, Spitsbergen; Reuterskiøldfjellet Sandstone, Siegenian.

Description. Holotype subtriangular, diameter $26\ \mu$. Lips extend almost to the equatorial margin. Exine $2\ \mu$ thick; proximal surface with twenty-five radially disposed ribs, $0\cdot5\text{--}1\ \mu$ wide.

Comparison. *Emphanisporites rotatus* McGregor 1961 (p. 3, pl. 1, figs. 1–4) is considerably larger and the laesurae are frequently unaccompanied by lips.

Occurrence. Fraenkelryggen Division and Reuterskiøldfjellet Sandstone, Gedinnian to Lower Emsian.

Emphanisporites patagiatus sp. nov.

Plate 97, fig. 21

Diagnosis. Miospores trilete; amb subcircular to subtriangular, periphery often undulating. Laesurae simple, straight, length $\frac{1}{2}\text{--}\frac{3}{4}$ spore radius. Exine $2\text{--}6\ \mu$ thick, homogeneous to infragranulate; proximal surface with $8\text{--}15$ radially disposed muri, $3\text{--}14\ \mu$ wide, up to $4\ \mu$ high, extending $\frac{1}{3}\text{--}\frac{1}{2}$ spore radius from the equatorial margin, proximal polar region and distal surface laevigate.

Dimensions. (Fifteen specimens) Equatorial diameter $33\text{--}50\ \mu$ (mean $45\ \mu$).

Holotype. Preparation KA 271/3, 38·1 99·3, K897, N277.

Locus typicus. South Munindalen, Central Dicksonland, Spitsbergen; Reuterskiøldfjellet Sandstone, Emsian.

Description. Holotype roundly triangular, diameter $49\ \mu$. Laesurae length two-thirds of spore radius. Exine $6\ \mu$ thick, finely infragranulate, nine proximal radial ribs, $4\text{--}13\ \mu$ wide, extend $\frac{1}{3}\text{--}\frac{1}{2}$ spore radius from the equatorial margin.

Comparison. *Emphanisporites robustius* McGregor 1961 (p. 4, pl. 1, fig. 13) is larger and lacks the laevigate proximal polar region.

Occurrence. Reuterskiøldfjellet Sandstone; Siegenian and Emsian.

Subturma ZONOTRILETES Waltz 1935
Infraturma TRICRASSATI Dettmann 1963
Genus CRASPEDISPOA gen. nov.

Type species. *Craspedispora craspeda* sp. nov.

Diagnosis. Miospores trilete; amb subcircular to roundly triangular. Laesurae usually

well defined, simple or accompanied by lips. Central area encompassed inter-radially by a narrow zona. Central area sculptured proximo-equatorially and distally.

Discussion. Differs from both *Reinschospora* Schopf, Wilson, and Bentall 1944 and *Diatomozonotriletes* (Naumova) Playford 1962 in having a more roundly triangular shape, and a nonfimbriate zona rather than a corona. *Camarozonotriletes* (Naumova) Potonié 1958 has a thick interradianal crassitude.

Derivation of name. Gr. *krespedon*—edge, border.

Craspedispora craspeda sp. nov.

Plate 97, figs. 22, 23

Diagnosis. Miospores trilete; amb subcircular to roundly triangular. Laesurae straight, distinct, length $\frac{1}{2}$ – $\frac{2}{3}$ spore radius, simple or accompanied by narrow, smooth lips individually 0.5–1 μ wide. Exine of central area 1–2.5 μ thick, sometimes slightly thicker inter-radially, homogeneous to finely infragranulate, extending interradianally as a thin, membranous zona 2–5 μ wide, the zona never develops in the radial regions. Contact areas often slightly darkened, laevigate, proximo-equatorial and distal surfaces of the central area with a distinct ornament of cones, 1.5 μ or less in height and basal diameter. Zona laevigate, or occasionally with a few small cones. Curvatural folds sometimes present.

Dimensions. (Thirty-four specimens) Equatorial diameter (including zona) 35–42 μ (mean 39 μ).

Holotype. Preparation KA 258/3, 42.8 89.4, K922, N278.

Locus typicus. South Mimerdalen, Central Dicksonland, Spitsbergen; Reuterskiøldfjellet Sandstone, Emsian.

Description. Holotype roundly triangular, diameter 41 μ . Laesurae length two-thirds of spore radius. Exine 2 μ thick, slightly less at the apices, zona 2.5 μ wide.

Remarks. Corrosion of the thin zona frequently occurs, giving the outer margin an irregular appearance. In oblique aspect, the zona is very difficult to see.

Occurrence. Reuterskiøldfjellet Sandstone, and Lower Mimer Valley Series; Emsian and Eifelian.

Genus DIATOMOZONOTRILETES (Naumova) Playford 1962

Type species. *Diatomozonotriletes saetosus* (Hacquebard and Barss 1957) Hughes and Playford 1961.

Diatomozonotriletes sp.

Plate 97, figs. 24, 25

Description of specimens. Miospores trilete; amb triangular, with straight to slightly concave sides, and rounded apices. Laesurae indistinct, simple, straight, length approximately three-quarters spore radius. Corona composed of discrete, closely spaced, pointed saetae, 2.5 to 3 μ long interradianally, diminishing in size towards the triangular apices, from which they are absent. Exine of central area approximately 1 μ thick, finely infragranulate, proximally laevigate, distally supporting an ornament of small discrete cones, 1.5 μ or less in height and basal diameter. Exine folded.

Dimensions. (Three specimens) Overall equatorial diameter 25–27 μ .

Remarks. Although too few specimens are present to warrant specific assignment, these specimens are interesting in that they provide the lowest stratigraphical record for this genus.

Occurrence. Planteklofta Conglomerate and Fiskeklofta Formation; probable Upper Givetian.

Infraturma CINGULATI (Potonié and Klaus) Dettmann 1963

Genus STENOZONOTRILETES (Naumova) Potonié 1958

Type species. *Stenozonotriletes conformis* Naumova 1953.

Stenozonotriletes furtivus sp. nov.

Plate 98, figs. 2, 3

Diagnosis. Miospores trilete; amb roundly triangular to subcircular. Laesurae distinct, straight, length $\frac{1}{2}$ – $\frac{2}{3}$ spore radius, simple or more frequently accompanied by low, flat-topped lips, individually 2–3 μ wide at the polar end, decreasing gradually equatorially. Exine laevigate to finely punctate; cingulum smooth, uniform or slightly narrower interradially.

Dimensions. (Seventeen specimens) Overall equatorial diameter 65–108 μ (mean 81 μ); width of cingulum 10–19 μ (mean 12 μ).

Holotype. Preparation KA 274/4, 44·8 94·4, K872, N281.

Description. Holotype roundly triangular, overall diameter 70 μ . Laesurae half spore radius, accompanied by low thickened lips, individually 3 μ wide. Cingulum uniform, 10 μ wide.

Remarks. Frequently the cingulum is eroded, giving it an irregular appearance.

Comparison. *Archaeozonotriletes subcompactus* Naumova 1955 (p. 84, pl. 13, fig. 14 and p. 35, pl. 13, fig. 9) is circular and has a sculpture of small protuberances. *Triletes dubius* Eisenack 1944 (p. 115, pl. 2, fig. 7, text-fig. 14) has a narrower cingulum and the exine thickens towards the polar axis, forming a darkened triangular area, unlike the lip formation in *S. furtivus* sp. nov.

Occurrence. Dicksonfjorden Sandstone, Reuterskiöldfjellet Sandstone, and Lower Mimer Valley Series; Upper Siegenian to Eifelian.

Stenozonotriletes insessus sp. nov.

Plate 98, fig. 1

Diagnosis. Miospores trilete; amb convexly subtriangular. Laesurae straight, extending almost to the equatorial margin, accompanied by narrow lips, each approximately 0·5 μ wide, up to 2·5 μ high. Exine homogeneous to finely infragranulate, laevigate. Cingulum uniform.

Dimensions. (Twenty specimens) Overall equatorial diameter 24–36 μ (mean 30 μ); width of cingulum 3–6 μ (mean 4 μ).

Holotype. Preparation KA 223/2, 35·5 89·7, K829, N283.

Locus typicus. South Mimerdalen, Central Dicksonland, Spitsbergen; Reuterskiöldfjellet Sandstone, Emsian.

Description. Holotype overall diameter $36\ \mu$, lips individually $0.5\ \mu$ wide, $2\ \mu$ high. Cingulum $4\ \mu$ wide.

Comparison. *Archaeozonotriletes pusillus* Naumova 1953 (p. 86, pl. 13, fig. 19) has simple laesurae which often have 'clavate endings'; but is otherwise similar. *Stenozonotriletes extensus* Naumova var. *minor* Naumova 1953 (p. 37, pl. 3, fig. 18; p. 72, pl. 10, fig. 21; p. 130, pl. 19, figs. 19, 20) is more coarsely infragranulate and has simple laesurae.

Occurrence. Reuterskiöldfjellet Sandstone, and Lower Mimer Valley Series; Siegenian to Eifelian.

Stenozonotriletes sp.

Plate 98, fig. 4

Description of specimens. Miospores trilete; amb convexly subtriangular. Laesurae straight or slightly sinuous, length three-quarters to full central area radius. Exine finely punctate; cingulum smooth, usually slightly thicker interradially.

Dimensions. (Six specimens) Overall equatorial diameter $54\text{--}66\ \mu$ (mean $58\ \mu$), width of cingulum $6\text{--}8\ \mu$ interradially, $4\text{--}6\ \mu$ radially.

Comparison. Too few specimens are present to warrant the erection of a new species. *Stenozonotriletes perforatus* Playford 1962 (p. 607, pl. 86, figs. 8–9, text-fig. 5c), has a narrower, laevigate cingulum, but is otherwise similar. *Stenozonotriletes* sp. cf. *S. recognitus* var. *recognitus* Naumova in Balme and Hassell 1962 (p. 14, pl. 3, figs. 3, 4) differs only in having a darker contact area.

Occurrence. Upper Reuterskiöldfjellet Sandstone, and Lower Mimer Valley Series; Upper Emsian, Lower Eifelian.

Genus LYCOSPORA (Schopf, Wilson, and Bentall) Potonié and Kremp 1954

Type species. *Lycospora micropapillata* (Wilson and Coe) Schopf, Wilson, and Bentall 1944.

EXPLANATION OF PLATE 98

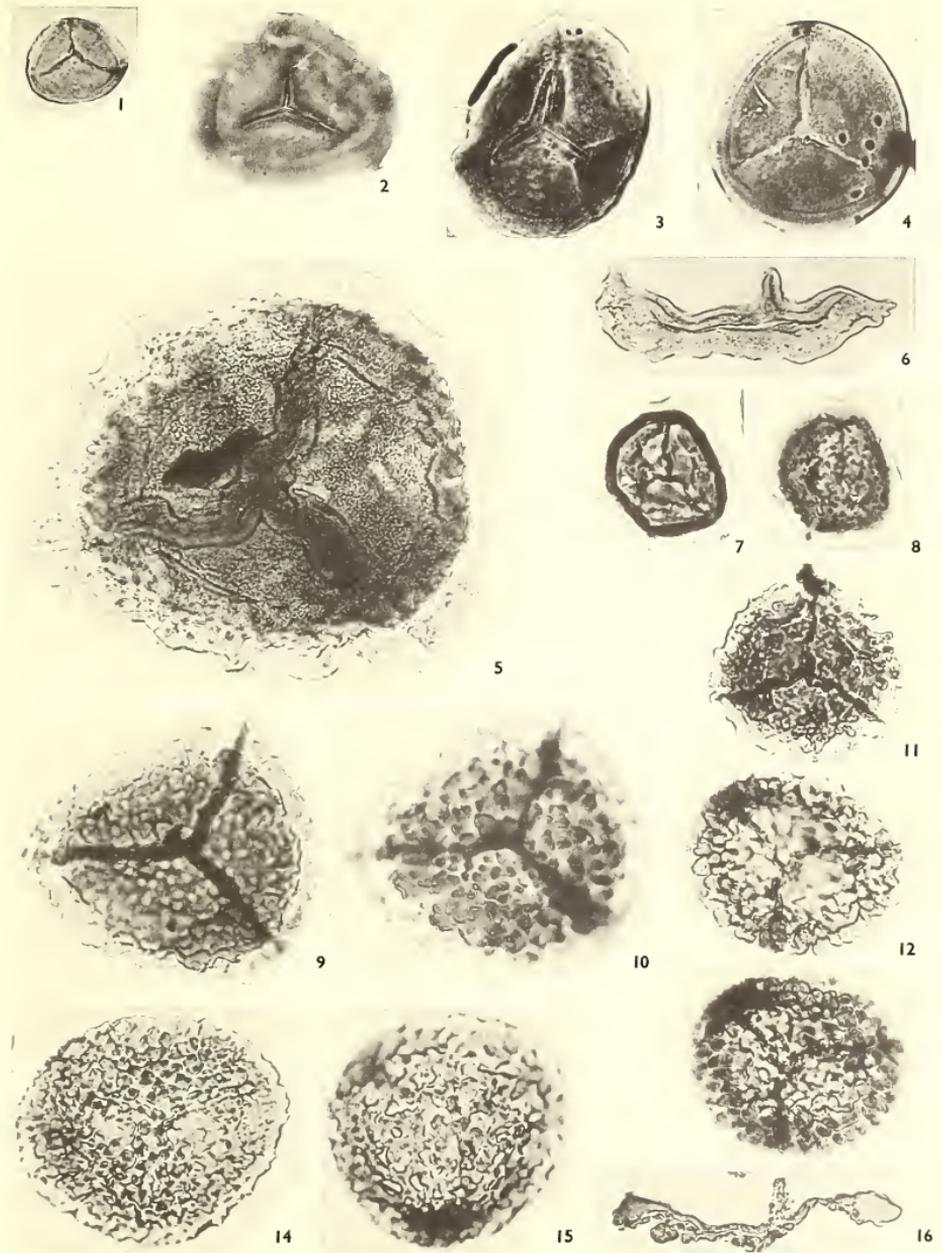
All figures $\times 500$; from untouched negatives.

Figs. 1–4. *Stenozonotriletes* spp. 1, *S. incessus* sp. nov. Holotype, sectional focus; KA 223/2, 35-5 89-7, K829, N283. 2–3, *S. furtivus* sp. nov. 2, Holotype, proximal surface; KA 274/4, 44-8 94-4, K872, N281. 3, Proximal surface; KA 209/2. 42-7 92-1, K519, N282. 4, *S. sp.* Sectional focus; KA 230/4, 36-0 101-7, K638, N284.

Figs. 5–6. *Densosporites devonicus* Richardson. 5, Proximal surface; KA 209/M1, 63-8 90-8, K519, N285. 6, Section; KA 286/S12, 32-6 95-8, K773, N286.

Figs. 7–8. *Lycospora culpa* sp. nov. Holotype, proximal and distal surfaces respectively; KA 262/4, 57-7 106-4, K908, N287.

Figs. 9–16. *Samarisporites* spp. 9–10, *S. praetervisus* (Naumova) comb. nov., Proximal and distal surfaces respectively; KA 243/1, 52-2 98-4, K767, N288. 11, *S. senotus* sp. nov. Holotype, sectional focus; KA 243/2, 32-8 105-3, K767, N289. 12–16, *S. hesperus* sp. nov. 12, 13, Holotype, proximal and distal surfaces respectively; KA 243/3, 51-7 102-7, K767, N290. 14, Distal surface; KA 243/3, 24-7 93-4, K767, N291. 15, Distal surface showing cristo-reticulate sculpture; KA 243/3, 37-6 103-4, K767, N292. 16, Section, showing the cingulate exine and distal sculpture; KA 243/S11, 43-4 90-8, K767, N293.



Lycospora culpa sp. nov.

Plate 98, figs. 7, 8

Diagnosis. Miospores trilete; amb roundly triangular with acute to broadly rounded apices, occasionally subcircular, conformable with the central area outline. Laesurae indistinct, straight, length two-thirds to full central area radius, accompanied by narrow, smooth, low lips, individually 0.5–1.5 μ wide, length three-quarters to full spore radius. Exine two-layered; intexine approximately 1 μ thick, closely appressed to the exoexine and usually indistinct, exoexine of both central area and equatorial flange finely infragranulate. Proximal surface laevigate, distal surface of central area sparsely covered with small cones and granules 1.5 μ or less in height and basal diameter, equatorial flange laevigate. Proximal surface usually with numerous folds.

Dimensions. (Twenty specimens) Overall equatorial diameter 33–60 μ (mean 47 μ), width of cingulum 2–14 μ (mean 6 μ).

Holotype. Preparation KA 262/4, 57-7 106-4, K908, N287.

Locus typicus. South Mimerdalen, Central Dicksonland, Spitsbergen; Lower Reuterskiøldfjellet Sandstone, Siegenian.

Description. Holotype roundly triangular with convex sides and acute apices, diameter 51 μ , width of cingulum 6 μ . Laesurae indistinct, lips 1 μ wide, extending full radius of the central area. Intexine 1 μ thick, exoexine proximally folded, distally with grana and small cones on the central area.

Remarks. Some specimens are slightly thicker at the very inner margin of the cingulum, but in no specimen is it truly bizonate. This species provides a very low stratigraphical record for the genus *Lycospora*.

Comparison. *Lycospora uber* (Hoffmeister, Staplin, and Malloy) Staplin 1960 (p. 20, pl. 4, figs. 13, 17, 18, 20) is smaller, and only faintly granulose. *Hymenozonotriletes milligranus* Naumova 1953 (p. 126, pl. 18, figs. 31, 32) is bizonate, and more densely sculptured. *Hymenozonotriletes mancus* Naumova 1953 (p. 63, pl. 8, fig. 17) has a laevigate distal central area. *Hymenozonotriletes limpidus* Naumova 1953 (p. 98, pl. 15, fig. 21) is circular, lacks lips, and is more densely sculptured.

Occurrence. Lower Reuterskiøldfjellet Sandstone, Siegenian.

Genus *DENSOSPORITES* (Berry) Potonié and Kremp 1954

Type species. *Densosporites covensis* Berry 1937.

Densosporites devonicus Richardson 1960

Plate 98, figs. 5, 6

Dimensions. (Forty specimens) Overall equatorial diameter 66–156 μ (mean 99 μ); total width of cingulum 18–40 μ (mean 26 μ), inner zone 12–27 μ (mean 18 μ).

Remarks. The section of *D. devonicus* Richardson (Pl. 98, fig. 6) demonstrates the raised lips, distal sculpture, and thick exoexine. The intexine cannot be seen in this section.

Occurrence. Upper Mimer Valley Series; Givetian.

Genus SAMARISPORITES Richardson 1965

Type species. *Samarisporites (Cristatisporites) orcadensis* (Richardson) Richardson 1965.

Discussion. *Samarisporites triangulatus* sp. nov. and *Samarisporites inusitatus* sp. nov. (see below) both have equatorial structures which vary from a zona to a cingulum (here referred to as an equatorial flange), giving evidence in support of Dettmann's (1963) emendation of the infraturma Cingulati (Potonié and Klaus 1954), to include zonate forms.

Samarisporites praetervisus (Naumova) comb. nov.

Plate 98, figs. 9, 10

1953 *Hymenozonotriletes praetervisus* Naumova, p. 40, pl. 4, fig. 8.

Description of specimens. Miospores trilete; amb roundly triangular to subtriangular. Laesurae indistinct, obscured by smooth elevated lips, individually 1–2 μ wide, 5–10 μ high, almost extending to the equatorial margin. Exine two-layered; intexine homogeneous 2 μ or less wide, closely appressed to the exoexine and often indistinct; exoexine of both central area and cingulum finely to coarsely infragranulate, proximally laevigate, distal surface densely ornamented with cones, 2–7 μ wide, 3–8 μ high. Cones on the central area variable both in shape and distribution, commonly with rounded apices, often supporting an apical capitate spine, the cones are usually closely spaced, with rounded polygonal or occasionally fused bases. Cones on the cingulum less dense, with pointed to slightly rounded apices, 33–52 cones round the equatorial margin. Cingulum uniform, tapering, differentiation from the central area distinct to obscure.

Dimensions. (Sixteen specimens) Overall equatorial diameter 70–124 μ (mean 86 μ); width of cingulum 16–30 μ (mean 21 μ).

Comparison. *Samarisporites orcadensis* (Richardson 1960, p. 58, pl. 14, fig. 12, text-fig. 8) Richardson 1965, is considerably larger.

Occurrence. Upper Mimer Valley Series; Givetian.

Samarisporites senotus sp. nov.

Plate 98, fig. 11

Diagnosis. Miospores trilete; amb convexly triangular, irregular, central area outline circular. Laesurae straight, length two-thirds to full radius of the central area, accompanied by smooth, narrow, often sinuous lips, individually 1–1.5 μ wide, extending on to the cingulum, usually to the equatorial margin. Exine two-layered; intexine thin, approximately 1 μ wide, closely appressed to the exoexine, and often indistinct; exoexine of both central area and cingulum finely infra-granulate. Proximal surface laevigate, distal surface very sparsely covered with small spines and cones, 1–4 μ wide, 2–4 μ high, the cones frequently support a small apical spine. Cingulum of uniform width, proximally occasionally raised above the central area, the inner distal margin may be slightly thickened, but the cingulum is never distinctly bizonate.

Dimensions. (Sixteen specimens) Overall equatorial diameter 50–64 μ (mean 57 μ); width of cingulum 12–16 μ (mean 15 μ).

Holotype. Preparation KA 243/2, 32.8 105.3, K767, N289.

Locus typicus. East Munindalen, Central Dicksonland, Spitsbergen; Plantekløfta Conglomerate, probable Upper Givetian.

Description. Holotype diameter $57\ \mu$, cingulum $12\ \mu$ wide. Laesurae straight, length two-thirds central area radius, lips each $1\ \mu$ wide, extending almost to the equatorial margin. Distal spines and cones $1\text{--}3\ \mu$ wide, $2\text{--}3\ \mu$ high, somewhat corroded.

Remarks. In corroded specimens, the sculptural elements may be partially or completely eroded.

Comparison. *Hymenozonotriletes spinosus* Naumova 1953 (p. 41, pl. 14, fig. 9) is much larger, and has a more regular ornament. *Zonotriletes deliquescens* Lubert, in Lubert and Waltz 1941 (p. 50, pl. 1, fig. 6), is larger, and the inner part of the cingulum is not thickened. *Hymenozonotriletes pusillus* (Ibrahim) Ishchenko 1952 (p. 50, pl. 13, fig. 122) is smaller, the lips are shorter, and there is a sparser ornament on the cingulum. *Densosporites laudesii* Staplin 1960 (p. 25, pl. 5, fig. 11) has an ornament only of cones, shorter lips, and a distinctly bizonate cingulum.

Occurrence. Upper Mimer Valley Series; Givetian.

Samarisporites hesperus sp. nov.

Plate 98, figs. 12–16

Diagnosis. Miospores trilete; amb circular to subcircular conformable with the central area outline. Laesurae indistinct, length three-quarters to full central area radius, accompanied and usually obscured by narrow, often slightly sinuous, elevated lips, individually $1\text{--}2.5\ \mu$ wide, extending to the inner margin of the cingulum. Exine one-layered, finely infra-granulate, proximally laevigate, distally with an even distribution of cones on both central area and cingulum. The cones $2\text{--}6\ \mu$ wide, $2\text{--}6\ \mu$ high, have rounded apices, and a capitate apical spine in well-preserved specimens; the bases of the cones on the central area are usually fused, often to such an extent as to form an imperfect reticulum. Cingulum uniform, tapering abruptly at the outer margin, differentiation from the central area is sometimes indistinct.

