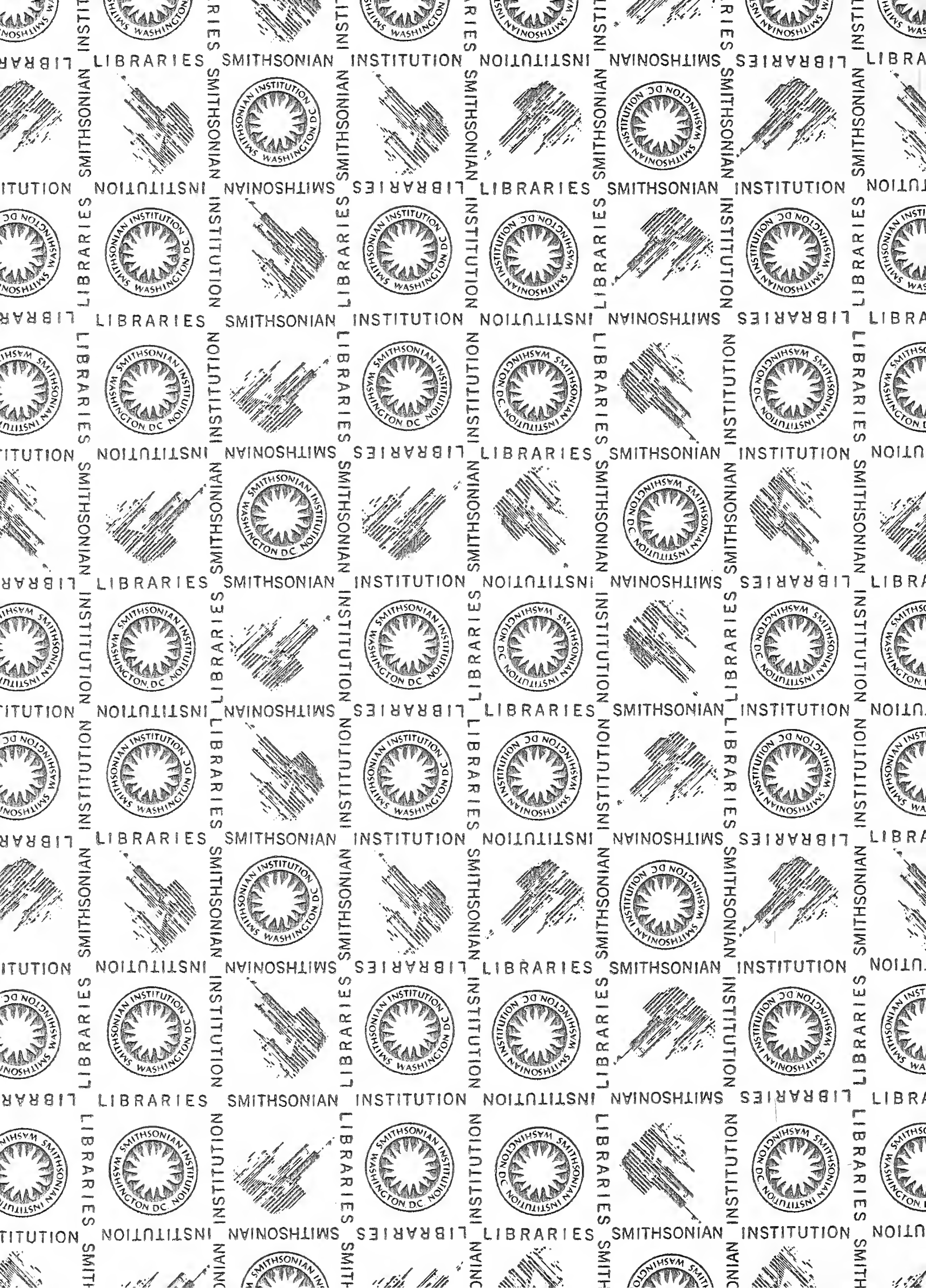

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PREDATION AND SHELL DAMAGE IN A VISÉAN BRACHIOPOD FAUNA

by HOWARD BRUNTON

ABSTRACT. A description is given of a variety of borings and signs of predation which occurred either during the life or after the death of some Viséan brachiopods. These structures, thought to have been produced by sponges, bryozoans, gastropods, and fish are of interest as indicators of environment and of the type of death assemblage met within these rocks.

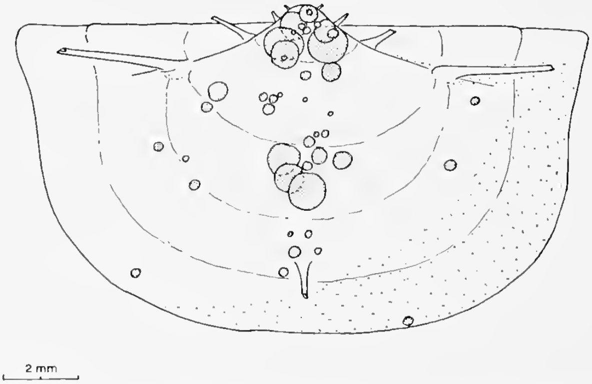
A RICH silicified brachiopod fauna obtained from Upper Viséan rocks in Co. Fermanagh, Northern Ireland, by the process of acid etching shows signs of predation or of having provided a habitat for organisms that required a hard surface upon or within which to live. The etched limestones were from a predominantly argillaceous series immediately underlying the widespread and prominent Dartry Limestone group. Within this fauna it is possible to distinguish damage indicating activity upon the living shells, and that reflecting settlement of organisms after death, in which only the shelly material was affected. It is assumed that any organism that lived wholly on the inner surfaces of valves, or which covered areas such as articulatory processes, or extended from the inner to the outer surfaces via the posterior margins must have colonized the valve after the death of the brachiopod.

Damage to living shells. One of the commonest signs of damage to brachiopod shells consists of neatly bored circular holes, usually penetrating the full thickness of the valve (Pl. 60, fig. 1). These holes vary from 0·1 mm. to just over 1 mm. in diameter and occur in as many as 50% of the collected pedicle valves of *Productina margaritacea*. However, the proportion is usually about 30% of pedicle valves and 15%, or less, of brachial valves, e.g. in *Rugosochonetes* cf. *celticus* about 35% of the pedicle valves and 7% of the brachial valves are bored. This higher occurrence of bored pedicle valves is probably a reflection of their accessibility to predators on or within the substratum, and of their immobility as compared to the free brachial valve. A surprising thing is that large valves may have three or four penetrating holes. It can only be assumed that the predators were only able to feed from the tissue close to the hole and bored in several places to expose more of the soft parts. The holes are commonly on the postero-median region of pedicle valves within about 6 or 7 mm. of the ventral beak, but not invariably so, and there seems to be no area in which they are particularly concentrated (text-fig. 1). Two borings out of forty-six into the pedicle valves of *P. margaritacea* were unsuccessful in that they do not penetrate the complete shell thickness. However, it is possible that these are the rare instances when predation was not successful in killing the brachiopod. This might have been possible if the boring took place just behind the shell edge and if the predator was unable to remove much of the internal mantle lobes. If this were so, the mantle could probably have repaired itself and subsequent deposition of secondary shell would have sealed the hole internally. From other evidence of damage to shells, it does seem that the

[Palaeontology, Vol. 9, Part 3, 1966 pp. 355–9, pl. 60.]

mantle was capable of repair allowing normal anterior growth to proceed and only leaving a temporary scar at the surface of the shell.

It is most probable that the predators involved were carnivorous gastropods living within the surface layer of the substratum. Modern gastropods, such as *Nucella*, bore similar holes, of about 1 mm. diameter, into lamellibranch shells. It is commonly noted that one valve of the lamellibranch is bored in preference to the other and this probably resulted from a preferred orientation of the shells, allowing greater accessibility to one valve. A comparable preference was shown by the Carboniferous predators for the pedicle valve of brachiopods. Fretter and Graham (1962) have pointed out that modern *Natica* only bores into shells when it is buried in sand. It is likely that the pedicle valves of the Fermanagh brachiopods were partially buried in a soft substratum and that gastropods, occupying a similar niche to *Natica*, bored these areas of accessible shell. A boring of particular interest, seen on a German Permian strophalosiid, is one in which the boring did not penetrate the shell and which has a small boss within the circular cavity. *Natica* is known to bore upon its prey by rasping away the shell at the edges of the hole, so leaving a central boss similar to that seen on the Permian shell. Within the etched faunas there is a paucity of gastropod remains, and only a few specimens of *Platyceras*, *Euomphalus*, *Bellerophon*, and Subulitidae are to be found in residues from near Derrygonnelly, Co. Fermanagh.