Dimensions. (Fifty-three specimens) Overall equatorial diameter $52\text{--}89\ \mu$ (mean $73\ \mu$); width of cingulum $7\text{--}12\ \mu$ (mean $10\ \mu$).

Holotype. Preparation KA 243/3, 51.7 102.7, K767, N290.

Locus typicus. East Munindalen, Central Dicksonland, Spitsbergen; Plantekløfta Conglomerate, probably Upper Givetian.

Description. Holotype subcircular, diameter $68\ \mu$, cingulum $9\ \mu$ wide. Laesurae indistinct, lips approximately $1\ \mu$ wide, cones $4\text{--}6\ \mu$ wide, $3\text{--}6\ \mu$ high, occasionally fused near the distal pole. Capitate spines eroded from many cones.

Remarks. The section (Pl. 98, fig. 16) clearly demonstrates the laevigate proximal surface, raised lips, one-layered exine, and abruptly tapering cingulum. In specimens where the cones are eroded, the fused bases are clearly seen (Pl. 98, fig. 15).

Comparison. *Archaeozonotriletes crassispinosus* Chibrikova 1959 (p. 62, pl. 8, fig. 5) is roundly triangular, lacks lips, and there is no evidence of small spines on the cones.

Lycospora magnifica McGregor 1960 (p. 35, pl. 12, fig. 5, pl. 13, figs. 2-4) is much larger, and has a smaller sculptural pattern. *Lycospora rugulatus* Vigran 1964 (p. 23, pl. 1, figs. 17, 18; pl. 2, fig. 15) is clearly similar, but lacking cones, has a rugulate rather than a cristate sculpture. The lack of cones in Vigran's specimens may be due to poor preservation; if this is proved to be so, then *Samarisporites hesperus* sp. nov. would be synonymous with *L. rugulatus*.

Occurrence. Upper Mimer Valley Series, particularly common in the Planteklofta Conglomerate; probable Givetian.

Samarisporites triangulatus sp. nov.

Plate 99, figs. 1-6

Diagnosis. Miospores trilete, amb triangular, with straight to moderately convex sides, central area outline circular to roundly triangular. Laesurae indistinct, length where seen two-thirds to full central area radius, accompanied by smooth, elevated lips, individually 0.5-3 μ wide, extending on to the equatorial flange, and frequently to the equatorial margin. Exine two-layered; intexine 1-2 μ wide, closely appressed to the exoexine, and often indistinct; exoexine of both central area and equatorial flange finely infragranulate. Proximal surface laevigate, distally the central area supports a closely spaced ornament of cones, 2-5 μ in height and basal diameter, the cones occasionally support a small apical spine. Variation occurs in the basal sculpture of the elements, which may be separate, occasionally fused, or more comprehensively associated, forming an imperfect reticulum; distally the equatorial flange is laevigate, or rarely with a sparse ornament of small cones. Equatorial flange acutely tapering, irregular, reaching its maximum width radially, frequently being only just perceptible in the inter-radial regions.

Dimensions. (Forty-five specimens) Overall equatorial diameter 46-78 μ (mean 62 μ); diameter of central area 32-54 μ (mean 43 μ); width of cingulum radially 10-20 μ (mean 13 μ), interradially 1-9 μ (mean 5 μ).

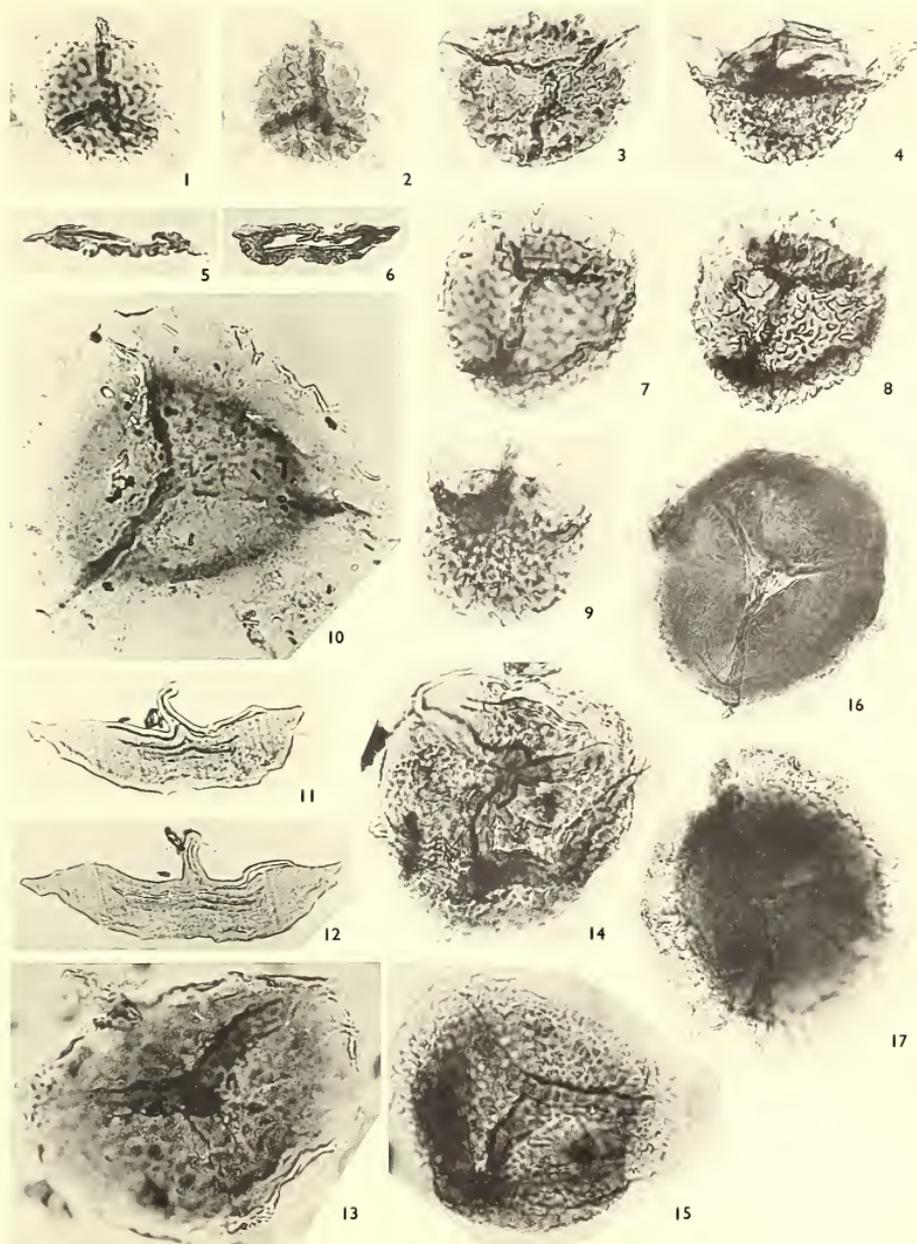
Holotype. Preparation KA 243/1, 39-6 97-6, K767, N294.

Locus typicus. East Munindalen, Central Dicksonland, Spitsbergen; Planteklofta Conglomerate, probable Upper Givetian.

EXPLANATION OF PLATE 99

All figures $\times 500$; from unretouched negatives.

- Figs. 1-9. *Samarisporites* spp. 1-6. *S. triangulatus* sp. nov. 1, 2, Holotype, proximal and distal surfaces respectively; KA 243/1, 39-6 97-6, K767, N294. 3, Proximal surface; KA 243/3, 57-8 108-3, K767, N295. 4, Lateral view; KA 243/3, 35-1 87-6, K767, N296. 5, 6, Sections showing the equatorial flange; KA 242/S3, 36-5 100-0, K772, N297 and KA 242/S3, 51-4 97-7, K772, N298 respectively. 7-9. *S. inusitatus* sp. nov. 7, 8, Holotype; proximal and distal surfaces respectively; KA 243/3, 52-2 101-3, K767, N299. 9, Lateral view; KA 243/1, 30-6 98-0, K767, N300.
- Figs. 10-13. *Cirratriradites avius* sp. nov. 10, Holotype, proximal surface; KA 242/1, 21-2 89-7, K772, N301. 11, 12, Sections showing the three-layered exine; KA 290/S11, 53-3, 105-0, K681, N302, and KA 290/S12, 32-9 90-5, K681, N303. 13, Proximal oblique aspect; KA 290/2, 45-9 108-4, K681, N304.
- Figs. 14-15. *Camptozonotrites asaminthus* sp. nov. 14, Holotype, proximal oblique aspect; KA 290/4, 53-0 91-2, K681, N307. 15, Proximal surface; KA 290/1, 38-8 103-2, K681, N308.
- Figs. 16-17. *Cirratriradites dissutus* sp. nov. 16, Holotype, the equatorial flange is somewhat eroded, as in all specimens; KA 251/3, 33-0 89-2, K905, N305. 17, Specimen showing the flange characteristically eroded in the inter-radial areas; KA 262/M5, 36-6 99-6, K908, N306.



Description. Holotype amb triangular, central area circular, overall diameter $54\ \mu$, central area $40\ \mu$, width of equatorial flange radially $12\ \mu$, inter-radially $1-4\ \mu$. Lips individually $2.5\ \mu$ wide, extend almost to equatorial margin. Distal central area cones $3-4\ \mu$ wide, $2-5\ \mu$ high, with separate bases, distal equatorial flange laevigate. Sculptural elements obscure the equatorial flange completely in one inter-radial region.

Remarks. There is some variation in the proximo-distal thickness of the cingulum, which may be very thin (Pl. 99, fig. 4) and represent a zona, or more definitely a cingulum, as demonstrated in the sections (Pl. 99, figs. 5, 6). Sections also show the intexine and exclusively distal ornament.

Comparison. The distinctive equatorial flange separates this species from others assignable to *Samarisporites*.

Occurrence. Upper Mimer Valley Series; Givetian.

Samarisporites inusitatus sp. nov.

Plate 99, figs. 7-9

Diagnosis. Miospores trilete; amb circular to roundly triangular, conformable with the central area outline. Laesurae obscured by smooth, elevated lips, individually $1-2\ \mu$ wide, $3-8\ \mu$ high, extending to the equatorial margin. Exine homogeneous to finely infragranulate, proximally laevigate, distally the central area supports an ornament of cones, $1-4\ \mu$ wide, $1-6\ \mu$ high, the cones often supporting a small apical spine. Considerable variation occurs in the basal sculpture of the cones which may be separate, fused, or more comprehensively associated as an imperfect reticulum; distally the equatorial flange is laevigate or rarely with a sparse ornament of small cones. Equatorial flange acutely tapering, uniform.

Dimensions. (Eighteen specimens) Overall equatorial diameter $60-66\ \mu$ (mean $62\ \mu$); width of equatorial flange $5-9\ \mu$ (mean $6.5\ \mu$).

Holotype. Preparation K243/3, 52.2 101.3, K767, N299.

Locus typicus. East Munindalen, Central Dicksonland, Spitsbergen; Plantekløfta Conglomerate, probable Upper Givetian.

Description. Holotype circular, overall diameter $62\ \mu$, equatorial flange $7\ \mu$. Lips each approximately $1\ \mu$ wide, $3\ \mu$ high. Distal cones $1-3\ \mu$ in height and diameter, occasionally fused basally.

Remarks. Specimens in oblique aspect (Pl. 99, fig. 9) demonstrate the thin equatorial flange.

Comparison. *Samarisporites hesperus* sp. nov. (Pl. 98, figs. 12-16) has a larger, denser sculpture, and a strong cingulum. *Hymenozonotriletes ceber* Chibrikova 1959 (p. 77, pl. 13, fig. 3) is considerably larger, and has a much wider equatorial flange.

Occurrence. Fiskekløfta Formation, Planteryggen Sandstone, and Plantekløfta Conglomerate; probable Upper Givetian.

Genus *CIRRATRIRADITES* Wilson and Coe 1940

Type species. *Cirratiradites saturni* (Ibrahim) Schopf, Wilson, and Bentall 1944.

Discussion. *Cirratiradites avius* sp. nov. (Pl. 99, figs. 10–13) and *Cirratiradites dissutus* sp. nov. (Pl. 99, figs. 16–17) are included within this genus on the basis of their apparently thin equatorial flange, and reduced sculpture.

Cirratiradites avius sp. nov.

Plate 99, figs. 10–13

Diagnosis. Miospores trilete; amb roundly triangular, with convex sides and sharply to broadly rounded apices. Laesurae indistinct, accompanied by smooth elevated lips, individually 1–3 μ wide, length three-quarters to full spore radius. Exine three-layered; intexine finely infra-granulate, approximately 2 μ thick, closely appressed to the exoexine, and seen only in over-macerated specimens or sections; exoexine two-layered, inner exoexine coarsely infra-granulate, outer exoexine homogeneous. Proximal surface laevigate, distal surface laevigate, or very sparsely ornamented with cones 1–2 μ wide, 1–4 μ high; equatorial flange moderately to acutely tapering, uniform, differentiation from the central area often indistinct.

Dimensions. (Twenty specimens) Overall equatorial diameter 84–172 μ (mean 123 μ), width of equatorial flange 16–36 μ (mean 27 μ).

Holotype. Preparation KA 242/1, 21·2 89·7, K772, N301.

Locus typicus. East Munindalen, Central Dicksonland, Spitsbergen; Plantekløfta Conglomerate, probable Upper Givetian.

Description. Holotype diameter 121 μ , equatorial flange approximately 22 μ wide. Lips narrow, total width 5 μ , inaperturate, extend on to the inner margin of the cingulum. Exine laevigate, equatorial flange corroded.

Remarks. Sections (Pl. 99, figs. 11, 12) show the three-layered exine, and the elevated lips formed as an extension of the homogeneous outer exoexine only, which in this specimen are inaperturate. The inner exoexine is very thick distally, which probably accounts for the indistinct intexine and central area outline. As demonstrated in *Cirratiradites elegans* by Hughes, Dettmann, and Playford (1962), sections of what appears in proximo-distal aspect to be a thin equatorial flange, is in fact surprisingly thick.

Comparison. *Cirratiradites elegans* (Waltz) Potonié and Kremp 1956 (p. 126) is clearly similar, but has a more distinct and scabrate central area, and as seen in section (Hughes, Dettmann, and Playford 1962, p. 251, pl. 38, figs. 6, 7), has a thinner intexine, and an undivided exoexine.

Occurrence. Upper Mimer Valley Series; Givetian.

Cirratiradites dissutus sp. nov.

Plate 99, figs. 16, 17

Diagnosis. Miospores trilete; amb circular, subcircular to oval, conformable with the central area outline. Laesurae straight often open, length equal to full central area

radius, accompanied by membranous, elevated lips, individually $1.5\text{--}6\ \mu$ wide, up to $8\ \mu$ high, extending on to the equatorial flange, and frequently to the equatorial margin. Exine apparently one-layered, coarsely infra-granulate, central area $4\text{--}10\ \mu$ thick, slightly thicker distally, punctate, occasionally microreticulate proximally, laevigate distally; equatorial flange much lighter in colour, thin, uniform, laevigate, often broken radially. Proximal and distal minor folds occasionally present.

Dimensions. (Twenty-one specimens) Overall equatorial diameter $71\text{--}123\ \mu$ (mean $90\ \mu$), diameter of equatorial flange $4\text{--}20\ \mu$ (mean $11\ \mu$).

Holotype. Preparation KA 251/3, 33-0 89-2, K905, N305.

Locus typicus. South Mimerdalen, Central Dicksonland, Spitsbergen; Lower Reuterskiöldfjellet Sandstone, Siegenian.

Description. Holotype subcircular, diameter $96\ \mu$, flange $10\ \mu$ wide. Laesurae open, lips up to $6\ \mu$ wide extend to the equatorial margin. Exine of central area $8\ \mu$ thick, proximally microreticulate.

Remarks. The majority of specimens are dark and ill preserved, and are very difficult to macerate satisfactorily. The breakdown of the equatorial flange radially (Pl. 99, fig. 17) in the majority of specimens, gives the spore a very distinctive appearance. Corrosion of the coarsely infra-granulate exine gives the spore a pseudosculpture of granules.

Comparison. *Hymenozonotriletes varius* Naumova 1953 var. *varius* (p. 38, pl. 4, fig. 10) is smaller, and has a very different lip construction.

Occurrence. Common in the Lower Reuterskiöldfjellet Sandstone, but extends up into the Lower Mimer Valley Series; Siegenian and Emsian.

Genus CAMPTOZONOTRILETES Staplin 1960

Type species. *Camptozonotriletes vermiculatus* Staplin 1960.

Camptozonotriletes asaminthus sp. nov.

Plate 99, figs. 14, 15

Diagnosis. Miospores trilete; proximally flattened, distally convex, amb circular, conformable in outline with the central area. Laesurae indistinct, straight, length two-thirds to full central area radius, accompanied and frequently masked by smooth, often sinuous, elevated lips, individually $3\text{--}5\ \mu$ wide, $7\text{--}12\ \mu$ high, extending on to the equatorial flange, and occasionally reaching the equatorial margin. Exine one-layered, coarsely infra-granulate, central area exine $2\text{--}10\ \mu$ thick, slightly thicker distally, equatorial flange lighter in colour, tapering equatorially; proximal surface laevigate, distal surface densely sculptured with low verrucae and occasional cones, $2\text{--}5\ \mu$ wide, $2\text{--}4\ \mu$ high, somewhat reduced and occasionally absent from the equatorial flange. Proximal surface frequently with conspicuous radially directed folds.

Dimensions. (Twenty-eight specimens) Overall equatorial diameter $80\text{--}108\ \mu$ (mean $89\ \mu$) equatorial flange $6\text{--}24\ \mu$ wide (mean $13\ \mu$).

Holotype. Preparation KA 290/4, 53-0 91-2, K681, N307.

Locus typicus. West Lagercrantzberget, Central Dicksonland, Spitsbergen; Upper Mimer Valley Series, Upper Givetian.

Description. Holotype diameter $96\ \mu$, equatorial flange $11\ \mu$ wide. Laesurae indistinct, lips each $3\ \mu$ wide, $7\ \mu$ high, extending to equatorial margin. Distal verrucae $3\text{--}4\ \mu$ in height and basal diameter, only slightly reduced on the equatorial flange.

Remarks. The majority of specimens are only slightly compressed, and as the proximal surface is flat, and the distal surface deeply convex, they are preserved in oblique aspect. The coarsely infra-granulate structure of the distal verrucae often results in their gradual corrosion and specimens with only a slightly undulose distal surface are frequent.

Comparison. *Hymenozonotriletes trichomirovii* Naumova 1953 (p. 62, pl. 8, fig. 12) is smaller, and has an ornament of spines on the equatorial flange. *Cirratriradites ornatus* Neves 1960 (p. 269, pl. 33, fig. 3) has a punctate central exine, and an ornament of cones.

Occurrence. Upper Mimer Valley Series; Givetian.

Camptozonotriletes aliquantus sp. nov.

Plate 100, figs. 1, 2

Diagnosis. Miospores trilete; amb roundly triangular, with moderately to strongly convex sides and well rounded or occasionally acute apices, conformable in outline with the central area. Laesurae distinct to discernible, simple, straight, length two-thirds to full central area radius. Exine two-layered; intexine $1\text{--}3\ \mu$ thick, infra-punctate, often slightly separate from the exoexine and usually distinct; exoexine homogeneous to infra-punctate extending beyond the intexine as a membranous flange. Proximal surface laevigate, distal central area comprehensively sculptured with high, narrow muri $1\text{--}3\ \mu$ wide, which frequently anastomose to form an imperfect reticulum; on the equatorial flange, the muri are somewhat lower, and are radially directed, occasionally extending to the equatorial margin. Major compressional folding frequent, the intexine is sometimes folded independently of the exoexine. All specimens are slightly corroded.

Dimensions. (Fifteen specimens) Diameter of exoexine $57\text{--}97\ \mu$ (mean $76\ \mu$); diameter of intexine $40\text{--}74\ \mu$ (mean $55\ \mu$); equatorial flange $9\text{--}16\ \mu$ (mean $12\ \mu$).

Holotype. Preparation KA 281/2, 37-0 96-4, K850, N309.

Locus typicus. Estheriahaugen, Central Dicksonland, Spitsbergen; Emsian.

Description. Holotype roundly triangular, diameter of exoexine $80\ \mu$, of intexine $50\ \mu$, equatorial flange $10\text{--}12\ \mu$ wide. Laesurae indistinct, only one laesura clearly seen. Intexine $3\ \mu$ thick, unfolded; distal exoexine with an imperfect reticulum centrally, muri slightly corroded; radially directed muri do not reach the equatorial margin of the flange. One major distal fold.

Remarks. The radially directed muri on the equatorial flange are an easily recognizable feature of this species. *Camptozonotriletes aliquantus* sp. nov. is included in this genus and not in *Cirratriradites* Wilson and Coe 1940, on the basis of the very prominent distal sculpture.

Occurrence. Reuterskiöldfjellet Sandstone, and Lower Mimer Valley Series; Siegenian to Lower Eifelian.

Infraturna PATINATI Butterworth and Williams 1958
Genus ARCHAEOZONOTRILETES (Naumova) emend.

1953 *Archaeozonotriletes* Naumova, p. 30.

1958 *Archaeozonotriletes* (Naumova) Potonié, p. 28.

Emended diagnosis. Miospores trilete; amb circular, subcircular to subtriangular. Laesurae usually long, simple, or accompanied by lips. Exine one- or two-layered, acavate, laevigate, or punctate; distally patinate. The patina may be of uniform thickness, or thickest in the distal polar region.

Type species. *Archaeozonotriletes variabilis* Naumova 1953, p. 30, pl. 2, fig. 12 (designated by Potonié 1958, p. 28).

Other species. The following species can probably be included within *Archaeozonotriletes* (Naumova) emend.

1. *Archaeozonotriletes accitus* Chibrikova 1959, p. 66, pl. 9, fig. 5. Occurrence: Western Bashkiria, U.S.S.R.: Givetian.

2. *Archaeozonotriletes tschernovii* Naumova 1953, p. 81, pl. 12, fig. 12. Occurrence: Chkalov province, U.S.S.R.; Lower Frasnian.

Discussion. The type species selected by Potonié 1958, is somewhat atypical amongst the large number of species recorded within *Archaeozonotriletes* by Naumova (1953). More typical, are thick-walled apiculate forms, which have an intexine partly separated from the exoexine; many of these latter species, however, can be included within *Geminospora* Balme 1962. Potonié 1958 (p. 28) interpreted the construction of *A. variabilis* as an irregular cingulum. Evidence from the Spitsbergen specimens, however, shows that *A. variabilis* has a very thick distal patina, and therefore is frequently preserved in oblique aspect, thus giving the impression of an irregular cingulum.

Comparison. The validation of *Archaeozonotriletes* by Potonié 1958, precedes by one month the erection of *Tholisporites* Butterworth and Williams 1958. In *Tholisporites*, however, the patina is thickest in the equatorial region, and is, according to Butterworth and Williams 1958 (p. 382) closely related to *Densosporites* and *Anulatisporites*; whereas the uniform or distal polar thickened patina of *Archaeozonotriletes* shows little constructive similarity to *Densosporites*. Also in *Tholisporites*, the patina appears to end abruptly on the proximal area, whereas in *Archaeozonotriletes*, the exine gradually thins over the proximal surface.