TEXT-FIG. 1. Diagram of the pedicle valve exterior of *Productina margaritacea* (Phillips) showing the positions and approximate sizes of 44 borings through the valves.

Modern boring naticids and muricacids have been traced back to the Triassic and Cretaceous periods respectively, and no Palaeozoic genera are known to have been borers. However, it is likely that this style of feeding was employed by gastropods, and Fenton and Fenton (1931) have discussed such borings found in American Palaeozoic brachiopods. They distinguish borings with bevelled edges, such as described in Tertiary lamellibranchs by Hayasaka (1933), from those with parallel sides, as described here. Fenton and Fenton suggested that *Platyceras* may have been related to naticids, and therefore a borer, but this concept is no longer commonly accepted.

On the external surfaces of some shells are slightly twisting open canal-like borings. In some specimens these extend right through the shell substance, in others they appear as simple pits and holes. In some specimens of *Eomarginifera* these borings more or less follow the radial ribbing and measure between 0·8 and 1·5 mm. wide (Pl. 60, fig. 2). Their alignment with the ribs may result from the shell substance being thinner in these regions because of the supposed underlying mantle canals, which may have provided nutrients to the predator. There is no clear evidence as to whether these borings were made during the brachiopod's life or after its death. But as the borings invariably seem to enter the shell from its external surfaces, and tend to be concentrated around the ventral umbo, it is more likely that they were made while the shell was alive. Had the borings been made purely as a protective habitat it is probable that the thicker parts of the shell, between the ribs, would have been excavated. The borings are quite unlike the neat holes described above or the ramifications of bryozoans described below, and are thought to have been made by sponges.

Distortion of the normal shell growth is not uncommonly seen, either locally confined to a small area, or more extensive and with scar shell material dwindling anteriorly into normal growth. Sarycheva (1949) described forms of damage to productoid brachiopods and distinguished several morphological types based upon the extent and position of the damage. She suggested that much of the damage resulted from mechanical action, such as waves and moving stones, but that the jaw action of predators (p. 288) may have caused the more sharply localized damage. Sarycheva also described the irregular internal morphology, such as muscle scars, seen on some specimens. I believe that predation and irregular growth resulting from the close proximity of a foreign object account for most of the distorted shells seen in the Fermanagh fauna.

Irregularities in growth commonly developed from an indentation in the shell, as if locally crushed, or as a cleft extending to the valve margin. In the former instance the point of crushing may be confined to one valve or involve both valves, as can be seen in a specimen of *Delepinea destinezi* (Pl. 60, figs. 6, 7) from limestones of Lower Viséan age bordering Lough Erne. In this example a series of points have scarred and crushed part of the dorsal valve, producing a similarly shaped series of protuberances from the surface of the pedicle valve. The damage must have been considerable and broken right through the shell from the dorsal surface. Secondary shell occurs anterior to the damaged areas, so that the shell must have survived and continued its growth. In the scar area, and beyond, the costellation is irregular and remains distorted for a distance of about 20 mm. It seems likely that death would have resulted had this damage been inflicted to the visceral region, but that the mantle epithelium of the brachial cavity was capable of reformation and continued growth. Growth-lines radiate antero-medianly from the lateral edges of the scars, showing the way in which growth must have continued sealing around the front of the damaged areas, and indicating that the mantle edge was probably damaged. A crest was formed where these two growing edges reunited in front of the broken shell. Signs of the mantle edge having been damaged are to be seen in some specimens of *Krotovia spinulosa* and *Eomarginifera* in which a continuous groove developed up to the anterior margin (Pl. 60, fig. 5). Here shell substance was only deposited from the sides and normal growth was not resumed. One specimen of *Eomarginifera* (Pl. 60, fig. 4) appears to have had a portion of its pedicle valve removed without having irrevocably damaged the mantle. Here shell growth was continued level with the inner surface of the existing shell, but was not only secondary shell, as the external ornament was soon redeveloped and the shell levels became equal towards the anterior margin. It seems, therefore, that even after having had part of its shell ripped away, the mantle and mantle edge were still capable of shell deposition. The continuation or redevelopment of the normal surface ornamentation is indicative of normal primary shell formation, at the mantle edge, while featureless scar material was probably the product of the mantle surface along with the normal secondary shell substance.

So far as is known, the only possible predators large enough to inflict damage on the scale described above would have been fishes, probably members of the cladodont sharks. The deep impression left in the brachial valve of *Delepinea*, described above, matches the shape that is typical for a cladodont tooth. The impression lacks the mark of the large central cusp because of the deposition of secondary shell in that region, but the smaller marginal cusps have all left their marks. The teeth of these vertebrates are to be found occasionally in nearby sediments.

Damage to Dead Shells. One of the commonest forms of damage to shells is that of infestation, most likely by ctenostomatous bryozoans, belonging to the subphylum Ectoprocta. These stoloniferous, zooid-bearing organisms usually appear on the inner surfaces of the valves as thin crack-like tubes of about 0·04 mm. diameter. Older regions of the colony increase in size to about 0·1 mm. diameter and are covered by minute pores, but a gradation between the two sizes is rare. The stolons may be on the valve surface or more or less sunk into the shell. Rarely they disappear completely into the shell and may penetrate to the outer surface. Branching is common and the stolons may cross one another. Colonization of the valves commonly took place in a more or less radial fashion from one or more centres of growth, which became enlarged and commonly deeply sunk into the shell. The surfaces of the stolons of these older regions are closely covered by minute pores, giving a granular appearance, as if the zooids were crowded over the entire surface rather than being arranged in single rows, as along the thin newly formed stolons.

Of the described ctenostomatous genera (Bassler 1953), the nearest in morphology is *Vinella* Ulrich 1890, although the Fermanagh ramifications have more than a 'single row of small pores' (1953, G35) on many of the stolons. Further study of these organisms may reveal that they should not be referred to *Vinella* and that the pores themselves housed polypides rather than being the scars from where the zooecia have broken.

EXPLANATION OF PLATE 60

All specimens are silicified and collected from Co. Fermanagh.

Fig. 1. *Krotovia sp.*, showing six holes bored through the pedicle valve. BB52878, ×4·1.

Fig. 2. *Eomarginifera sp.*, showing borings on the visceral region of the pedicle valve. BB52893, ×4·1.

Fig. 3. *Plicatifera plicatilis* (J. de C. Sowerby), damaged shell showing irregularly developed plication. BB52924, ×3·8.

Fig. 4. *Eomarginifera sp.*, damaged and bored pedicle valve. BB52925, ×3·7.

Fig. 5. *Krotovia spinulosa* (J. Sowerby), damaged pedicle valve. BB52923, ×4·1.

Figs. 6, 7. *Delepinea destinezi* (Vaughan), fragment of shell showing the damage believed to have been caused by a cladodont shark; viewed ventrally and dorsally. BB52927, ×1·2.

Fig. 8. *Schizophoria sp.*, fragment of pedicle valve showing worm tubes that developed over the dental plates. BB54634, ×4·1.

Fig. 9. Portion of the ventral interior of *Schizophoria* showing ctenostome infestation. BB52931, ×10·2.

Fig. 10. *Eomarginifera sp.*, portion of the upper, posteriorly directed, portion of the pedicle valve trail showing ctenostome infestation. BB52930, ×8·6.