Archaeozonotriletes variabilis (Naumova) emend.

Plate 100, figs. 3-6

1953 *Archaeozonotriletes variabilis* Naumova 1953, p. 30, pl. 2, figs. 12, 13, pl. 12, figs. 8-11; p. 83, pl. 13, figs. 7-9.

Emended diagnosis. Miospores trilete, amb circular to subcircular, conformable with the central area outline. Laesurae straight, length three-quarters to full central area radius. Exine homogeneous, laevigate to finely punctate, proximally 1.5-4 μ thick; distally strongly patinate, 5-23 μ thick.

Dimensions. (Nineteen specimens) Equatorial diameter 42–60 μ (mean 53 μ); polar diameter 49–74 μ (mean 61 μ).

Locus typicus. Kaluga province, Starooskol beds, U.S.S.R.: Givetian.

Description. (From the illustration in Naumova 1953, pl. 2, fig. 12.) Holotype diameter in oblique aspect 50 μ . Laesurae simple, straight, length equal to full central area radius exine patinate, proximal oblique aspect 6 μ , distal oblique aspect 20 μ .

Remarks. The thickness of the patina is often as much as 30 per cent. of the total polar diameter (Pl. 100, fig. 4). In well-preserved specimens, the punctate nature of the exine is not always obvious, whilst in poorly preserved specimens the punctae are clearly seen (Pl. 100, fig. 5). Spores with a thicker distal hemisphere, are common both in Devonian samples from Melville Island, Arctic Canada, McGregor 1960 (p. 38) and from Spitsbergen. It is quite possible that some of the species included within the genus *Stenozonotriletes* by many Russian authors, may in fact possess a patina. Specimens in oblique aspect are the most informative for distinguishing species of *Archaeozonotriletes* from thick-walled *Punctatisporites*, and *Stenozonotriletes*. Russian authors who use the term 'otorochka', appear to use it both for equatorial structures and normal exine thickness.

Comparison. *Tholisporites tenuis* McGregor 1960 (p. 38, pl. 13, fig. 9) has a proximal membranous veil and a thinner patina. *T. scoticus* Butterworth and Williams 1958 (p. 382, pl. 3, figs. 48–50) is smaller, and the patina has its greatest thickness equatorially. *Trematozonotriletes irregularis* (Andrejeva, in Lubert and Waltz 1941) Ishchenko 1959 (p. 79, pl. 9, fig. 116) appears very similar, but the punctae are confined to the inner margin of the patina. *Stenozonotriletes fixus* Ishchenko 1952 (p. 56, pl. 16, fig. 141) with its punctate exine, appears to be similar to poorly preserved specimens of *A. variabilis* (Naumova), but is cingulate rather than patinate.

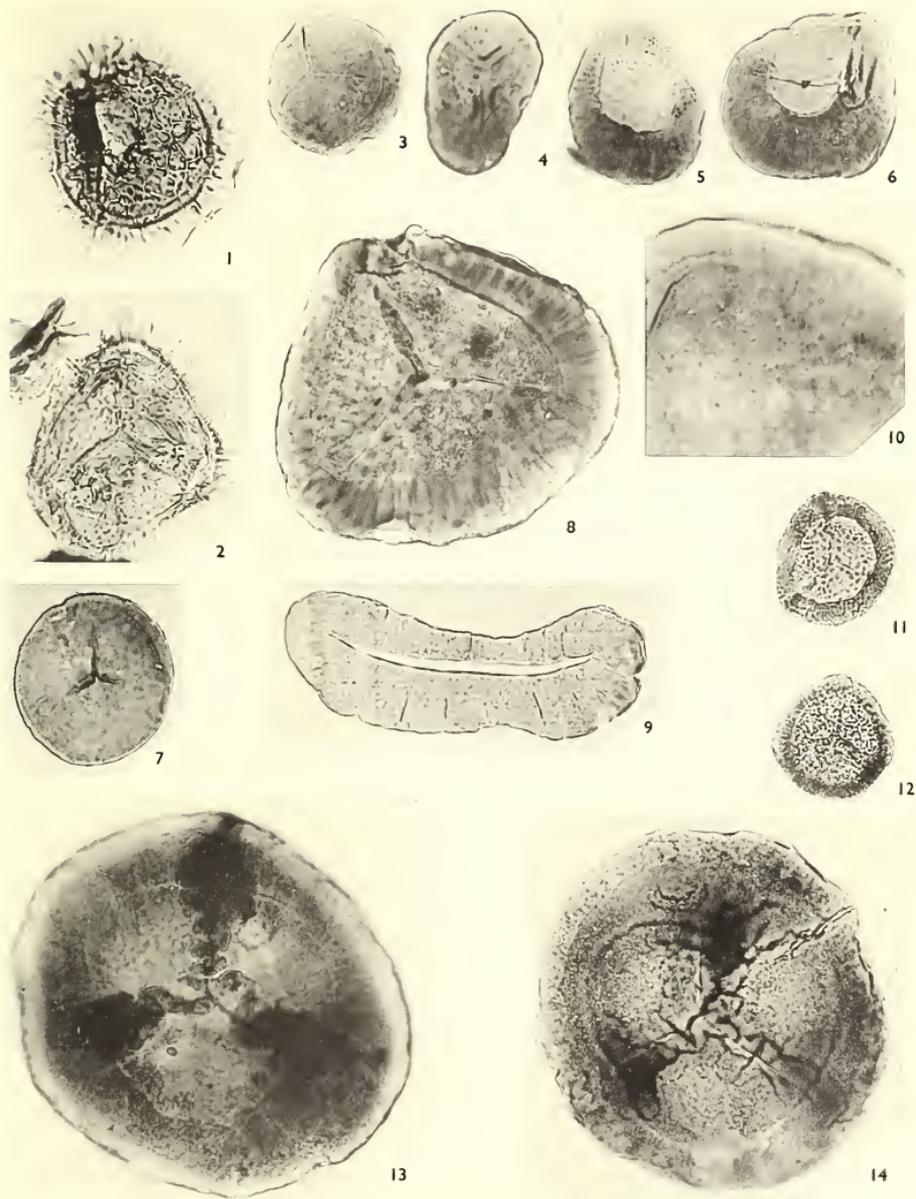
Occurrence. Upper Mimer Valley Series; Givetian.

Previous records. Recorded by Naumova (1953) from the Frasnian and Givetian of Kaluga, Chkalov, and Voronezh provinces, U.S.S.R., and by Kedo (1957) from the Famennian of Belorussia, U.S.S.R.

EXPLANATION OF PLATE 100

All figures $\times 500$ unless otherwise stated; from unretouched negatives.

- Figs. 1–2. *Camptozonotriletes aliquantus* sp. nov. 1, Holotype, distal surface, KA 281/2, 37-0 96-4, K850, N309. 2, Proximal surface, showing more distinct laesurae; KA 209/1, 34-1 97-2, K519, N310.
 Figs. 3–10. *Archaeozonotriletes* spp. 3–6. *A. variabilis* (Naumova) emend. 3, Proximal oblique aspect; KA 286/2, 27-5 107-3, K773, N311. 4, Lateral view, showing thick distal patina; KA 286/1, 20-6 99-6, K773, N312. 5, Showing corroded punctate exine; KA 286/3, 20-7 96-0, K773, N313. 6, Proximal oblique aspect; KA 286/1, 52-4 108-3, K773, N314. 7, *A. sarus* sp. nov. Holotype; KA 261/1, 32-4 103-2, K891, N315. 8–10. *A. columnus* sp. nov. 8, Holotype, proximal oblique aspect; KA 278/1, 27-6 101-8, K855, N316. 9, Section; KA 286/S4, 40-1 101-7, K773, N317. 10, ($\times 1000$) Showing punctate exine; KA 286/2, 28-8 87-6, K773, N318.
 Figs. 11–12. *Cymbosporites catillus* gen. et sp. nov. 11, Holotype; KA 287/2, 34-1 94-2, K846, N329. 12, Distal surface; KA 243/1, 28-5 95-1, K767, N330.
 Figs. 13–14. *Archaeozonotriletes meandricus* sp. nov. 13, Holotype, proximal surface; KA 209/2, 35-7 88-6, K519, N319. 14, Proximal surface; KA 209/M4, 24-7 100-5, K519, N320.



Archaeozonotriletes sarus sp. nov.

Plate 100, fig. 7

Diagnosis. Miospores trilete; amb circular. Laesurae short, distinct, length $\frac{1}{3}$ – $\frac{1}{2}$ spore radius, accompanied at least in part by narrow lips, individually $1\ \mu$ or less wide, the laesurae often extend equatorially beyond the lips. Exine infra-punctate, laevigate; proximally 2 – $3\ \mu$ thick, distal surface slightly patinate, 3 – $5\ \mu$ thick.

Dimensions. (Twenty-five specimens) Equatorial diameter 42 – $57\ \mu$ (mean $50\ \mu$).

Holotype. Preparation KA 261/1, 32-4 103-2, K891, N315.

Locus typicus. North Mimerdalen, Central Dicksonland, Spitsbergen; Fiskeløfta Formation, Givetian.

Description. Holotype diameter $56\ \mu$. Laesurae approximately half spore radius, lips individually $0.5\ \mu$ wide, length one-third spore radius. Proximal oblique aspect $2.5\ \mu$, distal oblique aspect $4.5\ \mu$.

Comparison. *Trematozonotriletes irregularis* (Andrejeva, in Luber and Waltz 1941) Ishchenko 1958 (p. 79, pl. 9, fig. 116) is smaller, has longer laesurae and a thicker patina. *Tholisporites tenuis* McGregor 1960 (p. 38, pl. 13, fig. 9) has simple laesurae and a thin membranous proximal surface. *T. densus* McGregor 1960 (p. 37, pl. 13, figs. 6, 7) has longer, simple laesurae, a thicker patina and a proximal membranous veil. *A. variabilis* (Naumova) emend. has longer, simple laesurae, and a thicker patina.

Occurrence. Upper Mimer Valley Series; Givetian.

Archaeozonotriletes columnus sp. nov.

Plate 100, figs. 8–10

Diagnosis. Miospores trilete; amb circular, subcircular to oval. Laesurae simple, straight, length three-quarters to full central area radius. Exine thick, homogeneous to infra-granulate, finely to coarsely punctate; proximally 4 – $10\ \mu$ thick, distally patinate 8 – $28\ \mu$ thick.

Dimensions. (Forty specimens) Equatorial diameter 76 – $145\ \mu$ (mean $107\ \mu$).

Holotype. Preparation KA 278/1, 27-6 101-8, K855, N316.

Locus typicus. Estheriahaugen, Central Dicksonland, Spitsbergen; Plantskløfta Sandstone, probably Upper Givetian.

Description. Holotype $116\ \mu$, laesurae extend full central area radius. Proximal oblique aspect $9\ \mu$, distal oblique aspect $21\ \mu$.

Remarks. The section (Plate 100, fig. 9) clearly demonstrates the overall thickness of the exine, together with the thickened distal hemisphere. Corrosion of the exine results in an increase in the diameter of the punctae and more drastically in their fusion.

Comparison. *Tholisporites punctatus* McGregor 1960 (p. 38, pl. 13, fig. 10) is somewhat smaller, and has the suggestion of a thin proximal membrane. *Archaeozonotriletes variabilis* (Naumova, p. 30, pl. 2, fig. 12) emend. is smaller, and in relation of its proximal hemisphere, is more strongly patinate. *A. vivax* Chibrikova 1959 (p. 69, pl. 10, fig. 4) has according to Chibrikova, a tuberculate ornament, though it would appear from the

illustration to be foveo-reticulate, rather than punctate. *Foveosporites pertusus* Vigran 1964 (p. 18, pl. 4, figs. 3, 4; pl. 5, figs. 1, 2*a-d*) is clearly similar, but although the thickness of the exine varies from 4–17 μ , Vigran gives no indication that this species is patinate.

Occurrence. Upper Mimer Valley Series; Givetian.

Archaeozonotriletes meandricus sp. nov.

Plate 100, figs. 13, 14

Diagnosis. Miospores trilete, amb circular. Laesurae straight, length $\frac{1}{2}$ – $\frac{3}{4}$ spore radius, accompanied by distinctive, smooth, sinuous, elevated lips, which increase markedly in width equatorially (total width at polar end 4–8 μ , at equatorial end 21–26 μ), length $\frac{2}{3}$ – $\frac{3}{4}$ spore radius. Exine probably one-layered, 4–9 μ thick equatorially and distally, thinning proximally, coarsely infra-granulate, laevigate (punctate in corroded specimens). Contact areas depressed, radial diameter 26–50 μ , bounded by distinct, low, curvatural ridges.

Dimensions. (Eighteen specimens) Equatorial diameter 82–173 μ (mean 117 μ).

Holotype. Preparation KA 209/2, 35.7 88.6, K519, N316.

Locus typicus. West Odellfjellet, North Dicksonland, Spitsbergen; Lower Mimer Valley Series, Lower Eifelian.

Description. Holotype 137 μ . Laesurae straight, lips totalling 5 μ wide proximally, 24 μ wide equatorially, length two-thirds spore radius, extending beyond the contact areas. Radial diameter of contact areas 40–42 μ .

Comparison. The very distinctive sinuous lips which increase in thickness equatorially, separate *A. meandricus* sp. nov. from other laevigate, patinate species.

Occurrence. Upper Reuterskiøldfjellet Sandstone, and Lower Mimer Valley Series; Emsian and Eifelian.

Genus THOLISPORITES Butterworth and Williams 1958

Type species. *Tholisporites scoticus* Butterworth and Williams 1958.

Tholisporites ancyclus sp. nov.

Plate 101, figs. 1–7

Diagnosis. Miospores trilete; amb subcircular to roundly triangular, with convex sides and broadly rounded apices, occasionally oval. Laesurae straight, length $\frac{1}{3}$ – $\frac{2}{3}$ spore radius, rarely accompanied by lips. Exine two-layered; the inner layer (? intexine) 2–5 μ thick, homogeneous, proximally minutely granulose, distally laevigate (seen only when the outer layer is absent); outer layer (? exoexine) laevigate, patinate, equatorially 4–18 μ wide, decreasing in thickness towards the distal pole, extends proximally only a short distance, its maximum extension being in the radial regions. The outer patinate layer is corroded in all specimens, and probably because of its structure, corrodes in a constant pattern, giving the spores a 'sculptured' appearance. Equatorially the corroded patina appears as large broadly rounded segments, and distally as irregular, partly anastomosing ridges, often radially directed.

Dimensions. (Twenty-one specimens) Overall equatorial diameter 80–116 μ (mean 94 μ), diameter of the inner layer 64–100 μ (mean 78 μ). Maximum proximal enclosure of the inner layer by the outer layer, radially 18 μ , inter-radially 6 μ .

Holotype. Preparation KA 240/2, 50·2 100·6, K582, N321.

Locus typicus. Manchesterbreen Spur, Central Dicksonland, Spitsbergen; Lower Mimer Valley Series; Upper Emsian.

Description. Holotype roundly triangular, with broadly rounded apices and convex sides, overall diameter 96 μ , diameter of inner layer 80 μ . Laesurae indistinct, length approximately one-third of spore radius. Inner layer 2 μ thick, outer layer equatorially approximately 16 μ thick, absent from the distal pole, where the laevigate inner layer can be seen. Proximal overlap of the outer layer 12 μ radially, 3 μ inter-radially.

Remarks. The author regards the 'sculpturing' as the effect of corrosion of a finely punctate exine rather than a true sculptural pattern primarily for two reasons. The considerable variation in the size of the 'sculptural' elements, being much larger and less numerous in the best preserved specimens (Pl. 101, fig. 5) suggesting further breakdown of the exinal layer with increased corrosion. True sculptural elements in miospores are frequently more homogeneous than the exine which supports them, and with corrosion they tend to become shorter and rounder, rather than breaking up into more numerous elements as in *Tholisporites ancyclus* sp. nov. If these were true sculptural elements, it is unlikely that they would extend completely to the base of the outer exinal layer, as demonstrated in the sections (Pl. 101, figs. 3, 4).

The corrosion pattern occurs in all specimens, and is a morphological feature easily recognizable, and is here included in the diagnosis. Sections (Pl. 101, figs. 3, 4) show the distal and proximo-equatorial extension of the outer layer. The outer layer occasionally breaks away from the inner layer.

Occurrence. Dicksonfjorden Sandstone, Reuterskiøldfjellet Sandstone, and Lower Mimer Valley Series; Emsian and Eifelian.

Genus CYMBOSPORITES gen. nov.

Type species. *Cymbosporites cyathus* sp. nov.

Diagnosis. Miospores trilete; amb circular, subcircular, to roundly triangular. Laesurae long, usually accompanied by lips. Exine thin proximally, equatorially and distally patinate, the patina of even thickness, or with its greatest thickness in the distal polar region. Patina variably sculptured with cones, spines, and granules.

Comparison. *Archaeozonotriletes* (Naumova) emend, has a laevigate or punctate patina. *Tholisporites* Butterworth and Williams 1958 has its greatest thickness equatorially, and is laevigate or with very small sculptural elements.

Derivation of name: L. *cymba* (Gr. *kymbe*)—cup, bowl.

Cymbosporites cyathus sp. nov.

Plate 101, figs. 8–11

Diagnosis. Miospores trilete; amb subcircular to roundly triangular with convex sides and broadly rounded apices, conformable with the central area outline. Laesurae

straight often indistinct, extending full central area radius, accompanied by smooth, elevated lips, individually 0.5–3 μ wide, 2–5 μ high. Exine proximally 1–3 μ thick, equatorially and distally patinate, 8–12 μ thick, homogeneous to finely infra-granulate. Proximal surface laevigate; patina supporting a variable concentration of cones, 2–5 μ wide, 1–5 μ high, often supporting a small apical spine; where densely packed, the cones have polygonal bases. Arcuate folding of the proximal exine at the central area margin is very common.

Dimensions. (Twenty-four specimens) Equatorial diameter 53–80 μ (mean 63 μ).

Holotype. Preparation KA 287/2, 55.2 94.0, K846, N326.

Locus typicus. Estheriahaugen, Central Dicksonland, Spitsbergen; Estheriahaugen Formation, Givettian.

Description. Holotype subcircular, diameter 61 μ . Laesurae indistinct, accompanied by narrow lips, individually 0.5 μ wide. Exine very thin proximally, patina equatorially 12 μ thick; patina densely covered with cones, 3–5 μ wide, 2–5 μ high, often with polygonal bases.

Remarks. The very thin proximal exine often sags into the 'cup-shaped' patina, resulting in arcuate folding along the central area margin.

Comparison. It is difficult to make exact comparisons with Russian species of similar appearance in proximo-distal aspect; unless mentioned in the description, or illustrated in oblique aspect, these species may appear cingulate. Many of the Russian species may in fact be patinate rather than cingulate. *Archaeozonotriletes famennensis* Naumova 1953 (p. 117, pl. 17, figs. 31–34) is probably of similar construction, but is smaller, and has lips which extend on to the thicker equatorial exine. *A. pustulatus* Naumova 1953 (p. 35, pl. 3, fig. 10) is smaller, lacks lips, and has a sparser ornament. *A. decorus* Naumova 1953 (p. 35, pl. 3, figs. 11, 12) lacks lips, and the equatorial exine is thicker. *Lepidozonotriletes subtriquetrus* (Luber, in Luber and Waltz 1941) Luber 1955 (pl. 5,

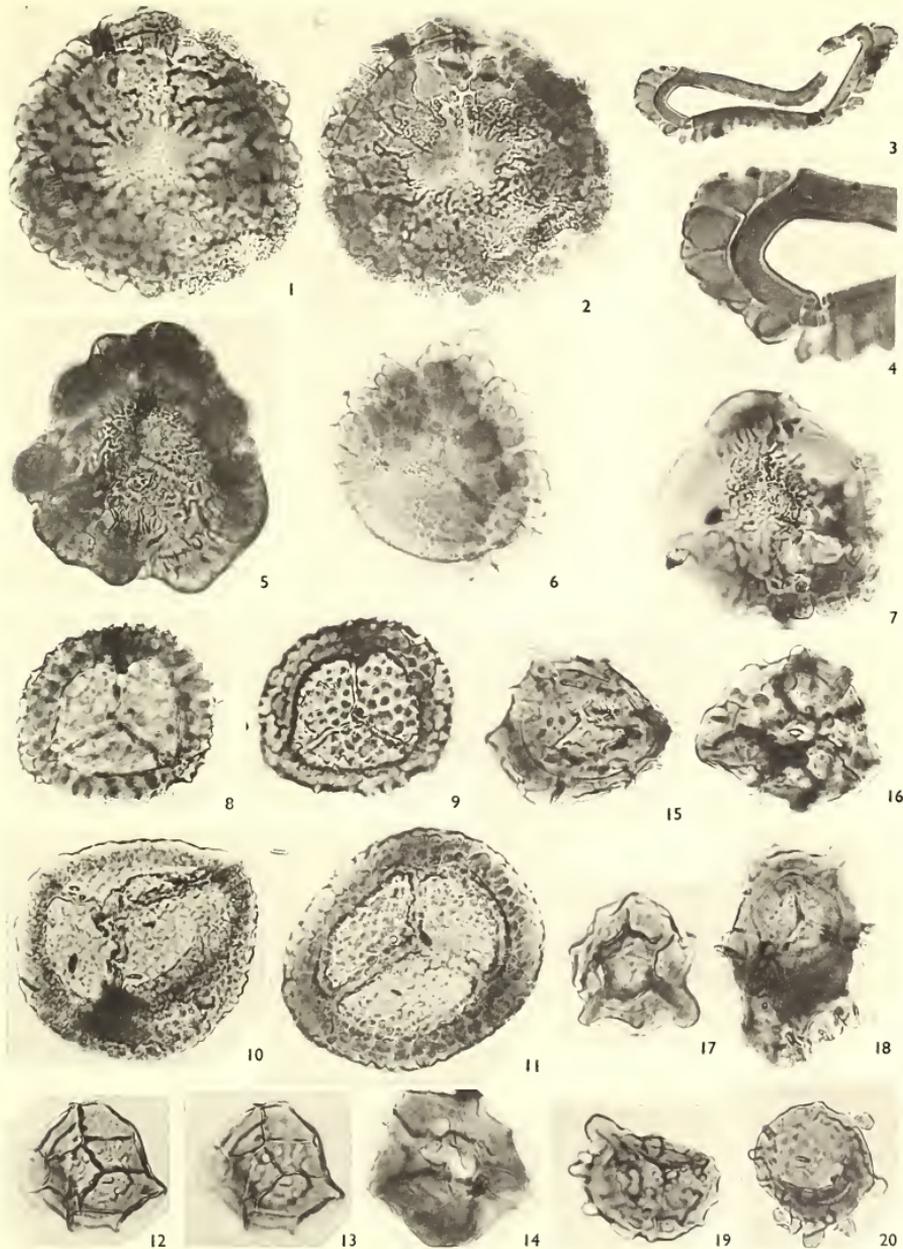
EXPLANATION OF PLATE 101

All figures $\times 500$, unless otherwise stated; from unretouched negatives.

Figs. 1–7. *Tholisporites ancylus* sp. nov. 1, 2, Holotype, proximal and distal surfaces respectively, the proximal view shows the extent of the outer layer; KA 240/2, 50.2 100.6, K582, N321. 3, Section showing extent of the outer layer; KA 274/S3, 24.2 94.8, K872, N322. 4, ($\times 1000$) the same. 5, Corrosion pattern; KA 202/5, 30.6 92.2, K555, N323. 6, Pseudo-ornament of verrucae formed by corrosion of the patina; KA 271/3, 23.8 87.8, K897, N324. 7, Corrosion pattern, much of the outer layer has corroded away; KA 274/6, 52.7 104.2, K872, N325.

Figs. 8–11. *Cymbosporites cyathus* gen. et sp. nov. 8, 9, Holotype, proximal and distal surfaces respectively; KA 287/2, 55.2 94.0, K846, N326. 10, Proximal oblique aspect, showing patina and distal sculpture; KA 293/1, 42.5 94.5, K556, N327. 11, Proximal surface; KA 243/3, 23.4 95.7, K767, N328.

Figs. 12–20. *Chelinospora concinna* gen. et sp. nov. 12, 13, Holotype, proximal and distal surfaces respectively, KA 293/1, 31.7 91.2, K556, N331. 14, Paratype, proximal oblique aspect, showing patina; KA 286/1, 50.3 105.0, K773, N332. 15, 16, Specimens showing proximally reduced sculpture; KA 243/2, 35.6 106.3, K767, N333, and KA 243/2, 55.0 90.0, K767, N334 respectively. 17, Distal surface; KA 243/1, 54.8 96.5, K767, N335. 18, Lateral view showing very thick corroded patina; KA 293/1, 26.9 90.7, K556, N336. 19, 20, Specimens showing corrosion of the patina; KA 243/2, 24.8 103.5, K767, N337, and KA 293/1, 35.4 89.7, K556, N338 respectively.



ALLEN, Lower and Middle Devonian miospores

figs. 94 and 95) is smaller, and is probably cingulate. *Lycospora magnifica* McGregor 1960 (p. 35, pl. 12, fig. 5, pl. 13, figs. 2-4) is considerably larger, and has some fusion of the basal ornament.

Occurrence. Upper Mimer Valley Series; Givetian.

Cymbosporites catillus sp. nov.

Plate 100, figs. 11-12

Diagnosis. Miospores trilete; amb circular, subcircular to roundly triangular, with moderately convex sides and broadly rounded apices, conformable with the central area outline. Laesurae straight, often indistinct, extend almost to the central area margin, accompanied by smooth, slightly elevated lips, individually 0.5-2 μ wide. Exine proximally 1-2 μ thick, distally and equatorially patinate, 6-9 μ thick, homogeneous. Proximal surface laevigate, patina sculptured with densely packed granules or small verrucae, 1.5 μ or less in height. Frequent arcuate folding of the thin proximal exine occurs at the central area margin.

Dimensions. (Thirty-five specimens) Equatorial diameter 34-50 μ (mean 40 μ).

Holotype. Preparation KA 287/2, 34:1 94:2, K846, N329.

Locus typicus. Estheriahaugen; Central Dicksonland, Spitsbergen; Estheriahaugen Formation, Givetian.

Description. Holotype roundly triangular, with convex sides and broadly rounded apices, diameter 44 μ . Laesurae indistinct, accompanied by lips, individually 0.5 μ wide. Exine very thin proximally, equatorial patina 7 μ thick, patina densely covered with granules.

Remarks. Specimens in oblique aspect clearly demonstrate the nature of the uniform distal patina. As in *Cymbosporites cyathus* sp. nov. the thin proximal surface sags into the 'cup-shaped' patina, resulting in arcuate folding of the proximal surface at the central area margin, which tends to support the thin proximal wall at this point.

Comparison. *Cymbosporites cyathus* sp. nov. (Pl. 101, figs. 8-11) is larger, and has an ornament of cones. Several Russian species included within *Archaeozonotriletes* and *Retusotriletes* have a similar proximo-distal appearance, descriptions make it difficult to interpret their construction, which may be patinate, cingulate, or thick-walled apiculate. Below are listed species with somewhat similar proximo-distal appearance, size range, and sculptural elements, which may prove to have a patinate construction similar to *C. catillus* sp. nov.:

Retusotriletes verrucosus Kedo 1955, p. 22, pl. 1, fig. 17.

Archaeozonotriletes basilaris Naumova 1953, p. 81, pl. 13, fig. 16; p. 33, pl. 3, fig. 30; p. 128, pl. 19, fig. 8.

Retusotriletes accuratus Chibrikova 1959, p. 51, pl. 5, fig. 6.

Archaeozonotriletes subpusillus Chibrikova 1959, p. 61, pl. 8, fig. 2.

Archaeozonotriletes truncatus Naumova 1953, p. 34, pl. 3, fig. 7.

Occurrence. Upper Mimer Valley Series, particularly common in shale samples; Givetian.

Genus *CHELINOSPORA* gen. nov.

Type species. Chelinospora concinna sp. nov.

Diagnosis. Miospores trilete; amb circular to roundly triangular. Laesurae distinct, usually long, simple or accompanied by narrow folds. Exine one or two-layered, acavate, thin proximally, equatorially and distally patinate, the patina may be of even thickness, or with its maximum thickness either equatorially or distally. Patina reticulate or foveoreticulate, contact areas laevigate or with a reduced sculpture of muri, granules, and cones.

Comparison. Differs from other patinate genera in having a reticulate or foveoreticulate patina.

Derivation of name. Gr. *Chelinos*—netted.

Chelinospora concinna sp. nov.

Plate 101, figs. 12–20

Diagnosis. Miospores trilete; amb circular to subcircular, conformable with the central area outline. Laesurae distinct to discernible, straight, length three-quarters to full central area radius, simple or accompanied by low, smooth, narrow lips, less than $1\ \mu$ wide. Exine homogeneous to infra-punctate, equatorially $3\text{--}12\ \mu$ thick (including muri), proximal oblique aspect $2\text{--}5\ \mu$ thick, distal surface variably patinate $5\text{--}32\ \mu$ thick, the patina is usually thickest in the distal polar region, and occasionally extends on to the proximal surface. Contact areas support a sparse ornament of small verrucae or granules, $2\ \mu$ or less in width and height, and less frequently rugulae or muri, $4\text{--}6\ \mu$ long, $0\cdot5\text{--}2\ \mu$ wide. Patina coarsely reticulate, muri $0\cdot5\text{--}2\ \mu$ wide, $1\text{--}4\ \mu$ high, enclosing large polygonal to irregularly rounded lumina $5\text{--}22\ \mu$ in longest diameter.

Dimensions. (Thirty specimens) Equatorial diameter $32\text{--}54\ \mu$ (mean $41\ \mu$), polar diameter $36\text{--}74\ \mu$.

Holotype. Preparation KA 293/1, 31·7 91·2, K556, N331.

Paratype. Preparation KA 286/1, 50·3 105·0, K773, N332.

Locus typicus. North ridge of Kinanderfjellet, Central Dicksonland, Spitsbergen; Upper Mimer Valley Series, Givetian.

Description. Holotype subcircular, equatorial diameter $48\ \mu$. Laesurae straight, length three-quarters central area radius, accompanied by narrow lips. Exine $6\text{--}11\ \mu$ thick equatorially (including muri), patina thins abruptly on the proximal surface. Contact areas with a sparse ornament of verrucae and granules $2\ \mu$ or less wide, distal muri $1\ \mu$ or less wide, $2\ \mu$ high, lumina 10 to $22\ \mu$ in longest diameter.

Paratype in oblique aspect, proximally $2\text{--}3\ \mu$ thick, distally $12\text{--}13\ \mu$ thick. Laesurae straight, length two-thirds spore radius. Muri $1\ \mu$ wide, approximately $1\ \mu$ high, lumina $10\text{--}24\ \mu$ wide. Reduced muroid ridges proximally.

Remarks. There is considerable variation in width of the patina, thickness of muri and size of lumina. Corrosion of the reticulum and patina is common, giving spores an unusual appearance (Pl. 101, figs. 19, 20).

Comparison. *Knoxisporites reticulatus* Vigran 1964 (p. 22, pl. 1, figs. 10–12; pl. 2, figs. 8, 9) is similar but has a laevigate proximal surface. *Verrucosisporites variabilis* McGregor 1960 (p. 30, pl. 11, fig. 15) resembles ill-preserved specimens, in which the patina has broken down, and the variable ornament recorded, including large flat-topped elements, may be the result of a corroded patina. However, there is no mention by McGregor of any reticulate sculpture. *Archaeozonotriletes strangulatus* Naumova 1953 (p. 73, pl. 11, figs. 22, 23) is subtriangular, has shorter laesurae, is proximally laevigate, and there is no mention of variable exine thickness.

Occurrence. Mimer Valley Series; Givetian and probable Upper Eifelian.

Chelinospora ligurata sp. nov.

Plate 102, figs. 1–7

Diagnosis. Miospores trilete; amb circular to roundly triangular, with convex sides and broadly rounded apices. Laesurae simple, straight, length three-quarters to full central area radius. Exine at least in some specimens two-layered; intexine 1–2 μ thick, homogeneous; exoexine homogeneous to infra-punctate, proximally thin, distally patinate 10–21 μ thick (including muri), maximum thickness either equatorially or in the distal polar region; the patina occasionally extends on to the proximal surface, where it may thin gradually or abruptly. Proximal surface laevigate or with a sparse ornament of small verrucae or cones, 2 μ or less in height and basal diameter; patina with a high indistinct reticulum, muri 1–3 μ wide, 2–7 μ high, lumina 4–9 μ wide.

Dimensions. (Thirty specimens) Equatorial diameter 42–70 μ (mean 55 μ).

Holotype. Preparation KA 243/2, 53.5 91.0, K767, N339.

Locus typicus. East Munindalen, Central Dicksonland, Spitsbergen; Plantekløfta Conglomerate, probable Upper Givetian.

Description. Holotype roundly triangular, diameter 58 μ . Laesurae equal full central area radius. Intexine indistinct; exoexine proximal surface sparsely sculptured with small cones and verrucae 1–2 μ in height and basal diameter, equatorially patina 10 μ wide (excluding muri), muri 2–3 μ wide, 5–6 μ high; distal reticulate pattern indistinct.

Remarks. Corrosion in the majority of specimens results in both the reticulum and the patina breaking down, giving the spore a very distinctive 'sculptured' appearance of high, close bacula (Pl. 102, figs. 6, 7).

Comparison. *Chelinospora concinna* sp. nov. (Pl. 101, figs. 12–20) has a coarser, lower reticulum.

Occurrence. Fiskekløfta Formation, Planteryggen Sandstone, and Plantekløfta Conglomerate; probable Upper Givetian.

Chelinospora perforata sp. nov.

Plate 102, figs. 8–10

Diagnosis. Miospores trilete; amb roundly triangular, to subcircular, conformable with the central area outline. Laesurae straight, length three-quarters to full central area radius, accompanied and frequently obscured by smooth, narrow lips, individually 0.5–

2 μ wide. Exine infra-granulate, thin proximally, distally patinate, equatorially 11–17 μ thick, gradually thinning towards the distal pole. Contact areas laevigate, patina foveoreticulate, fovea 2–6 μ in longest diameter, circular, oval, or occasionally irregular, 1–5 μ apart.

Dimensions. (Sixteen specimens) Equatorial diameter 58–86 μ (mean 71 μ).

Holotype. Preparation KA 272/2, 30.0 97.6, C626, N344.

Locus typicus. Huginaspiskardet, Central Dicksonland, Spitsbergen; Lower Mimer Valley Series, Lower Eifelian.

Description. Holotype roundly triangular, diameter 58 μ . Laesurae length two-thirds of spore radius, lips each 1–5 μ wide. Equatorial patina 11 μ thick. Fovea 2–5 μ in longest diameter.

Comparison. *Perforosporites robustus* Scott and Rouse 1961 (p. 978, pl. 113, figs. 1–6, pl. 114, figs. 1–5) is smaller, lacks lips, is frequently sculptured with papillae, and lacks a patina.

Occurrence. Upper Reuterskiøldfjellet Sandstone, and Lower Mimer Valley Series; Emsian and Eifelian.

Subsuperturma PERINOTRILITI (Erdtman) Dettman 1963
Genus AURORASPORA Hoffmeister, Staplin, and Malloy

Type species. *Auroraspora solisortis* Hoffmeister, Staplin, and Malloy 1955.

Auroraspora macromanifestus (Hacquebard) Richardson 1960

Dimensions. (Six specimens) Diameter of exoxine 192–216 μ ; diameter of intexine 107–26 μ .

Occurrence. Fiskekløfta Formation and Planteryggen Sandstone; Upper Givetian.

Genus PEROTRILITES (Erdtman) ex Couper 1953

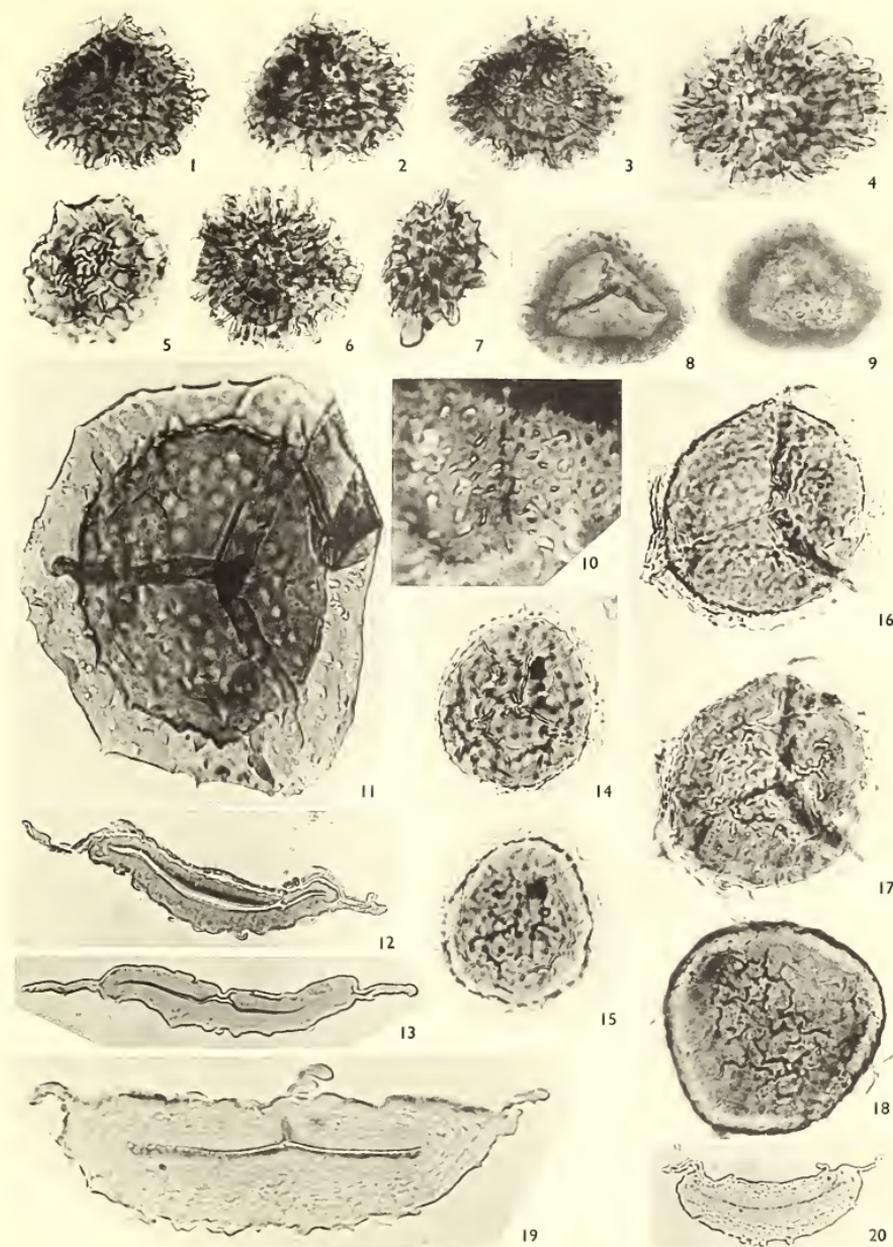
Type species. *Perotrilites granulatus* Couper 1953.

EXPLANATION OF PLATE 102

All figures $\times 500$ unless otherwise stated; from unretouched negatives.

Figs. 1–10. *Cheliospora* spp. 1–7. *C. ligurata* sp. nov. 1–3, Holotype, proximal, sectional and distal foci; KA 243/2, 53.5 91.0, K767, N339. 4, Proximal oblique aspect, showing thick corroded patina; KA 243/1, 41.8 105.3, K767, N340. 5, Showing distal reticulum; KA 243/2, 46.8 91.8, K767, N341. 6, 7, Corroded specimens; KA 243/1, 26.0 96.4, K767, N342, and KA 243/3, 35.8 107.5, K767, N343 respectively. 8–10. *C. perforata* sp. nov. 8, 9, Holotype; proximal and distal surfaces respectively, KA 272/2, 30.0 97.6, C626, N344. 10, ($\times 1000$) detail of distal foveo-reticulate exine; KA 271/3, 37.9 109.3, K897, N345.

Figs. 11–20. *Perotrilites* spp. 11–13. *P. eximius* sp. nov. 11, Holotype, proximal surface; KA 295/M4, 49.2 96.1, K922, N346. 12, Section showing the three-layered sclerine; KA 258/S2, 22.8 92.1, K922, N347. 13, Section showing outer sculptine only partly separate from inner sculptine; KA 258/S3, 28.5 90.2, K922, N348. 14–15. *P. pannosus* sp. nov. Holotype, proximal and distal surfaces respectively; KA 243/1, 29.2 96.6, K767, N353. 16–20. *P. ergatus* sp. nov. 16, 17, Holotype, proximal and distal surfaces respectively; KA 261/4, 53.0 98.5, K891, N349. 18, Showing distal muroid fold pattern; KA 290/5, 54.9 103.6, K681, N350. 19, 20, Sections showing the very thick inner sculptine; 19, ($\times 1000$) KA 290/S8, 30.8 106.4, K681, N351. 20, KA 290/S9, 35.0 99.5, K681, N352.



Discussion. The species listed below are included within *Perotrilites* (Erdtman) ex Couper 1953, on the basis that they possess a thin homogeneous or finely infra-granulate outer layer, in comparison with the much thicker infra-granulate inner layer. As the exact nature of this outer layer is not known (it may in fact be an outer exoexine layer), the term perine is not used, and the terms inner and outer sculptine (Erdtman 1952, p. 468) are employed for these two layers. Where an intexine is also demonstrated, the term sclerine (Erdtman 1952, p. 468) is used for all three layers. The cavity occurs between the outer and inner sculptine, and not between the inner sculptine and intexine. Sectioned species included in *Grandispora* (Pl. 103, fig. 9) and *Calyptosporites* (Pl. 103, fig. 11), show an exoexine and intexine of approximately equal thickness.

Perotrilites eximius sp. nov.

Plate 102, figs. 11–13

Diagnosis. Miospores trilete; cavate; amb and inner sculptine outline convexly triangular to circular. Laesurae straight, short, length $\frac{1}{3}$ – $\frac{2}{3}$ central area radius, often accompanied and exceeded equatorially by triradiate folds of the outer sculptine, total width 4–12 μ . Exine three-layered; intexine thin, 0.5–1.5 μ , homogeneous, closely appressed to the inner sculptine, and seen only in sections; inner sculptine 4–9 μ thick, homogeneous to finely infra-granulate, laevigate; outer sculptine 1–2.5 μ thick, homogeneous. Proximal surface laevigate, distal surface supporting a variable ornament of cones and occasional spines, 3–7 μ wide, 4–8 μ high, the majority of cones supporting a smaller apical cone or bifurcate-tipped spine. Proximal surface often with numerous minor folds.

Dimensions. (Forty-four specimens) Diameter of outer sculptine 80–160 μ ; diameter of inner sculptine 52–105 μ (mean 90 μ).

Holotype. Preparation KA 295/M4, 49.2 96.1, K922, N346.

Locus typicus. South Mimerdalen, Central Dicksonland, Spitsbergen; Reuterskiöldfjellet Sandstone, Emsian.

Description. Holotype roundly triangular, outer sculptine diameter 136 μ ; inner sculptine diameter 102 μ . Laesurae approximately half inner sculptine radius, elevated lips 11 μ high, length four-fifths spore radius. Inner sculptine 9 μ thick, outer sculptine 2 μ thick. Distal cones 3–6 μ wide, 3–8 μ high, somewhat smaller on the outer sculptine extension.

Remarks. The section (Pl. 102, fig. 12) clearly shows the three-layered sclerine, composed of an intexine and an inner and outer sculptine. Although the outer sculptine is not diaphanous, the thick inner sculptine is undoubtedly an exoexinal layer, and the species is included within *Perotrilites* (Erdtman) ex Couper 1953, on the basis of having a much thinner layer outside this exoexinal layer.

Occurrence. Dicksonfjorden Sandstone, Upper Reuterskiöldfjellet Sandstone, and Lower Mimer Valley Series; Emsian and Eifelian.

Perotrilites ergatus sp. nov.

Plate 102, figs. 16–20

Diagnosis. Miospores trilete; cavate; amb and inner sculptine outline convexly triangular to circular. Laesurae straight, length $\frac{2}{3}$ – $\frac{4}{5}$ central area radius, usually obscured by

triradiate folds of the outer sculptine, totalling 1–2 μ wide, 2–7 μ high, extending to the equatorial margin. Inner sculptine inter-radially 6–10 μ thick, radially 4–7 μ thick, coarsely infra-granulate, laevigate; outer sculptine 1–2 μ thick, homogeneous to finely infra-granulate, extends 4–14 μ beyond the inner sculptine, proximally laevigate, distally supporting a sparse ornament of cones, 1–3 μ in height and basal diameter. Distal surface frequently with small muroid folds, 1–3 μ wide, occasionally anastomosing as an imperfect reticulum.

Dimensions. (Thirty-two specimens) Diameter of outer sculptine 71–124 μ (mean 91 μ); diameter of inner sculptine 60–108 μ (mean 79 μ).

Holotype. Preparation KA 261/4, 53-0 98-5, K891, N349.

Locus typicus. Estheriahaugen, Central Dicksonland, Spitsbergen; Fiskekløfta Formation, Givetian.

Description. Holotype amb and inner sculptine roundly triangular, outer sculptine diameter 84 μ , inner sculptine diameter 69 μ . Laesurae length three-quarters inner sculptine radius. Inner sculptine 4 μ thick radially, 8 μ thick inter-radially, outer sculptine 1–2 μ thick. Distal surface with occasionally anastomosing muroid folds.

Remarks. Sections (Pl. 102, figs. 19, 20) show clearly the cavate nature of the sculptine, the thick infra-granulate inner sculptine, and the triradiate folds. It is not certain from the strongly compressed sections whether an intexine is present as seen in *Perotrilites eximius* sp. nov. (Pl. 102, fig. 12).