Fig. 11. *Schizophoria sp.*, portion of the ventral interior showing a young ctenostome colony. BB52932, ×17.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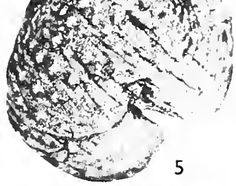
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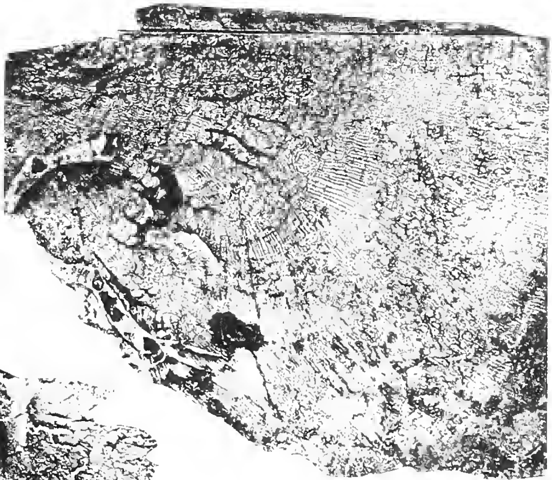
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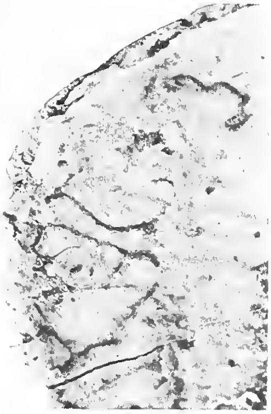
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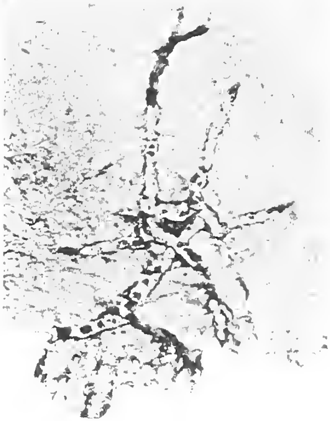
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BRUNTON, Predation and damage in Viséan brachiopods

As colonization of the shells always started on their inner surfaces and because the stolons extended over articulatory surfaces, it is clear that infestation took place after the death of the brachiopod. It is possible, therefore, to distinguish some of the shells that died and lay upon the sea floor prior to burial. An investigation into the sizes of shells and valves colonized within each species shows that the ctenostomes are commonly restricted to the larger specimens of the Fermanagh faunas. Juvenile and immature specimens of most species are rarely colonized and this suggests that only adult shells were being added to the death assemblage. Two species, a *Schizophoria* and *Rugosochonetes*, do provide young valves, down to about 3 mm. long, which are colonized by the bryozoans. These must have had a higher infant mortality rate than other species in the fauna and this may indicate that the habitat was not the optimum for these species.

The presence of these colonizing epifaunas can be taken as evidence of a period in which the skeletal parts lay unburied upon the sea floor. Thus, it cannot be assumed that such a community was killed by the sudden advent of sediment and consequent burial.

Valves in which the stoloniferous Ctenostomata are developed commonly have superficial irregularly winding and slightly coiled tubes of 0·1 to 0·25 mm. diameter. These show no external ornament or structure, but appear to incorporate fine sediment and are probably the remains of tubiferous marine worms similar to the polychaetes *Serpula* and *Spirobis*. It is quite clear that these worm tubes were late in development as they are adherent to the free inner surfaces of shells, and commonly cover bryozoan stolons. Like the stolons, they may partially fill the sockets or cover the teeth of *Schizophoria* or *Rhipidomella* (Pl. 60, fig. 8). The tubes were probably calcareous, with a little adherent fine sediment, and the silicification has bonded the two together.

It may be significant that brachiopods seen in the older black bituminous and pyritic limestones of Lower Viséan age, or those from the overlying reefal limestones of Knockmore, 3¼ miles south-south-west of Bunnahone, do not appear to have been subjected to attack by boring organisms other than gastropods.

It is clear that the brachiopods of the communities studied were not only prey to carnivorous animals, but provided a habitat for other organisms after their death, when their shells were added to the skeletal debris on the sea floor. Such debris was in turn of value to larval brachiopods of subsequent generations when they settled to the sea floor and became attached by their pedicles, cementation, or clasping spines.

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FOSSIL WOOD OF ANACARDIACEAE FROM THE BRITISH EOCENE

by DONALD W. BRETT

ABSTRACT. Silicified wood from the sands of the Woolwich Series (Landenian) at Herne Bay, Kent, is described as *Edenoxylon aemulum* sp. nov. (Anacardiaceae). The specimen closely resembles wood described from the Lower Eocene Green River Formation of Wyoming, U.S.A., as *Edenoxylon parviareolatum* Kruse. The character of the wood is essentially that of a tropical type with no strongly marked seasonal increments in its radial growth.