Comparison. *Perotrilites eximius* sp. nov. (Pl. 102, figs. 11–13) has much larger sculptural elements, and a uniformly thick inner sculptine. *Diaphanospora* sp. Balme and Hassell 1962 (p. 22, pl. 4, figs. 8, 9) is smaller, and has a laevigate outer sculptine. *Archaeozonotrilites arduus* Archangelskaya 1963 (p. 23, pl. 8, figs. 1–5) has a thicker distal surface, and the muroid folds are in the contact areas and not proximo-equatorial and distal.

Occurrence. Dicksonfjorden Sandstone, Upper Reuterskioldfjellet Sandstone, and Mimer Valley Series; Emsian to Givetian.

Perotrilites pannosus sp. nov.

Plate 102, figs. 14, 15

1964 *Perotrilites* cf. *perinatus* Vigran, p. 19, pl. 3, figs. 7, 8.

Diagnosis. Miospores trilete; cavate; amb and inner sculptine outline convexly triangular to circular. Laesurae straight, $\frac{3}{8}$ – $\frac{4}{5}$ central area radius, usually masked by triradiate folds of the outer sculptine, totalling 2–3 μ wide, 2–5 μ high. Inner sculptine 3–5 μ thick, infra-granulate, laevigate; outer sculptine 1–2 μ thick, homogeneous, loose-fitting. Contact areas laevigate, proximo-equatorial and distal surfaces with a distinct pattern of muroid folds, 0.5–2 μ wide, which may be arcuate, or anastomosing to form an imperfect reticulum. Distal surface with a sparse ornament of small cones, 1–2.5 μ in height and basal diameter, the cones frequently support a small apical spine.

Dimensions. (Forty-one specimens) Diameter of outer sculptine 40–74 μ (mean 62 μ); diameter of inner sculptine 37–64 μ (mean 54 μ).

Holotype. Preparation KA 243/1, 29-2 96-6, K767, N353.

Locus typicus. East Munindalen, Central Dicksonland, Spitsbergen; Plantekløfta Conglomerate, probable Upper Givetian.

Description. Holotype amb and inner sculptine outline subcircular, outer sculptine diameter $63\ \mu$, inner sculptine diameter $56\ \mu$. Laesurae straight, length half inner sculptine radius, triradiate folds $\frac{1}{2}$ – $\frac{2}{3}$ outer sculptine radius. Muroid folds on proximo-equatorial and distal surfaces, forming an imperfect reticulum. Distal cones 1 – $2\ \mu$ wide, 1 – $2.5\ \mu$ high.

Comparison. *Perotrilites bifurcatus* Richardson 1962 (p. 174, pl. 25, figs. 4, 5, text-fig. 3) is considerably larger, has a larger ornament of spines and the outer sculptine is not folded in a definite pattern. *Perotrilites* sp. McGregor 1960 (p. 35, pl. 12, fig. 8) has a granulate outer sculptine. *Diaphanospora riciniata* Balme and Hassell 1962 (p. 22, pl. 4, figs. 1–4; text-fig. 5) has a laevigate outer sculptine, and a cingulate inner sculptine. *Perotrilites ergatus* sp. nov. (Pl. 102, figs. 16–20) is larger and lacks a uniformly thick inner sculptine.

Occurrence. Dicksonfjorden Sandstone, Upper Reuterskiöldfjellet Sandstone, and Mimer Valley Series; Emsian to Givetian.

Genus GRANDISPORA Hoffmeister, Staplin, and Malloy 1955

Type species. *Grandispora spinosa* Hoffmeister, Staplin, and Malloy 1955.

Grandispora diamphida sp. nov.

Plate 103, figs. 1–6

Diagnosis. Miospores trilete; cavate; amb and intexine outline circular to subcircular. Laesurae straight, often indistinct, length three-quarters to full radius of the intexine, accompanied and usually masked by narrow elevated lips, 0.5 – $2\ \mu$ wide, 10 – $26\ \mu$ high, extending on to the exoexinal extension, frequently reaching the equatorial margin and occasionally separating equatorially. Intexine 1 – $4\ \mu$ thick, finely infra-granulate. Exoexine 2 – $4\ \mu$ thick, infra-granulate, proximal surface laevigate, distal surface sculptured with cones and spines of variable shape, 3 – $6\ \mu$ wide basally, 3 – $10\ \mu$ high, the cones are often flask-shaped, and may possess a small bifurcate tip. The cones and spines are often more concentrated on the exoexinal extension.

Dimensions. (Twenty-three specimens) Diameter of exoexine 67 – $90\ \mu$ (mean $75\ \mu$); diameter of intexine 54 – $66\ \mu$ (mean $59\ \mu$).

Holotype. Preparation KA 281/5, 55.3 98.8, K850, N354.

Locus typicus. Estheriahaugen, Central Dicksonland, Spitsbergen; Reuterskiöldfjellet Sandstone, Emsian.

Description. Holotype circular, exoexine diameter $71\ \mu$, intexine diameter $55\ \mu$. Laesurae indistinct, raised lips $1.5\ \mu$ wide, $8\ \mu$ high, separating equatorially and extending to the equatorial margin. Distal spines and cones 3 – $5\ \mu$ wide, 3 – $6\ \mu$ high; few cones have a small bifurcate tip.

Remarks. *Grandispora diamphida* sp. nov. resembles species of *Calyptosporites* Richardson 1962 in having cones and spines with bifurcate tips; but is here assigned to *Grandispora* Hoffmeister, Staplin, and Malloy on the basis of its smaller size and circular outline.

Comparison. *Hymenozonotrites polyacanthus* Naumova 1953 (p. 41, pl. 4, figs. 11, 12) has similar ornament, but appears to possess a bizonate cingulum.

Occurrence. Upper Reuterskiøldfjellet Sandstone, and Lower Mimer Valley Series; Emsian and Eifelian.

Grandispora inculta sp. nov.

Plate 103, figs. 7-9

Diagnosis. Miospores trilete; cavate; amb and intexine outline subcircular to roundly triangular. Laesurae indistinct, length $\frac{1}{3}$ – $\frac{2}{3}$ intexine radius, accompanied and frequently masked by smooth, narrow lips, total width 1–4 μ , 2–6 μ high, extending one-third to full radius of the exoexine. Intexine 1.5–3 μ thick, infra-granulate, laevigate, rarely folded; exoexine 1–3 μ thick, homogeneous to infra-granulate, often folded. Proximal surface laevigate, distal surface densely covered with cones 1–2 μ in height and basal diameter. Minor folds frequent on the exoexine.

Dimensions. (212 specimens) Diameter of exoexine 51–86 μ (mean 70 μ); diameter of intexine 34–63 μ (mean 49 μ).

Holotype. Preparation KA 261/4, 39-6 88-8, K891, N359.

Locus typicus. Estheriahaugen, Central Dicksonland, Spitsbergen; Fiskekløfta Formation, Givetian.

Description. Holotype amb roundly triangular, exoexine diameter 72 μ , intexine outline subcircular, diameter 42 μ . Laesurae indistinct, lips individually 1–1.5 μ wide, length of two lips one-third of exoexine radius, the third extending almost to the exoexinal margin. Distal cones 1–2 μ in height and basal diameter.

Remarks. The section (Pl. 103, fig. 9) demonstrates the cavate nature of the exine, the approximately equal thickness of the exoexine and intexine, and the exclusively distal ornament. The short laesurae and infra-granulate nature of the intexine is well seen in broken specimens or where the exoexine is removed.

Comparison. *Zonotrites explanatus* Lubert, in Lubert and Waltz 1941 (p. 10, pl. 1, fig. 4) has 'the entire surface of the exine covered with small tubercles', but is otherwise similar, although it may not be cavate. *Hymenozonotrites brevimanus* Naumova 1953 (p. 39, pl. 4, fig. 3) has a verrucose ornament. *Spore number 4* Apiculatozonales Group Thompson 1940, figured in Thompson 1952 (p. 10, fig. 14) is larger, and although the exine is clearly two-layered, it appears to have an equatorial flange.

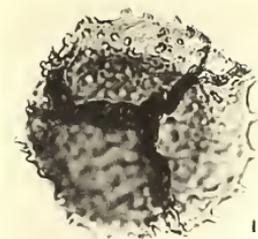
Occurrence. Upper Mimer Valley Series; Givetian.

EXPLANATION OF PLATE 103

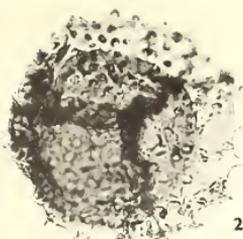
All figures $\times 500$ unless otherwise stated; from unretouched negatives.

Figs. 1–9. *Grandispora* spp. 1–6. *G. diamphida* sp. nov. 1, 2, Holotype, proximal and distal surfaces respectively; KA 281/5, 55-3 98-8, K850, N354. 3, Proximal surface; KA 281/5, 43-0 100-1, K850, N355. 4, Showing distal arcuate folds; KA 240/M1, 39-6 98-7, K582, N356. 5, 6, Sections showing raised lips and cavate exine; 5, KA 274/S7, 25-6 103-7, K872, N357. 6, ($\times 1000$) KA 274/S7, 43-4 88-9, K872, N358. 7–9. *G. inculta* sp. nov. 7, Holotype, sectional focus; KA 261/4, 39-6 88-8, K891, N359. 8, Distal surface; KA 261/1, 37-5 98-4, K891, N360. 9, Section showing cavate exine and exclusively distal sculpture; KA 290/S2, 59-3 93-6, K681, N361.

Figs. 10–11. *Calyptosporites proteus* (Naumova) comb. nov. 10, distal surface; KA 290/M1, 48-4 96-6, K681, N362. 11, Section showing cavate exine and exclusively distal sculpture; KA 290/S21, 34-5 91-6, K681, N363.



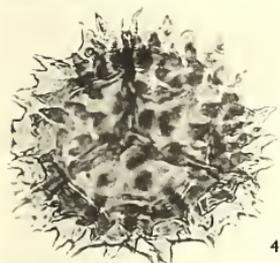
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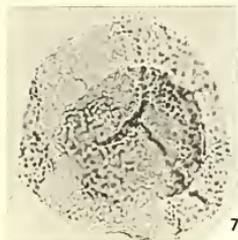
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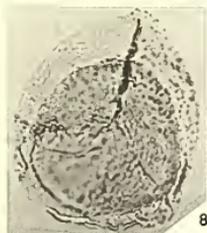
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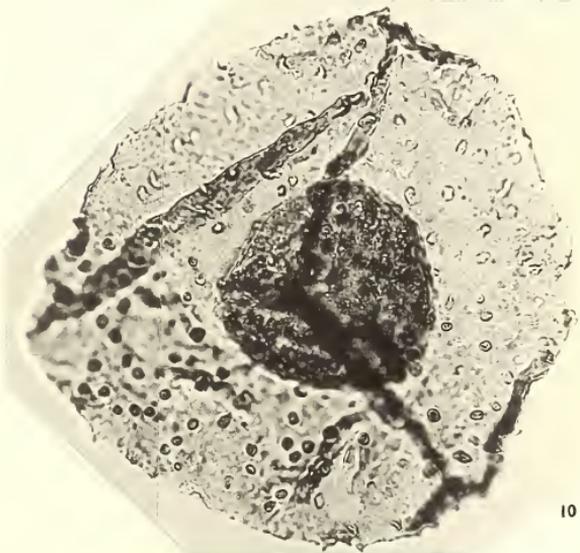
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11

Genus CALYPTOSPORITES Richardson 1962

Type species. Calyptosporites velatus (Eisenack) Richardson 1962.

Calyptosporites microspinosus (Richardson) emend. Richardson 1962

1960 *Cosmosporites microspinosus* Richardson, p. 53, pl. 14, figs. 5, 6.

1962 *Calyptosporites microspinosus* Richardson, p. 192.

Dimensions. (Fifteen specimens) Diameter of exoexine 216–301 μ (mean 264 μ); diameter of intexine 70–120 μ (mean 100 μ).

Remarks. Occasionally one or more of the lips are absent, presumably the result of compression or corrosion. Cone coverage is never dense, but in some corroded specimens as few as two cones are present. None of the Spitsbergen specimens exhibit the bifurcate tips noted by Richardson (p. 53).

Occurrence. Fiskekløfta Formation; Givetian.

Calyptosporites proteus (Naumova) comb. nov.

Plate 103, figs. 10, 11

1953 *Hymenozonotriletes proteus* Naumova, p. 40, pl. 14, fig. 5.

1955 *Hymenozonotriletes proteus* Naumova var. *eximius* Kedo, p. 31, pl. 4, fig. 3.

Description of specimens. Miospores trilete; cavate, amb subtriangular with moderately to strongly convex sides and acute to well-rounded apices, intexine outline roundly triangular to subcircular. Laesurae often indistinct, straight, length half to full intexine radius, usually masked by smooth, elevated lips, individually 2.5–6 μ wide, 4–9 μ high, length half to full exoexine radius. Intexine distinct, 1–4 μ thick, infra-granulate, laevigate; exoexine 2–4 μ thick, infra-granulate. Proximal surface laevigate, distal surface sculptured with cones 3–5 μ wide, 3–7 μ high, the rounded apices frequently supporting a small spine. The ornament is usually sparse, but is occasionally more dense. Distal folding of the exoexine frequent.

Dimensions. (Twenty-three specimens) Diameter of exoexine 110–170 μ (mean 144 μ); diameter of intexine 58–100 μ (mean 79 μ).

Remarks. Sections demonstrate the cavate nature of the spore, the absence of a limbus, the approximately equal thickness of the two exine layers, and the infra-granulate intexine.

Comparison. *Calyptosporites velatus* (Eisenack) Richardson 1962, p. 192, in Richardson 1960 (p. 52, pl. 14, fig. 4, text-fig. 3) has very similar dimensions, but has an ornament of much smaller cones, which have acute rather than rounded apices. *Hymenozonotriletes ventosus* Kedo 1957 (pl. 3, fig. 1) is much smaller. *Calyptosporites microspinosus* Richardson 1962 (p. 192) in Richardson 1960 (p. 53, pl. 14, figs. 5, 6) is considerably larger (the mean of the Spitsbergen specimens of *C. microspinosus* being over 100 μ greater than the mean of *C. proteus*).

Occurrence. Mimer Valley Series; Givetian and probably Upper Eifelian.

Calyptosporites optivus (Chibrikova) comb. nov.

Plate 104, figs. 1-4

1959 *Archaeozonotrilletes optivus* Chibrikova, p. 60, pl. 7, fig. 9.1960 *Retusotrilletes* sp. Taugourdeau-Lantz, p. 145, pl. 1, fig. 5.1964 *Biharisporites spitsbergensis* Vigran, p. 12, pl. 2, figs. 1-4.

Description of specimens. Megaspores trilete; cavate; amb and intexine outline sub-circular to roundly triangular, with convex sides and rounded apices. Laesurae straight, often indistinct, length three-quarters to full intexine radius, accompanied by smooth, elevated lips, individually 6-17 μ wide, 7-30 μ high, extending on to the exoexinal extension, and occasionally to the equatorial margin. Intexine 2-5 μ thick, homogeneous, laevigate; exoexine 3-5 μ thick, infra-granulate. Contact areas laevigate, proximo-equatorial and distal surfaces support an ornament of cones of very variable size and distribution 1-10 μ wide, 2-8 μ high; the ornament may be sparse, or closely packed and with polygonal bases, often supporting a small apical spine or cone. Arcuate folds 7-20 μ wide are usually present, which separate the raised contact area from the proximo-equatorial region; the intexine is positioned within this raised central region.

Dimensions. (Forty-five specimens) Diameter of exoexine 160-384 μ (mean 273 μ); diameter of intexine 112-230 μ (mean 160 μ).

Remarks. The section (Pl. 104, fig. 4) demonstrates the cavate nature of the spore, but not the proximal arcuate folds. This species is included within *Calyptosporites* on the basis of its large size, ornament of cones, and approximately equal thickness of the two exine layers. *Biharisporites* Potonié 1956 includes specimens with a very thin, membranous intexine (mesosporium).

Comparison. *Triletes* sp. A. Winslow 1962 (p. 38, pl. 19, fig. 10) is clearly very similar, but there is no mention of an intexine, and the exine is considerably thicker. *Biharisporites submamillarius* McGregor 1960 (p. 33, pl. 11, fig. 16, pl. 12, figs. 1-3) is larger, lacks the prominent arcuate folds and raised contact area, and has a much thinner intexine.

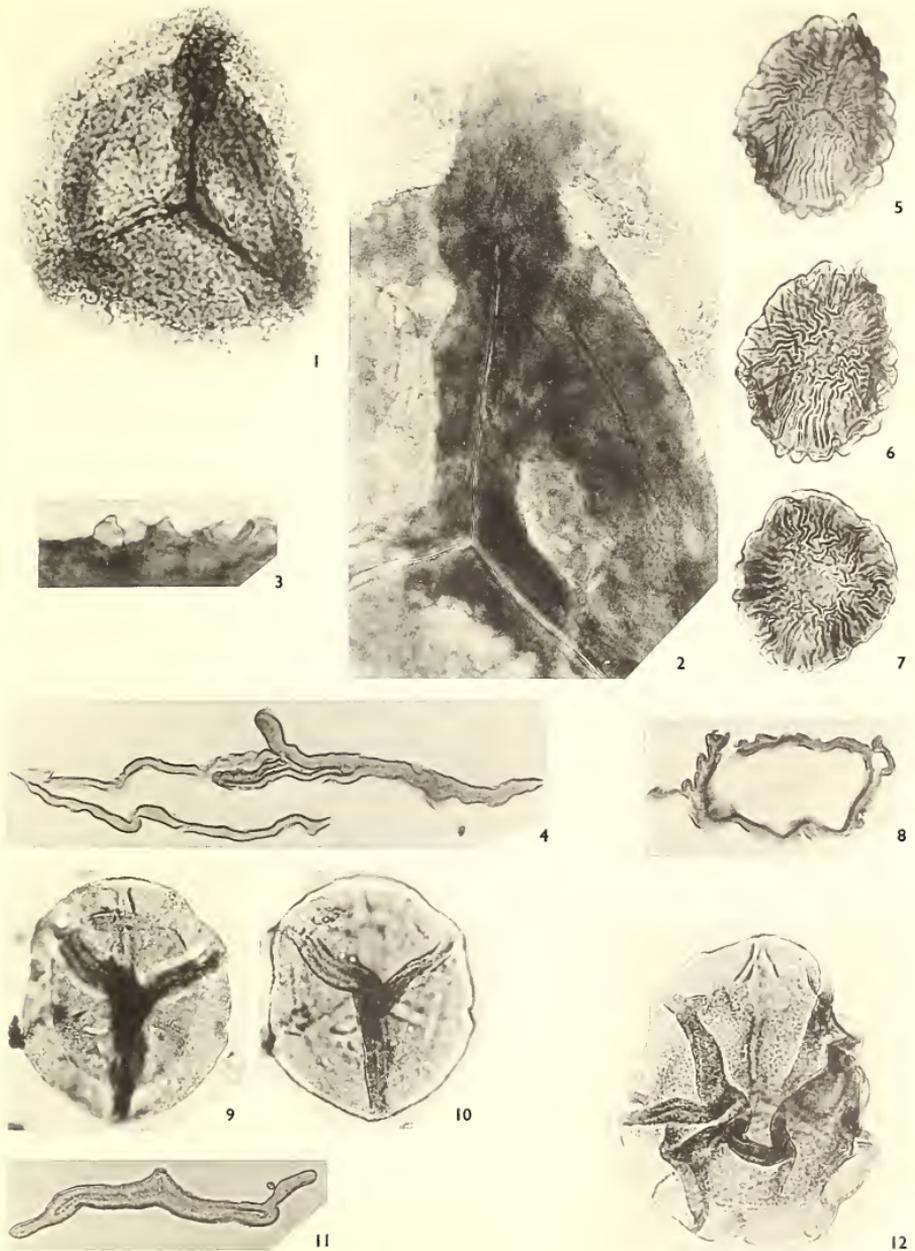
Occurrence. Upper Mimer Valley Series; Givetian.

EXPLANATION OF PLATE 104

All figures $\times 500$ unless otherwise stated; from unretouched negatives.

Figs. 1-4. *Calyptosporites optivus* (Chibrikova) comb. nov. 1, ($\times 200$) Proximal surface; KA 269/M1, 48.8 104.1, K558, N364. 2, ($\times 500$) the same. 3, ($\times 1000$) Showing cones with papillate apices; KA 242/M1, 32.7 98.2, K772, N365. 4, Section showing the cavate nature of the exine; KA 203/S2, 50.8 105.1, K555, N366.

Figs. 5-12. *Rhabdosporites* spp. 5-8. *R. cymatilus* sp. nov. 5, 6, Holotype, proximal and distal surfaces respectively; KA 274/4, 21.9 104.2, K872, N372. 7, Distal surface; KA 274/2, 51.6 93.3, K872, N373. 8, Section, showing cavate exine and folded exoexine; KA 251/S2, 57.2 88.4, K905, N374. 9-12. *R. scamnus* sp. nov. 9, 10, Holotype, proximal and distal surface respectively; KA 290/2, 38.7 100.0, K681, N369. 11, Section, very compressed; the cavate nature of the exine is not clearly seen; KA 290/S5, 29.8 91.6, K681, N370. 12, Distal surface showing numerous folds; KA 290/4 37.8 100.3, K681, N371.



Calyptosporites indolatus sp. nov.

Plate 106, figs. 1, 2

Diagnosis. Megaspores trilete; cavate; amb irregular, subcircular to roundly triangular, occasionally oval or roundly rectangular. Laesurae straight, length $\frac{1}{2}$ – $\frac{3}{4}$ intexine radius, frequently obscured by smooth lips, individually 2–5 μ wide, extending half to full spore radius. Intexine approximately 6–12 μ thick, laevigate, outline usually indistinct; exoexine 2–4 μ thick, infra-granulate, with a sparse distal ornament of cones and spines, 2–10 μ wide, 5–24 μ high. Exoexine strongly folded.

Dimensions. (Twenty-seven specimens) Diameter of exoexine 156–540 μ (mean 290 μ); diameter of intexine 90–278 μ (mean 155 μ).

Holotype. Preparation KA 235/M1, 45·7 104·1, K590, N367.

Locus typicus. Gonvillebreen–Horbyebeen Col, Central Dicksonland, Spitsbergen; Lower Mimer Valley Series, Lower Eifelian.

Description. Holotype diameter 408 μ , exoexinal extension 98 μ . Laesurae indistinct, elevated lips totalling 7 μ wide. Distal cones and spines 2–10 μ wide, 5–24 μ high. Exoexine with irregular prominent folds.

Remarks. Sections of this species appear to be zonate and prove to be somewhat confusing; evidence from broken and dissected specimens, from excentric intexines, and from independent cross-folding on the exoexinal extension, demonstrate that the spore is clearly cavate. It would appear that specimens are sometimes so compressed, that there has been fusion of the equatorial exoexine; even the spore cavity (Pl. 106, fig. 2) is represented only by a faint line.

Occurrence. Upper Mimer Valley Series; Givetian.

Genus RHABDOSPORITES Richardson 1960

Type species. *Rhabdosporites langii* (Eisenack) Richardson 1960.

Rhabdosporites scannus sp. nov.

Plate 104, figs. 9–12

Diagnosis. Miospores trilete; cavate; amb and intexine outline roundly triangular to circular. Laesurae straight, length two-thirds to full intexine radius, accompanied by low thickened lips, 1–2 μ wide, frequently extending beyond the laesurae on to the exoexinal extension. Intexine distinct, 1·5–4 μ thick, homogeneous, laevigate; exoexine 1·5–3 μ thick, infra-granulate, sculptured with a dense ornament of minute granules. Distal surface with a distinctive, variable distribution of muroid folds, frequently three in number, radially directed and usually situated inter-radially, but occasionally with a more comprehensive pattern. Short minor folds particularly on the equatorial exoexine are common.

Dimensions. (Fifty-eight specimens) Diameter of exoexine 54–119 μ (mean 82 μ); diameter of intexine 42–84 μ (mean 60 μ).

Holotype. Preparation KA 290/2, 38·7 100·0, K681, N369.

Locus typicus. West Lagercrantzberget, Central Dicksonland, Spitsbergen; Upper Mimer Valley Series, Givetian.

Description. Holotype roundly triangular, exoexine diameter $80\ \mu$, intexine diameter $58\ \mu$. Exoexine and intexine of approximately equal thickness. Three large distal inter-radial muroid folds present.

Remarks. The section (Pl. 104, fig. 11) demonstrates the two-layered exine, both layers of approximately equal thickness. Because of strong compression, the cavate nature of the equatorial exine is not clearly seen.

Comparison. *Camptozonotriletes velatus* (Waltz) Playford 1963 (p. 645, pl. 93, figs. 1-3) closely resembles *Rhabdosporites scammus* sp. nov. Sections of *C. velatus* (Waltz) Playford, in Dettmann and Playford 1962 (p. 680, pl. 96, figs. 10-12) are clearly similar, and are probably cavate, as they have tentatively suggested. However, *R. scammus* sp. nov. lacks the 'spanner like' lips, and except in a few specimens, also lacks the more comprehensive distal folding. *Rhabdosporites langi* (Eisenack) Richardson 1960 (p. 54, pl. 14, figs. 8-9) is larger, and lacks lips. *Rhabdosporites parvulus* Richardson 1965, is of similar size, but lacks the major folding so prominent in *R. scammus* sp. nov. Naumova (1953) assigned to *Archaeozonotriletes* and *Hymenozonotriletes* probable cavate forms, several of which exhibit major distal folding. *Archaeozonotriletes notatus* Naumova 1953 (p. 84, pl. 13, fig. 12) and *Hymenozonotriletes angulatus* Naumova 1953 (p. 65, pl. 8, fig. 21) both have three major radially directed distal folds, but are considerably smaller. Naumova has clearly misinterpreted the radially directed folds as 'the bordered aperture of the perispodium', and the real trilete mark as the 'aperture of the spore body' only. Size alone is not usually a criterion for specific separation, but insufficient details of the exact construction of *A. notatus* Naumova and *H. angulatus* Naumova makes closer comparison impossible. *Hymenozonotriletes facetus* Archangelskaya 1963 (p. 28, pl. 15, figs. 5, 6) has muroid folds proximally and lacks the major distal folds.

Occurrence. Upper Mimer Valley Series; Givetian.

· *Rhabdosporites cymatilis* sp. nov.

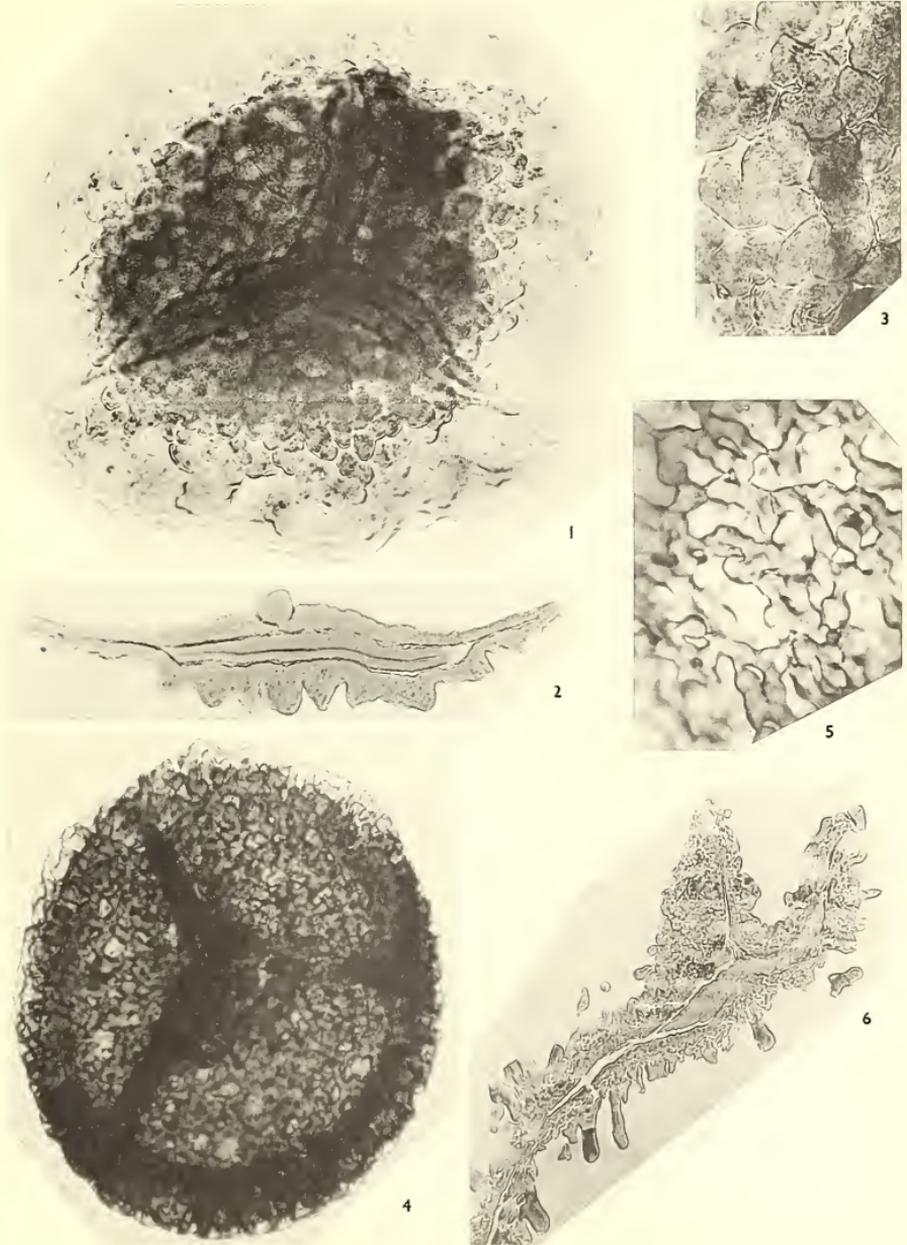
Plate 104, figs. 5-8

Diagnosis. Miospores trilete; cavate; amb and intexine outline roundly triangular, subcircular to oval, undulating. Laesurae often indistinct, straight, $\frac{1}{2}$ - $\frac{2}{3}$ spore radius, frequently accompanied and often obscured by sinuous lips, individually $1-3\ \mu$ wide, $5-10\ \mu$ high. Intexine indistinct, $1-3\ \mu$ thick, infra-granulate, unfolded; exoexine

EXPLANATION OF PLATE 105

All figures $\times 500$ unless otherwise stated; from unretouched negatives.

Figs. 1-6. *Aulicosporites* spp. 1-3. *A. aulicus* gen. et sp. nov. 1, Holotype, proximal surface; KA 209/M1, 63.3 98.8, K519, N375. 2, Section, showing cavate exine and exclusively distal sculpture; KA 240/S1, 37.6 101.6, K582, N376. 3, ($\times 1000$) Details of distal sculpture; KA 209/M3, 36.7 91.2, K519, N377. 4-6. *A. vitabilis* sp. nov. 4, Holotype, proximal surface ($\times 250$); KA 243/M1, 30.3 94.5, K767, N378. 5, ($\times 1000$) Details of the cristo-reticulate ornament; KA 243/M1, 41.0 100.2, K767, N379. 6, Section, showing sharp raised lips, and intexine; KA 243/S4, 40.7 100.4, K767, N380.



ALLEN, Lower and Middle Devonian miospores

2–4 μ thick, coarsely infra-granulate, laevigate, with a regular pattern of slightly sinuous muroid folds, 2–8 μ wide, 2–4 μ high, more or less radially directed (at least equatorially), and frequently absent from the contact areas.

Dimensions. (Twenty-four specimens) Diameter of exoexine 64–172 μ (mean 112 μ); diameter of intexine 68–92 μ (mean 79 μ).

Holotype. Preparation KA 274/4, 21·9 104·2, K872, N372.

Locus typicus. Reuterskiöldfjellet, Central Dicksonland, Spitsbergen; Reuterskiöldfjellet Sandstone, Emsian.

Description. Holotype subcircular, exoexine diameter 64 μ , intexine diameter 58 μ . Laesurae simple, straight, length approximately half intexine radius. Exoexine and intexine of approximately equal thickness. Muroid folds confined to the proximo-equatorial and distal surfaces, being very sinuous in the distal polar region, and being straighter and radially directed equatorially.

Remarks. The majority of the specimens are dark; and it is often difficult to see details of the intexine. Further maceration fails to clear the spores; however, even in dark specimens the regularly undulating exoexinal margin, the result of the radially directed folds, is an easily recognizable feature. Sections are difficult to cut from spores in this low horizon, but Plate 104, fig. 8 shows clearly the intexine and the folded exoexine.

Comparison. *Rhabdosporites langii* (Eisenack) Richardson 1960 (p. 54, pl. 14, figs. 8, 9, text-figs. 4, 6B) lacks the intricate and regular fold pattern, a feature present in all specimens of *Rhabdosporites cymatilus* sp. nov.; a distinctive diagnostic feature justifying its specific separation.

Occurrence. Reuterskiöldfjellet Sandstone, and Lower Mimer Valley Series; Siegenian, Emsian and probably Lower Eifelian.

Genus AULICOSPORITES gen. nov.

Type species. *Aulicosporites aulicus* sp. nov.

Diagnosis. Megaspores trilete; cavate; amb circular to roundly triangular. Intexine and exoexine of approximately equal thickness, intexine laevigate, exoexine sculptured at least distally with a cristate or cristo-reticulate ornament, with cones or occasional spines.

Discussion. Differs from both *Calyptosporites* Richardson 1962 and *Biharisporites* Potonié 1956, in having a cristate or cristo-reticulate ornament.

Derivation of name. Gr. *aulakos*—with small furrows.

Aulicosporites aulicus sp. nov.

Plate 105, figs. 1–3

Diagnosis. Megaspores trilete; cavate; amb and intexine outline circular, subcircular to roundly triangular. Laesurae distinct, straight, length one-third to full radius of the intexine, accompanied by conspicuous, smooth, elevated lips, 5–12 μ wide, 6–10 μ high, length three-quarters to full spore radius. Intexine 6–9 μ thick, infra-granulate; exoexine

7–12 μ thick, coarsely infra-granulate, proximally laevigate, distally sculptured with cones, variable both in size and distribution. The cones (6–40 μ wide, 6–24 μ high) have rounded apices, occasionally supporting a very small cone or spine; usually more densely packed in the distal polar region, where they are fused basally or have a polygonal outline. Distally the exoexinal extension is often laevigate.

Dimensions. (Thirty-eight specimens) Diameter of exoexine 180–306 μ (mean 217 μ); diameter of intexine 90–190 μ (mean 146 μ).

Holotype. Preparation KA 209/M1, 63·3 98·8, K519, N375.

Locus typicus. Odellfjellet, North Dicksonland, Spitsbergen; Lower Mimer Valley Series, Lower Eifelian.

Description. Holotype diameter of exoexine 208 μ , diameter of intexine 120 μ . Laesurae approximately half intexine radius. Lips each 8–10 μ wide, extend almost to the equatorial margin. Distal cones 6–12 μ wide, 6–10 μ high, with both separate polygonal and fused bases, and occasionally with small apical spines. Small folds present on exoexinal extension.

Remarks. The section (Pl. 105, fig. 2) demonstrates the cavate nature of the spore, the thick intexine, and the exclusively distal sculpture of cones.

Occurrence. Dicksonfjorden Sandstone, Upper Reuterskiøldfjellet Sandstone, and Lower Mimer Valley Series; Emsian and Eifelian.

Aulicosporites vitabilis sp. nov.

Plate 105, figs. 4–6

Diagnosis. Megaspores trilete, amb circular to roundly triangular with convex sides and broadly rounded apices. Laesurae straight, length $\frac{3}{4}$ – $\frac{4}{5}$ spore radius, accompanied and often obscured by acute, thickened lips, individually 5–25 μ wide, 25–44 μ high at the proximal pole, 16–26 μ high equatorially. Intexine seen only in sections, approximately 5 μ thick, homogeneous, laevigate; exoexine 8–10 μ thick (excluding ornament), infra-punctate. Contact areas occupying most of the proximal surface, laevigate or punctate, except adjacent to the lips, where they may support an ornament of cones; contact areas bounded by curvaturae, up to 20 μ wide, formed by a fusion of cones. Distal surface cristo-reticulate, with cones and occasional spines 6–12 μ wide, 7–20 μ high.

Dimensions. (Seventeen specimens) Diameter of exoexine 265–364 μ (mean 322 μ); diameter of intexine approximately 70 μ .

Holotype. Preparation KA 243/M1, 30·3 94·5, K767, N378.

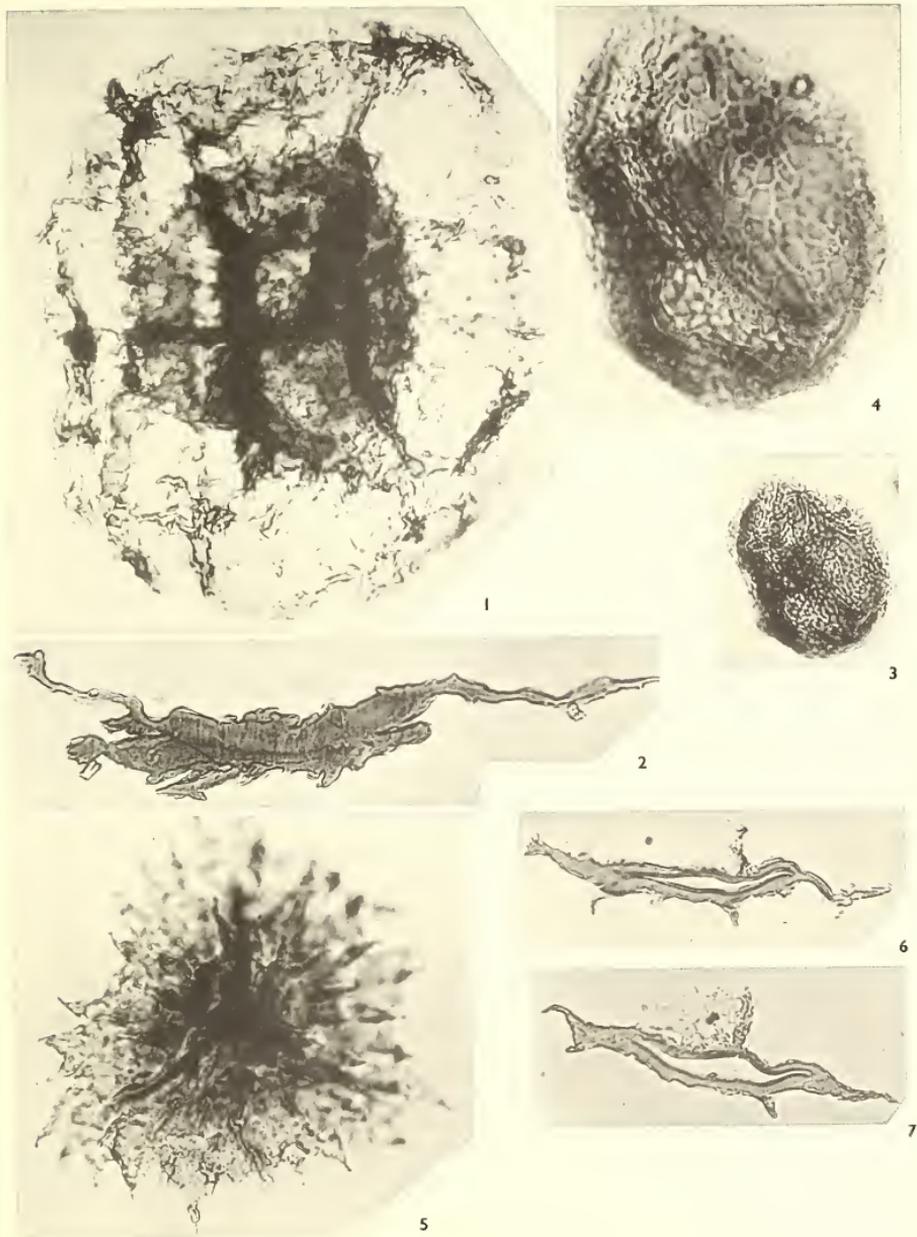
EXPLANATION OF PLATE 106

All figures $\times 500$ unless otherwise stated; from unretouched negatives.

Figs. 1–2. *Calyptosporites indolatus* sp. nov. 1, Holotype ($\times 250$), proximal surface; KA 235/M1, 45·7 104·1, K590, N367. 2, Compressed section; KA 235/S1, 49·7 105·0, K590, N368.

Figs. 3–4. *Retialetes* sp. 3, KA 251/1, 18·9 94·1, K905, N381. 4, ($\times 1000$) the same.

Figs. 5–7. *Ancyrospora langii* (Taugourdeau-Lantz) comb. nov. 5, Distal surface; KA 243/3, 47·7 92·1, K767, N386. 6, 7, Sections, showing the raised lips, equatorial flange, and intexine; KA 243/S8, 52·3 104·6, K787, N387 and KA 243/S8, 33·9 103·4, K767, N388, respectively.



Locus typicus. East Munindalen, Central Dicksonland, Spitsbergen; Plantekløfta Conglomerate, probable Upper Givetian.

Description. Holotype subcircular, exoexinal diameter 296μ , intexine not seen. Laesurae straight, length four-fifths spore radius, accompanied by lips each up to 24μ wide. Contact areas laevigate, except for an ornament of cones adjacent to the lips. Distal cristoreticulum well developed.

Remarks. The section (Pl. 105, fig. 6) clearly shows the intexine, the raised sharp lips formed by an upward extension and thickening of the exoexine, the infra-punctate (here corroded) nature of the exoexine, and the homogeneous sculptural elements.

Comparison. *Biharisporites ellesmerensis* Chaloner 1959 (p. 322, pl. 55, fig. 2, text-fig. 1) is smaller, and has smaller sculptural elements, which are not fused basally. No intexine appears to be present, but this feature is very indistinct in *Aulicosporites vitabilis* sp. nov.

Occurrence. Planteryggen Sandstone, and Plantekløfta Conglomerate; probable Upper Givetian.

Turma ALETES Ibrahim 1933

Subturma AZONALETES (Luber) Potonić and Kremp 1954

Infraturma RETICULONAPITA (Erdtman) Vimal 1952

GENUS RETIALETES Staplin 1960

Type species. *R. radforthii* Staplin 1960.

Retialetes sp.

Plate 106, figs. 3, 4

Description of specimens. Spores alete, ellipsoidal. Exine (excluding ornament) thin, 1.5μ or less, finely sculptured with low, narrow muri, 1μ or less wide, $0.5-2 \mu$ high. Lumina uniform, usually polygonal, small, typically $2-4 \mu$ wide (range $1-8 \mu$). Exine strongly plicated with major folds.

Dimensions. (Seven specimens) $40-64 \mu$ (mean 51μ) by $31-44 \mu$ (mean 38μ).

Comparison. *Retialetes radforthii* Staplin 1960 the only other species recorded for this genus, is considerably larger.

Occurrence. Lower Reuterskiøldfjellet Sandstone; Siegenian.

Previous records. The genus has previously been recorded only from the Lower Carboniferous.

INCERTAE SEDIS

Genus NIKITINSPORITES Chaloner 1959

Type species. *Nikitinsporites canadensis* Chaloner 1959.

Nikitinsporites spitsbergensis sp. nov.

Plate 108, figs. 1-5

Diagnosis. Megaspores trilete, amb subtriangular to subcircular. Laesurae obscured by greatly elevated lips (sometimes broken), individually $7-15 \mu$ wide, $74-160 \mu$ high. Exine

two layered; intexine 2–4 μ thick, homogeneous, closely appressed to the exoexine, and seen only in sections; exoexine 18–45 μ thick, coarsely infra-granulate. Contact areas laevigate, proximo-equatorial and distal surfaces supporting thick, more or less parallel-sided spines, structurally composed of rod-shaped elements parallel to the long axis; apically the spines narrow abruptly, ending with an homogeneous grapnel-tip, this tip is never wider than the main shaft of the spine; typically the spines are 100–50 μ long (range 48–250 μ), typically 40–60 μ wide (range 14–80 μ wide) the equatorial margin supports 8–20 spines. A pseudoflange up to 80 μ wide, formed by the fused bases of the spines, is occasionally present.

Dimensions. (Twenty-four specimens) Equatorial diameter (excluding spines) 240–440 μ (mean 342 μ); polar diameter (including apical prominence) 240–416 μ (mean 303 μ).

Holotype. Preparation KA 203/M4, 30.4 107-1, K555, N382.

Locus typicus. North ridge of Kinanderfjellet, Central Dicksonland, Spitsbergen; Upper Mimer Valley Series, Givetian.

Description. Holotype equatorial and polar diameter (excluding elevated lips) both 256 μ , elevated lips 160 μ . Spines 28–40 μ wide, 80–240 μ long, only a few with the grapnel-tips preserved, basal fusion of spines (pseudoflange) up to 20 μ wide.

Remarks. Sections (Pl. 108, figs. 4, 5) show the very thick exoexine, and very thin closely appressed intexine; the spore cavity appears somewhat irregular in shape. This species is included within *Nikitinспорites* Chaloner 1959, primarily on the shape and structure of the grapnel-tipped spines. Large size and greatly elevated lips, are features of *Nikitinспорites* which are also seen in some species included within *Hystricosporites* McGregor 1960 and *Ancyrospora* Richardson 1960 emend Richardson 1962. For example *Hystricosporites porrectus* (Balme and Hassell) comb. nov. (Pl. 95, figs. 1–3) has elevated lips, but the spines are homogeneous throughout, and with their large grapnel-tips, are clearly different from the spines of *Nikitinспорites* which are homogeneous only at the very apex, with a small grapnel tip never exceeding the diameter of the main shaft of the spine. A pseudoflange (also present in some species of *Ancyrospora*) may be absent, partially developed or strongly developed (Pl. 108, fig. 2) in otherwise identical specimens, and *Nikitinспорites* Chaloner 1959 is therefore included within *Incertae sedis*.

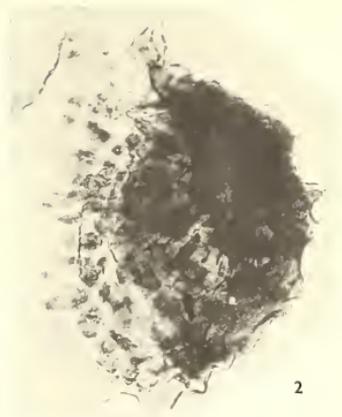
Comparison. *Nikitinспорites* sp. Vigran 1964 (p. 20, pl. 2, figs 11–13) has a variable sculpture of conical-based spines, coni and verrucae. *Nikitinспорites canadensis* Chaloner 1959 (p. 328, pl. 55, fig. 5, text-fig. 4) is circular, and is considerably larger. *Dicrospora* sp. Winslow 1962 (p. 55, pl. 10, figs. 1 and 1a) illustrated but not described, is probably assignable to *N. spitsbergensis* sp. nov.

Occurrence. Fiskekløfta Formation and Planteryggen Sandstone; Givetian.

EXPLANATION OF PLATE 107

All figures $\times 500$ unless otherwise stated; from unretouched negatives.

Figs. 1–6. *Ancyrospora* spp. 1, *A. trocha* sp. nov., Holotype, proximal surface; KA 209/M6, 39.2 103.3, K519, N389. 2–5. *A. reuta* sp. nov. 2, Holotype, lateral view; KA 209/4, 34.0 88.1, K519, N390. 3, 4, Sections, showing equatorial flange and thick exine; KA 204/S1, 21.0 90.4, K838, N391 and KA 204/S1, 62.0 105.5, K838, N392. 5, ($\times 1000$) Details of grapnel-tipped spines; KA 204/M2, 32.3 106.6, K838, N393. 6. *A. sp.* ($\times 250$) Proximal surface; KA 242/M1, 33.2 95.1, K772, N394.



Genus *ANCYROSPORA* Richardson 1960 emend Richardson 1962

Type species. *Ancyrospora grandispinosa* Richardson 1960 emend Richardson 1962.

Ancyrospora langii (Taugourdeau-Lantz) comb. nov.

Plate 106, figs. 5-7

1960 *Archaeotriletes langii* Taugourdeau-Lantz, p. 145, pl. 3, figs. 33, 34, 39.

1964 *Ancyrospora* cf. *simplex* Vigran, p. 26, pl. 6, figs. 1-3.

Dimensions. (Twenty specimens) Overall equatorial diameter 66-140 μ (mean 86 μ); central area diameter 40-81 μ (mean 55 μ); equatorial flange (excluding ornament) 12-48 μ wide. Grapnel-tipped spines typically 12-25 μ long (range 8-38 μ), typically 7-12 μ wide basally (range 5-20 μ).

Remarks. The spines narrow gradually from the base to the apex, ultimately widening into a grapnel-tip. The spines except for the homogeneous grapnel-tip, are infra-granulate. Sections (Pl. 106, figs. 6, 7) demonstrate the elevated membranous lips, thin intexine, and equatorial flange composed only of exoexine. In *Archaeotriletes* (Naumova) Potonié 1958 the spines are confined to the central area, and are absent from the flange.

Comparison. *Hymenozonotriletes incisus* Naumova 1953 (p. 68, pl. 9, fig. 11) is similar, and should this species prove to have grapnel-tipped spines, then it would be conspecific.

Occurrence. Upper Mimer Valley Series; Givetian.

Ancyrospora trocha sp. nov.

Plate 107, fig. 1

Diagnosis. Miospores trilete; amb and central area outline circular to subcircular. Laesurae straight, length three-quarters to full central area radius, accompanied and often obscured by sinuous, membranous, elevated lips, individually 2-4 μ thick, usually closely appressed to the exoexine, but occasionally separated and folded; exoexine coarsely infra-granulate 7-20 μ thick centrally, extending as an equatorial flange, typically 20-32 μ wide (range 15-50 μ). Contact areas occupy most of the proximal surface inside the flange, and support an ornament of low, broad, flat-topped radial muri, 6-13 μ wide, 4-12 on each contact area; proximo-equatorial and distal surfaces sparsely sculptured with short spines, typically 15-30 μ long (range 10-58 μ), the majority with large bulbous bases, 10-24 μ wide.

Dimensions. (Twenty-five specimens) Overall equatorial diameter (excluding spines) 154-272 μ (mean 189 μ).

Holotype. Preparation KA 209/M6, 39-2 103-3, K519, N389.

Locus typicus. Odellfjellet, North Dicksonland, Spitsbergen; Lower Mimer Valley Series, Lower Eifelian.

Description. Holotype circular, diameter 178 μ . Laesurae straight, length equals full intexine radius, elevated lips 16 μ high. Intexine 3 μ thick, folded; exoexine 16 μ thick, equatorial flange 22 μ wide. Radial muri 8-13 μ wide, 6-8 on each contact area; proximo-

equatorial and distal spines sparse, short, 14–18 μ high, frequently with the grapnel tip broken.

Comparison. *Ancyrospora grandispinosa* Richardson 1960 emend Richardson 1962 (p. 175, pl. 27, figs. 3–5, text-fig. 4) is clearly similar, but lacks the proximal radial muri. *Hystriospores porcatus* comb. nov. has longer spines, a curvatural ridge formed in part from the bases of the spines (zonarial ridge of Winslow 1962, p. 52), and lacks the membranous equatorial flange.

Occurrence. Upper Reuterskiöldfjellet Sandstone, and Lower Mimer Valley Series; Emsian and Eifelian.

Ancyrospora reuta sp. nov.

Plate 107, figs. 2–5

Diagnosis. Miospores trilete; amb and central area outline circular to subcircular. Laesurae indistinct, length half to full radius of the central area, occasionally accompanied by smooth lips, individually 1–3 μ wide. Exine two-layered; intexine infra-granulate 1–4 μ thick; exoexine infra-granulate 7–15 μ thick, extending as an equatorial flange, typically 25–40 μ wide (range 14–54 μ); proximal surface laevigate, distal surface densely covered with short grapnel-tipped spines, 6–20 μ long, frequently with large bulbous bases, 6–10 μ wide.

Dimensions. (Sixteen specimens) Overall equatorial diameter 111–180 μ (mean 151 μ); central area diameter 83–128 μ (mean 96 μ).

Holotype. Preparation KA 209/4, 34-0 88-1, K519, N390.

Locus typicus. Odelfjellet, North Dicksonland, Spitsbergen; Lower Mimer Valley Series, Lower Eifelian.

Description. Holotype in oblique aspect, subcircular, overall equatorial diameter 128 μ , central area diameter 100 μ . Laesurae indistinct. Exine 10 μ thick centrally, equatorial flange 14–22 μ wide. Distal spines 6–10 μ long, only a few grapnel-tips being preserved.

Remarks. Specimens are very dark, and difficult to macerate, tending to break down with increased maceration, rather than becoming lighter in colour. Frequently, the grapnel-tip is not preserved. The sections (Pl. 107, figs. 3, 4) demonstrate the equatorial flange and thick exine. No intexine is seen in this specimen.

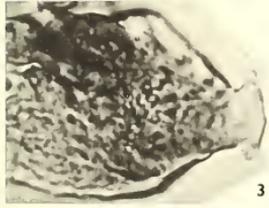
Comparison. *Ancyrospora grandispinosa* Richardson 1960 emend Richardson 1962 (p. 175, pl. 27, figs. 3–5, text-fig. 4) is considerably larger, and has much longer spines. *Ancyrospora trocha* sp. nov. (Pl. 107, fig. 1) has proximal radial muri.

Occurrence. Dicksonfjorden Sandstone, Upper Reuterskiöldfjellet Sandstone, and Lower Mimer Valley Series; Emsian to Eifelian.

EXPLANATION OF PLATE 108

All figures $\times 200$ unless otherwise stated; from unretouched negatives.

Figs. 1–5. *Nikitinsporites spitsbergensis* sp. nov. 1, Holotype, lateral view; KA 203/M4, 30-4 107-1, K555, N382. 2, Proximal surface showing pseudoflange; KA 282/M2, 33-9 96-4, K854, N383. 3, ($\times 1000$) bifurcate tipped spine from the holotype. 4, 5, Sections showing the thick exoexine and thin intexine. 4, ($\times 500$) KA 235/S17, 43-2 99-4, K590, N384. 5, ($\times 1000$), KA 235/S11, 20-7 106-0, K590, N385.



ALLEN, Middle Devonian megaspores

Ancyrospora sp.

Plate 107, fig. 6

Description of specimens. Megaspores trilete; amb triangular to roundly triangular, deeply incised, central area outline triangular. Laesurae indistinct, straight, length two-thirds to full spore radius, accompanied by smooth elevated lips, individually 4–12 μ wide, 10–40 μ high. Exine two-layered; intexine approximately 3 μ thick, closely appressed to the exoexine and usually indistinct; exoexine infra-granulate, centrally 15–20 μ thick, thinning and extending equatorially as a pseudoflange up to 60 μ wide. Proximal surface laevigate; equatorially and distally sculptured with flexuous spines, 40–100 μ long, basally 10–40 μ wide, each narrowing gradually towards the apex, where it widens slightly into a grapnel-tip. The spines, except for the homogeneous grapnel-tip, are infra-granulate.

Dimensions. (Six specimens) Overall equatorial diameter (excluding spines) 222–80 μ ; central area diameter 120–44 μ .

Remarks. Structurally the spines are similar to those in *Nikinisporites* Chaloner 1959, but differ in sculpture.

Comparison. *Archaeotriletes villosus* Chibrikova 1959 (p. 44, pl. 2, fig. 1) is clearly similar, and may prove to be identical, but the sculpture is reduced in size towards the distal pole, and there is no evidence of grapnel-tips to the spines, although this may be due to preservation.

Occurrence. Fiskekløfta Formation, Planteryggen Sandstone, and Plantekløfta Conglomerate; probable Middle and Upper Givetian.

SOME GENERAL COMMENTS

The Spitsbergen succession is one of the few Devonian continental successions which extends from the Lower Devonian into the Middle Devonian without a stratigraphical break.

Botanical affinities can tentatively be suggested on the basis of spores of similar construction found *in situ* in Devonian and Carboniferous plants, but many species, including those with proximal radial muri, grapnel-tipped spines, and patinate thickenings, which are restricted to, or abundant in, the Devonian, are as yet unassigned to any plant group.

Dispersed spores of diverse construction, included within the Infraturmae Laevigati, Apiculati, Murornati, Tricrassati, Cingulati, Patinati, and many cavate forms are described from the Lower Devonian. The majority of Lower Devonian plants described by Hoeg (1942) from Spitsbergen are assignable to the Psilophytales, and from the evidence of spores *in situ* described from the Devonian, the majority of Psilophytales produced simple laevigate or apiculate forms. This diversity of dispersed spores recovered from the Lower Devonian, suggests that there must have been a greater diversity of parent plants than have as yet been described from, or preserved in, the Lower Devonian of Spitsbergen or elsewhere.

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FRESHWATER OSTRACODS FROM THE BATHONIAN OF OXFORDSHIRE

by R. H. BATE

ABSTRACT. Eight species of freshwater ostracod are described from the Bathonian of Oxfordshire as exposed in the Old Cement Quarry, Kirtlington, near Oxford. Because of the number of specimens available only two, *Timiriasevia mackerrowi* sp. nov. and *Theriosynoecum kirtlingtonense* sp. nov., are identified specifically. Other genera represented are:—*Bisulcocypsis*; *Darwinula*; and *Limnocythere*. The presence of these freshwater ostracods in marine sediments and associated with marine ostracods is considered to be due to their being brought into the area by rivers. The occurrence of two species of *Timiriasevia* from this country is the first recorded identification of the genus outside the U.S.S.R.

DURING an excursion organized by the Palaeontological Association and led by Dr. W. S. McKerrow to the Oxford district in 1958, the marine marls and limestones of Bathonian age were examined in the Old Cement Quarry, Kirtlington (Grid Reference SP/495200). The presence of freshwater ostracods associated with an otherwise marine fauna led to a more detailed sampling the following year. Whilst it is intended to describe the complete ostracod fauna in a subsequent publication the presence of this freshwater fauna is considered to be of sufficient importance to warrant its prior description here.

The Kirtlington quarry section has been previously described by Arkell (1931, p. 570 and 1947, p. 57) and need not be discussed in detail. The samples from which the ostracods are described were obtained from the *Fimbriata-waltoni* clay at the top of the Bladon Beds and from three horizons within the Wychwood Beds (see text-fig. 1). These beds are of Middle to Upper Bathonian age.

During Bathonian times the period of marine deposition in the Oxford area was greatly influenced by the land nearby. This is evidenced by the presence of abundant lignite, reptilian bones, and charophytes; all these being brought into the area by rivers draining the land surface. It is not surprising, therefore, that freshwater ostracods should be abundant at several horizons throughout the succession.

All specimens referred to in the text have been deposited in the collections of the Department of Palaeontology, British Museum (Natural History).

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SYSTEMATIC DESCRIPTIONS

Subclass OSTRACODA Latreille 1806

Order PODOCOPIDA Müller 1894

Suborder PODOCOPINA Sars 1866

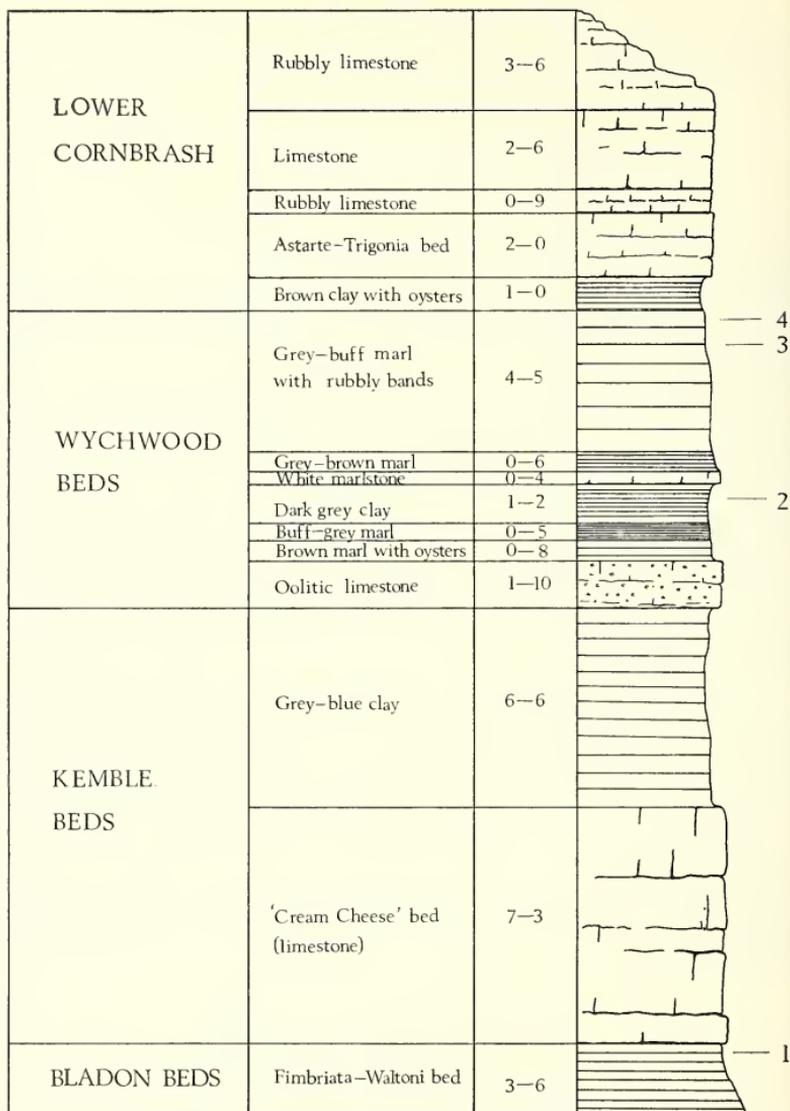
Superfamily DARWINULACEA Brady and Norman 1889

Family DARWINULIDAE Brady and Norman 1889

Genus DARWINULA Brady and Robertson 1885

Type species. *Polycheles stevensoni* Brady and Robertson 1870, by original designation.

[Palaeontology, Vol. 8, Part 4, 1965, pp. 749–59, pls. 109–11.]



TEXT-FIG. 1. Section of north-east face of Old Cement Quarry, Kirtlington, showing the four horizons from which fresh-water ostracods have been obtained.

Darwinula sp. A

Plate 109, figs. 1-4

Material. Two specimens (Io2715-16), a right valve from horizon no. 3 and a complete carapace from horizon no. 4.

Description. Carapace small, elongate-oval in outline with the greatest height and width in the posterior third. Greatest length passes through mid-point. Anterior narrowly rounded, posterior broadly rounded. Dorsal margin straight with convex antero-dorsal and postero-dorsal slopes. Ventral margin broadly incurved antero-medially. Left valve larger than the right which it overlaps strongly around the posterior and along the ventral margin. Hinge adont, consisting of a simple straight groove in the right valve. Other internal details not observed.

Dimensions. Carapace, BMNH Io2715, length 0.64 mm.; height 0.30 mm. Right valve BMNH Io2716, length 0.64 mm.; height 0.27 mm.

Remarks. Although close to *Darwinula leguminella* (Forbes in Lyell 1855, p. 294, text-fig. 334c) *Darwinula* sp. A may be distinguished by the more evenly rounded anterior margin, the line of greatest length passing through or slightly below mid-point. *D. leguminella* on the other hand has a more acuminate anterior margin, extended antero-ventrally so that the line of greatest length passes below mid-point. Until further material becomes available it is preferred to avoid giving the present series a specific name.

Superfamily CYTHERACEA Baird 1850

Family LIMNOCYTHERIDAE Klie 1938

Genus LIMNOCYTHERE Brady 1868

Type species. *Cythere inopinata* Baird 1843 by subsequent designation Brady and Norman 1889.

Limnocythere sp. A

Plate 109, figs. 8, 9

Material. A single left valve (Io2713) occurring at horizon no. 4.

Description. Valve subrectangular in outline with the ventral margin strongly concave and the greatest height situated in the posterior third. A deep, narrow, vertical sulcus is situated just anterior of mid-point. Greatest length of valve extends through mid-point. Anterior broadly rounded, posterior slightly more obliquely rounded. Dorsal margin long, slightly convex with prominent cardinal angles. The strong incurvature of the ventral margin is antero-median in position, the postero-ventral margin of the valve being strongly convex with a flat, distinct, marginal border. An oval swelling is situated just below and behind the vertical sulcus; posterior part of valve also prominently swollen. Shell surface granular, possibly originally punctate but now not clearly determinable because of preservation. Internally the lophodont type hinge consists of simple terminal sockets open ventrally to the inside of the valve, and a median element formed by the dorsal edge of the valve. Inner margin and line of concrescence coincide, duplication of moderate width. Muscle scars and radial pore canals not determined.

Dimensions. Left valve, BMNH Io2713, length 0.83 mm.; height 0.43 mm.

Remarks. *Limnocythere* sp. A appears to be close to *Limnocythere fragilis* Martin (1940, p. 348, pl. 7, figs. 105–9, pl. 9, fig. 152) in general appearance although it can be distinguished by the much stronger ventral incurvature and correspondingly more convex postero-ventral margin. The posterior is also more obliquely rounded in the present species which is further differentiated by the presence of a small oval swelling below and behind the vertical sulcus.

Limnocythere sp. B

Plate 109, figs. 5–7

Material. A single left valve (Io2714) found at horizon no. 2 in the Kirtlington section.

Description. Valve subrectangular with the greatest height in the anterior third. Greatest length through mid-point. Dorsal margin straight with prominent cardinal angles, the anterior angle in particular being noticeably upstanding. Ventral margin medially incurved. Anterior broadly rounded, posterior more narrowly rounded. Valve bi-sulcate with a median vertical sulcus and a shorter antero-median sulcus. Shell surface reticulate and rather irregularly swollen, giving a warty appearance. A short, pointed spine, backwardly projected, is situated below and slightly behind the median sulcus. Anterior and posterior margins flattened to form distinct marginal borders. Hinge lophodont, the terminal sockets being open to the interior of the valve. Median bar long and narrow. Inner margin and line of concrescence coincide, the duplicature being of moderate width. Radial pore canals long and straight, 8 anteriorly and 7 posteriorly. Muscle scars not observed.

Dimensions. Left valve, BMNH Io2714, length 0.83 mm.; height 0.44 mm.

Remarks. The ornamentation, warty appearance, and the presence of a ventro-lateral spine as well as the bi-sulcate development distinguish this species from all others previously described.

Genus *BISULCOCYPRIS* Pinto and Sanguinetti 1958

Type species. *Bisulcoocypris pricei* Pinto and Sanguinetti 1958, by original designation.

Remarks. The genus *Bisulcoocypris*, exclusively freshwater in habit, has a surface ornamentation consisting of pitting or reticulation with a tendency towards the development of small nodes or tubercles. Possibly the degree of tubercular development might reflect some variation in the environment (e.g. salinity or pH) although some species appear to be characteristically ornamented in this way. However, the development of nodes

EXPLANATION OF PLATE 109

All figures $\times 65$ unless otherwise stated.

- Figs. 1–4. *Darwinula* sp. A. Right, left, dorsal, and ventral views, complete carapace, Io2715.
 Figs. 5–7. *Limnocythere* sp. B. External and internal views (fig. 7, showing radial pore canals), left valve, Io2714.
 Figs. 8, 9. *Limnocythere* sp. A. External and internal views, left valve, Io2713.
 Figs. 10–12. *Bisulcoocypris* sp. B. Internal view to show hinge, external view (ventral margin broken on this illustration) and internal view to show radial pore canals, left valve. Io2718.
 Figs. 13, 14. *Bisulcoocypris* sp. A. Muscle scars and external view, broken right valve, Io2717. Fig. 13, $\times 170$.



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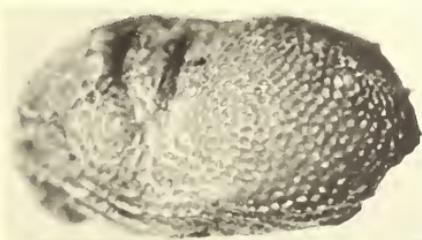
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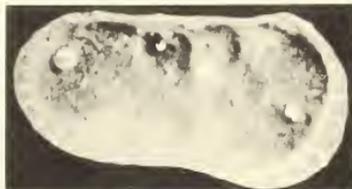
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within *Bisulcoypris* is never carried to such an extent as is considered here to be found in *Theriosynoecum*. Of the number of species placed by Pinto and Sanguinetti (1962) into *Bisulcoypris* one, *B. fittoni* (Mantell), is tuberculate not only as an adult but also throughout its ontogeny (see Sohn and Anderson 1964) and is to be more accurately referred to *Theriosynoecum*. Both genera are freshwater in habit so there is no objection to this. Pinto and Sanguinetti's statement (p. 76, which will be discussed later) that *Theriosynoecum* is a marine genus is not accepted here.

The presence in the Kirtlington section of two species of *Bisulcoypris* and the occurrence of *B. tenuimarginata* (Oertli 1957, p. 765) in Bathonian sediments of Poitou, France, extends the range of this genus below that indicated by Pinto and Sanguinetti (p. 76).

As there is some confusion at the present time concerning the separate identity of the genera *Bisulcoypris* and *Theriosynoecum* it is relevant to state here that only strongly tuberculate species (throughout their ontogeny) are considered to belong to *Theriosynoecum* irrespective of the possession or absence of an accommodation groove. There appears to be no real justification for their separation on any other grounds.

Bisulcoypris sp. A

Plate 109, figs. 13, 14

Remarks. A broken right valve (Io2717) from horizon no. 1 is all that has been found of this particular species. Shell surface is strongly punctate with longitudinal ridges developed along the ventral and ventro-lateral surfaces.

Bisulcoypris sp. B

Plate 109, figs. 10-12

Material. Two left valves (Io2718-19) occurring at horizon no. 4.

Description. Valve subquadrate in outline with the greatest length passing through mid-point and the greatest height in the posterior third. Anterior and posterior broadly rounded. Ventro-lateral margin convex, overhanging the ventral surface. Ventral margin with shallow antero-medial incurvature; dorsal margin strongly concave medially with broadly rounded anterior cardinal angle and sharply acute posterior angle. Posterior part of valve strongly inflated, the inflation being obliquely angled below the posterior cardinal angle to leave a flattened area. Shell surface uniformly reticulate with a series of short spines and nodes. In both left valves a short spine is present on the posterior cardinal angle, two further spines occur on the upper part of the posterior and a number around the anterior margin where they are found just to the inside of the narrow marginal border. The area between the two antero-dorsal sulci is noticeably swollen and two low nodes occur in the anterior half of the valve. In the posterior half three low nodes may occur one above the other just behind the second of the two sulci. These are present, however, only on one of the two valves and in this case a prominent tubercle is also developed just above the line of greatest length and in front of the two posterior spines. Longitudinal striae extend along the ventral and ventro-lateral surfaces and around the posterior. Hinge lophodont, the posterior socket in the left valve being short and triangular in shape whilst the anterior socket is elongate and rather narrow. Median bar

smooth, long, and strongly developed. An accommodation groove is present only over the posterior half of the hinge. Inner margin and line of concrescence do not coincide around the anterior margin where a narrow vestibule is developed. Radial pore canals (approximately 30 anteriorly) short, straight, and rather slender, posterior canals not seen. A narrow flange extends, outside the selvage, around the free margin from the anterior to the posterior cardinal angle. Muscle scars not observed.

Dimensions. Left valve, BMNH Io2718, length 1.03 mm.; height 0.63 mm.

Remarks. It is impossible to contrast sp. *A* and sp. *B* on the amount of material available but it would appear that in the case of sp. *B* the ornamentation is reticulate rather than punctate with the tendency to develop small tubercles, the two sulci are also separated by a distinct swelling. In sp. *A* the area between the sulci is flattened. *Bisulcoypris tenuimarginata* (Oertli 1957, p. 765, pl. 23, figs. 15–24) is a much smaller, compact ostracod, showing no tendency to develop small nodes.

Genus *THERIOSYNOECUM* Branson 1936

Type species. *Morrisonia wyomingensis* Branson 1935, by monotypy.

Remarks. The genus *Theriosynoecum* was originally described from Wyoming, U.S.A., under the preoccupied name of *Morrisonia* by Branson from freshwater sediments of the Morrison formation.

Pinto and Sanguinetti (1962, p. 76) suggest that *Theriosynoecum* is a marine ostracod because of its association with marine forms in Bathonian and Callovian sediments of England. A few years ago when Professor Pinto was visiting this country he examined my material from Kirtlington, where the association of this ostracod with marine ostracods is beyond dispute. However, when the complete evidence, both stratigraphical and palaeontological, is taken into consideration it can be seen that the presence of *Theriosynoecum*, as well as specimens of *Darwinula*, *Bisulcoypris*, and *Timiriasevia*, in marine sediments at Kirtlington is due entirely to their being brought into the area by rivers.

Theriosynoecum kirtlingtonense sp. nov.

Plate 110, figs. 1–11, Plate 111, fig. 1

Material. Fourteen specimens (Io2720–33) from horizons nos. 1–4.

Diagnosis. Carapace rectangular with well-rounded anterior and posterior margins. Posterior cardinal angle acute, anterior angle rounded. Shell surface strongly reticulate anteriorly, generally weakly reticulate posteriorly. Vento-lateral margin projected as thinly developed ridge, particularly postero-laterally. 8 strong tubercles are developed in

EXPLANATION OF PLATE 110

All figures $\times 65$ unless otherwise stated.

Figs. 1–11. *Theriosynoecum kirtlingtonense* sp. nov. Figs. 1–3, 11. External, internal, and dorsal views and internal view ($\times 110$) to show anterior radial pore canals, male left valve, holotype Io2720.

Figs. 4–7. External, internal, dorsal, and ventral views male right valve, paratype Io2726. Figs. 8, 9. External and internal views, female right valve, paratype Io2725. Fig. 10. Muscle scars ($\times 120$), female right valve, paratype Io2730.



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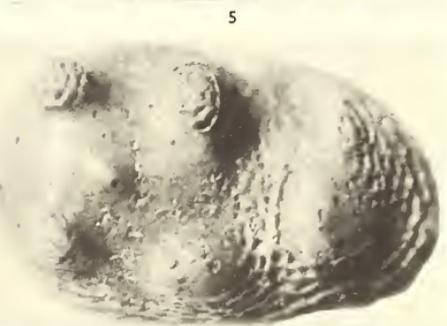
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BATE, Bathonian freshwater ostracods

both male and female dimorphs, 3 in the anterior half and 5 in the posterior half. Small additional nodes may be present close to the anterior and posterior margins and at the posterior cardinal angle. A narrow anterior vestibule is present. Radial pore canals short, thin, and numerous, approximately 27 anteriorly. Muscle scars an oblique row of 4 oval scars, no anterior scars observed.

Holotype. A male left valve BMNH Io2720, from horizon no. 4.

Description. Carapace bi-sulcate, oval-rectangular in outline with well-rounded anterior and posterior margins. Dorsal margin slightly convex in the left valve, the outline being broken posteriorly by the development of an accommodation groove, medially concave in the right valve. Ventral margin with a broad median incurvature. Vento-lateral margin projected ventrally, overhanging the ventral surface in side view, particularly well developed postero-laterally. Cardinal angles prominent with the posterior angle of the left valve being particularly acute, and possessing a short spine. Sexual dimorphism strongly apparent, the females being quite swollen posteriorly. Greatest length of carapace through mid-point, greatest height in the male dimorph either in the anterior or the posterior third, in the female dimorph the greatest height occurs in the posterior third. Although a complete carapace has not been found the greatest width would be in the posterior third. A flattened marginal border extends round the anterior. Carapace strongly tuberculate, possessing a maximum of 8 tubercles, one of which separates the two antero-dorsal sulci. This oval tubercle may, however, be missing, in which case the two sulci fuse to form a single broad depression. In front of the short anterior sulcus a low oval tubercle is developed just below the anterior cardinal angle. A second rounded tubercle occurs just below this anterior sulcus. Behind the second of the two sulci 5 tubercles may be developed. In position there is a vertical row of 3 tubercles immediately behind the sulcus and of these the dorsal and ventral ones are the most strongly developed, being directed to the rear. The median tubercle is often found out of position, further towards the posterior, or may be missing altogether. Two prominent tubercles are situated further back on the posterior part of the valve and again are situated one above the other. Shell surface is reticulate but often only in the anterior half, the ornamentation fading away towards the posterior. In some specimens, however, the reticulation is present over the whole of the valve, and in all specimens continues over the tubercles. Young instars show the same number and positioning of the tubercles. Ventral and underside of ventro-lateral surface strongly ornamented with about 4 longitudinal ridges. Particularly in the females further ridges may also be present on the ventro-lateral surface and around the posterior. Hinge lophodont: left valve with smooth terminal sockets of which the posterior socket is triangular in shape and the anterior socket is more elongate. Median bar long, smooth, and strongly developed. Above the median element an accommodation groove is developed in the posterior half of the valve only. Right valve with a terminal blade-like tooth and a smooth median groove which follows the outline of the dorsal margin by bending downwards medially and is most broadly developed in the anterior half. Inner margin and line of concrescence coincide except for around the anterior margin where medially a narrow vestibule is apparent. Radial pore canals numerous, short, and straight, approximately 27 in number anteriorly. Occasionally the canals can be seen to occur in pairs diverging towards the outer margin. Selvage prominent with a well-developed flange outside. This flange

extends completely around the free margin but is only poorly developed in the region of the ventral incurvature. An oblique row of 4 oval adductor scars has been observed, but so far no scars anterior to these.

Dimensions. Holotype: Male left valve, BMNH Io2720, length 1.03 mm.; height 0.56 mm. Paratypes: Male right valve, BMNH Io2726, length 1.05 mm.; height 0.59 mm. Female right valve, BMNH Io2725, length 1.15 mm.; height 0.70 mm.

Remarks. *Theriosynoecum kirtlingtonense* is the first species of the genus to be described from Bathonian sediments and is readily distinguished from other members of the genus by the number of tubercles present and their position on the carapace. For example *T. fittoni* (Mantell 1844, p. 545, fig. 2) from the English Weald Clay (Lower Cretaceous) possesses 10 tubercles whilst *T. wyomingense* (Branson 1935, p. 521, pl. 57, figs. 17-21) from the Morrison formation (Upper Jurassic), U.S.A. possesses 4 tubercles in the dorsal region of the carapace and a crescentic ventro-lateral ridge.

Genus TIMIRIASEVIA Mandelstam 1947

Type species. *Timiriasevia epidermiformis* Mandelstam 1947, by original designation.

Remarks. *Timiriasevia* is found in freshwater sediments of Mesozoic age and as such has only been described from the U.S.S.R., where some 16 species, all of relatively small size, are known. The species described here, *T. mackerrowi* sp. nov. and *Timiriasevia* sp. A constitute the first record of the genus outside the U.S.S.R.

Timiriasevia mackerrowi sp. nov.

Plate 111, figs. 2-12

Derivation. The species is named after Dr. W. S. McKerrow.

Material. Ten specimens (Io2734-43) from horizons nos. 1-4.

Diagnosis. Carapace oval in side view slightly constricted anterior of mid-point, greatly expanded posteriorly; heart-shaped in dorsal view. Valves taper to anterior. Left valve larger than right. Adult instars with prominently developed carapace in postero-ventral region. Ornamentation consists of a series of fine longitudinal ridges which follow the outline of the carapace to give a finger-print arrangement. Hinge lophodont. Inner margin and line of concrescence do not coincide anteriorly and posteriorly. Radial pore canals short, straight, simple, and fairly numerous, exact number not determined.

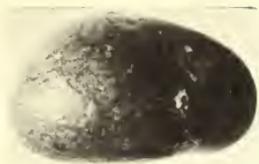
EXPLANATION OF PLATE 111

All figures $\times 65$.

Fig. 1. *Theriosynoecum kirtlingtonense* sp. nov. Dorsal view of right valve to show terminal hinge teeth, female paratype Io2725.

Figs. 2-12. *Timiriasevia mackerrowi* sp. nov. Figs. 2-5. Right, dorsal, ventral, and left views, complete carapace, holotype Io2734. Fig. 6. External view, right valve, paratype Io2740. Figs. 7, 12. Internal and dorsal views, right valve, paratype Io2741. Fig. 8. Internal view, juvenile right valve, showing narrow duplicature, paratype Io2737. Figs. 9-11. External, internal, and dorsal views, left valve, paratype Io2736.

Figs. 13-15. *Timiriasevia* sp. A. External, internal, and dorsal views, right valve, Io2744.



2



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15



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14



1



12

Muscle scars consist of a subvertical row of 4 oval adductor scars, a rounded antero-dorsal antennal scar, and a larger rounded antero-ventral mandibular scar.

Holotype. A complete carapace, BMNH Io2734, from horizon no. 1.

Description. Carapace oval in side view slightly constricted mid-dorsally just anterior of mid-point and with broadly convex dorsal margin and rounded anterior and posterior margins. Ventro-lateral margin convex, overhanging the ventral surface. Ventral margin convex, incurved antero-medially. Anterior narrower than posterior, greatest height being situated just behind valve mid-point. Greatest length of carapace passes very slightly below mid-point; greatest width in posterior third. Carapace heart-shaped in dorsal view tapering to the anterior, where there is a flattened marginal border; broadly expanded to the rear. The posterior expansion is most prominently developed in adult instars where the selvage moves inwards relative to the postero-ventral margin. Shell surface laterally ornamented by a series of fine longitudinal ridges which tend to follow the outline of the valve and are therefore somewhat concentrically arranged towards the outer margins. The result is to produce an ornament reminiscent of a finger-print. The ventral surface is similarly ornamented by fine longitudinal ridges. Left valve slightly larger than the right which it overlaps mid-ventrally and around the anterior and posterior. Postero-ventrally the left valve may have originally overlapped the right, but this is not clear in the present material. Hinge lophodont: left valve with long, narrow anterior socket and a shorter, wider, posterior socket. Both sockets are smooth and terminally open, being continuous with a narrow groove extending around the anterior and posterior, below the selvage. Median bar smooth and short. In the right valve the smooth terminal hinge elements are simply the anterior and posterior terminations of the prominent selvage. Median groove short but quite broad. Inner margin and line of concrescence do not coincide around the anterior and posterior margins, although the vestibule is extremely narrow. Radial pore canals short, straight, and simple anteriorly, the exact number has not been determined. Selvage very prominent around the free margin, in adults with a broad anterior and posterior flange outside. This flange is essentially composed of a broad flange groove and a narrower flange proper which extends along the ventral surface. Posteriorly, in adult specimens, because of the development of the postero-ventral part of the valve, the flange groove becomes broad and extends obliquely across that part of the valve. In more juvenile instars the flange groove is narrower and follows the outline of the posterior margin. It is only in these instars that the relationship of the inner margin to the line of concrescence may be determined posteriorly, as in adults the flange groove completely extends over the inner termination of the duplicature. Muscle scars as seen in a single specimen consist of an oblique row of 4 oval adductor scars, a smallish, round, antero-dorsal antennal scar, and a larger, apparently also rounded, antero-ventral mandibular scar.

Dimensions. Holotype: Carapace, BMNH Io2734, length 0.58 mm.; height 0.36 mm.; width 0.43 mm. Paratypes: Left valve, BMNH Io2736, length 0.60 mm.; height 0.37 mm. Juvenile right valve, BMNH Io2737, length 0.51 mm.; height 0.34 mm. Right valve, BMNH Io2740, length 0.63 mm.; height 0.37 mm. Right valve, BMNH Io2741, length 0.57 mm.; height 0.34 mm.

Remarks. *Timiriasevia mackerrowi* closely resembles *T. polymorpha* Mandelstam (*in*

Galeeva 1955, p. 61, pl. 15, figs. 4a, b, B) although it may, however, be distinguished by ornamentation which in *T. polymorpha* consists of a neat reticulation. *Gomphocythere* sp. l. Oertli (1957, p. 763, pl. 22, figs. 24-31) which is, in fact, a species of *Timiriasevia*, has a similar although much weaker ornament to that of the present species but differs in outline, tending to be much more square with the greatest height in the anterior and not the posterior third.

Timiriasevia sp. A

Plate 111, figs. 13-15

Material. A single right valve (Io2744) from horizon no. 4.

Description. Valve sub-rectangular in outline with the greatest length passing very slightly below mid-point and greatest height being in the anterior third. Dorsal margin convex with fairly prominent cardinal angles; anterior and posterior rounded; ventral margin convex with a shallow antero-median incurvature. Ornamentation consists of longitudinal low ridges along the ventral surface which laterally become terminally oblique V-ing towards the dorsal margin and tending to branch at about valve centre. A prominent lateral ridge extends along the ventro-lateral margin. Hinge lophodont, consisting of smooth terminal elements formed by the selvage, and an elongate, smooth, median groove. Inner margin and line of concrescence appear to be almost coincident anteriorly, not clear posteriorly. Radial pore canals short, straight, and simple, exact number not determinable. Selvage prominent with a flange outside. Flange groove of moderate width postero-ventrally. Muscle scars not seen.

Dimensions. Right valve, BMNH Io2744, length 0.50 mm.; height 0.27 mm.

Remarks. *Timiriasevia* sp. A is found associated with *T. mackerrowi* sp. nov., from which it is easily distinguished by shape, position of greatest height, presence of a prominent ventro-lateral ridge, and a more pronounced V-ing of the lateral ornament. These characters also distinguish this species from others previously described from the U.S.S.R.

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Manuscript received 25 November 1964

THE PALAEOONTOLOGICAL SOCIETY

Extracts from the Annual Report of the Council for 1964-5

MEMBERSHIP. On 31 December 1964 there were 1,269 members (646 Ordinary, 108 Student, and 515 Institutional), a net increase of 79 members during the year.

FINANCE. The year's working shows an excess of income over expenditure of £1,415 in contrast with the slight deficit estimated at the beginning of the year. This excess has been transferred to the Publications Reserve Account to cover the cost of the increased numbers of *Palaeeontology* to be printed in future. There has been a small under-expenditure on *Palaeeontology* compared with the estimates, and a sum of £343 unspent from the last part of Volume 6 in the previous year has also been brought forward. Sales of back numbers, etc., from Messrs. Blackwells have brought in a much larger amount than anticipated, but this is partly due to their changing over during the year from paying for parts as sold, to paying for stocks as received. The income from subscriptions has been approximately as expected, and so has the interest received. Administrative expenditure has been slightly less than anticipated.

'PALAEOONTOLOGY'. The four parts of Volume 7 (for 1964) were published during 1964-5. They contained 45 papers.

MEETINGS. Four meetings took place during 1964-5. The Association is grateful to the Council of the Geological Society of London, Professor J. F. Kirkaldy (Queen Mary College, London), and Professor E. A. Vincent (University of Manchester) for generously granting facilities for meetings, and to the Local Secretaries for their efficient services.

- a. The **Seventh Annual General Meeting** was held in the Rooms of the Geological Society of London, Burlington House, London, W. 1. on Wednesday, 4 March 1964, at 5.0 p.m. The Annual Report of the Council for 1963-4 was adopted and the Council for 1964-5 was elected. Professor T. Neville George delivered the **Seventh Annual Address** on 'Morphogeny in the Spirifers'.
- b. A **Field Demonstration Meeting** was held at Dudley on Saturday, 23 May 1964. The theme was 'The Wenlockian faunas of the Wren's Nest'. Dr. I. Strachan was Leader and Local Secretary.
- c. A **Discussion and Demonstration Meeting** was held in the Department of Geology, Queen Mary College, London, E. 1 on Saturday, 17 October 1964 at 2.30 p.m. There were twenty-one exhibits and about seventy persons attended. The Local Secretary was Dr. F. A. Middlemiss.
- d. A **Discussion Meeting** on 'Chemistry and Microstructure of Fossils' was held in the Department of Geology, University of Manchester, on Friday/Saturday, 18/19 December 1964. About eighty persons attended. Ten papers were read during three sessions and there were twenty-three exhibits. A Palaeeontological Association Dinner was held at Woolton Hall, University of Manchester on 18 December. Dr. F. M. Broadhurst was Local Secretary.

COUNCIL. The following were elected members of the Council of the Association for 1964-5 at the Annual General Meeting on 4 March 1964; *President*: Dr. L. R. Cox. *Vice-Presidents*: Professor T. Neville George, Dr. W. S. McKerrow, Professor F. H. T. Rhodes. *Treasurer*: Dr. T. D. Ford. *Assistant Treasurer*: Dr. C. Downie. *Secretary*: Dr. C. H. Holland. *Editors*: Mr. N. F. Hughes, Dr. Gwyn Thomas, Dr. I. Strachan, Dr. M. R. House. *Other members*: Dr. C. G. Adams, Dr. F. M. Broadhurst, Professor O. M. B. Bulman, Professor P. M. Butler, Dr. W. J. Clarke, Dr. G. Y. Craig, Dr. W. T. Dean, Dr. B. M. Funnell, Dr. F. A. Middlemiss, Mr. M. Mitchell, Dr. A. J. Rowell, Dr. R. J. G. Savage, Professor Scott Simpson.

BALANCE SHEET AND ACCOUNTS
FOR THE YEAR ENDING 31 DECEMBER 1964

BALANCE SHEET		£	s.	d.	£	s.	d.	
<i>Liabilities</i>								
Publications Reserve Account								
Balance as per Annexed Account					6,083	2	3	
Amounts Received In Advance								
Subscriptions for 1965					375	1	4	
Provision for Cost of Publication of <i>Palaeontology</i> , Vol. 7 as per Income and Expenditure Account					6,437	0	7	
Less Expenditure incurred to 31 December 1964					3,886	18	11	
						2,550	1	8
Sundry Creditors						10	10	0
 <i>Note:</i> No amount has been included in these Accounts for Subscriptions unpaid at 31 December 1964.								
						£9,018	15	3
 <i>Assets</i>								
Office equipment at cost					27	6	6	
Less Depreciation to date					4	5	4	
						23	1	2
Investments at cost:								
Equities Investment Fund for Charities—958 Units					999	18	3	
5% Defence Bonds					4,000	0	0	
						4,999	18	3
Sundry Debtors and Payments in Advance:								
Authors for reprints					137	14	0	
Advance payments <i>re Palaeontology</i> , Vol. 8					411	7	6	
						549	1	6
Cash at Bank—Deposit Account					2,686	11	10	
Current Account					760	2	6	
						3,446	14	4
						£9,018	15	3

Report of the Auditors to the Members of the Palaeontological Association. We have examined the above Balance Sheet and annexed Income and Expenditure Account which in our opinion give respectively a true and fair view of the state of the Association's affairs as at 31 December 1964 and of its income and expenditure for the year ended on that date.

BAKER BROS. HALFORD & CO.
Chartered Accountants.

INCOME AND EXPENDITURE ACCOUNT

<i>Expenditure</i>	£	s.	d.	£	s.	d.
<i>To Provision for Cost of Publication of Palaeontology</i>						
Vol. 7, Part 1	1,558	3	10			
Part 2	1,578	16	9			
Part 3	1,650	0	0			
Part 4	1,650	0	0			
	<u>6,437</u>	0	7			
<i>Less Excess provision for Vol. 6 not required</i>		343	0	6		
					6,094	0
						1
<i>Administrative Expenses:</i>						
Postage and stationery	76	3	4			
Insurance	1	16	3			
Audit Fee	10	10	0			
Miscellaneous	5	3	6			
Cost of distribution of publications	44	16	6			
Honorarium to Assistant Treasurer	25	0	0			
Duplicating and dispatching circulars, etc.	156	5	4			
						319 14 11
<i>Excess of Income over Expenditure for the year transferred to Publications Reserve Account</i>				1,415	15	7
				<u>£7,829</u>	10	7
<i>Income</i>						
<i>By Subscriptions</i>				4,923	18	4
Sales of publications				1,785	10	2
Interest received:						
5% Defence Bonds	200	0	0			
Bank Deposit Account	60	12	1			
Equities Investment Fund for Charities	35	18	6			
					296	10
						7
Special donations					16	10
						0
General donations:						
British Petroleum Co. Ltd.	250	0	0			
Texaco	175	0	0			
Burmah Oil Co. Ltd.	100	0	0			
Mobil Oil Co. Ltd.	100	0	0			
					625	0
						0
Miscellaneous receipts:						
Commission on sales of American Treatise	147	8	6			
Sundries	34	13	0			
					182	1
						6
				<u>£7,829</u>	10	7
PUBLICATIONS RESERVE ACCOUNT						
<i>To Balance as per Balance Sheet</i>				6,083	2	3
				<u>£6,083</u>	2	3
<i>By Balance at 31 December 1963</i>				4,667	6	8
<i>Less General Donations not received</i>				0	0	0
Excess Income over Expenditure for the year transferred from Income and Expenditure Account				1,415	15	7
				<u>£6,083</u>	2	3

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