THE fossil wood described in this paper is closely similar to the wood of *Edenoxylon parviareolatum* Kruse (1954) which is founded on small stems and roots from the Lower Eocene of Wyoming, U.S.A. The following diagnoses are based on the holotype (stem) of *E. parviareolatum* Kruse, which I have examined, and the new British material which is named *E. aemulum* sp. nov.

Family ANACARDIACEAE
Organ-genus EDENOXYLON Kruse

Diagnosis. Fossil secondary wood, or stems or roots with some secondary wood. Rays of two kinds: narrow 1–2 seriate, and wider fusiform rays containing ducts. Vessels solitary and in radial multiples (2–9), about 50 per sq. mm; diameter 20–140 μ; intervascular pitting typically alternate but opposite in places, minute (about 5 μ); perforations simple, more or less oblique. Wood parenchyma scanty paratracheal. Pitting between vessels and ray cells and between vessels and parenchyma irregularly elliptical, about twice as long as broad, or sub-circular. Remainder of wood tissue narrow fibres, mostly septate.

Type species. *Edenoxylon parviareolatum* Kruse.

Description of type specimen. Stem about 3 cm. wide with medulla, secondary xylem, and phloem. Vessels about 50 per sq. mm; 20–70 μ diameter. Narrow rays mostly uniseriate, rarely biseriate in part; 2–20 cells high; about 20 per mm. Secondary phloem containing vertical ducts mainly in concentric rows, fibres, and stone cells. (Pl. 61, figs. 1, 2.)

Holotype. B-3280 in Palaeobotanical Collection, University of Cincinnati, Ohio, U.S.A.

Horizon. Lower Eocene of Eden Valley, Wyoming, U.S.A.

Edenoxylon aemulum sp. nov.

Plate 61, figs. 3–7

Diagnosis. Secondary xylem. Vessels about 44 per sq. mm; 30–140 μ diameter. Narrow rays almost all uniseriate nearer centre of axis; further out almost all biseriate and 5–9 cells high, or higher when including uniseriate parts. Rays average about 8 per mm.

Holotype. V44297 in Department of Palaeontology, British Museum (Nat. Hist.), London.

Horizon. Lower Eocene, Landenian; Herne Bay, Kent, England.

[Palaeontology, Vol. 9, Part 3, 1966, pp. 360–4, pl. 61.]

Description. The material consists of several fragments taken from a large piece of silicified wood lying on the beach at Bishopstone, Herne Bay, Kent. Borings through the wood made by a species of *Teredo* are infilled with a greyish sand quite unlike that of the existing beach but matched in the lower beds of the Woolwich Series which overlie the Thanet Sands in the cliffs at Herne Bay. It is deduced from this that the fossil derives from the Woolwich beds.

The wood is diffuse porous. There is an indistinct and irregular periodicity evident in the dimensions of the fibres and vessel chains; and some broader rings have a definite late-wood with smaller and fewer vessels. In transverse section the vessels are solitary and in radial multiples and chains of 2–6 (exceptionally 8); solitary vessels and groups together average 44 per sq. mm.; tangential diameter averages 95 μ but the range is wide, 30–140 μ. Perforations are simple, more or less oblique; intervascular pitting is alternate, about 5 μ. Pits to the ray cells are irregularly elliptical, about twice as long as broad, commonly obliquely inclined or horizontal, or sub-circular and little wider than the intervascular pitting. Pitting between vessels and wood parenchyma is similar to the ray pitting but more commonly horizontal and elliptical (i.e. scalariform). Tyloses fill all the vessels. The fibres are narrow, mostly less than 15 μ wide, thin walled, septate and with dark contents, in strict radial rows forming a uniform tissue. Pits not seen. Wood parenchyma is scanty paratracheal. The rays are of two types, low narrow rays and larger fusiform rays containing radial ducts, together about 8 per mm. (range 6–12). Nearer the centre of the axis the narrow rays are almost uniseriate, 3–16 cells high, and the fusiform rays are only a little higher than the taller of the narrow rays and 3–4 cells wide at the duct. In the more mature wood the narrow rays are almost all biseriate, 5–9 cells high, the rarer uniseriate rays being only 3–4 cells high. Where the biseriate rays include a uniseriate portion they may reach a height of 14 cells. These narrow rays are markedly heterogeneous in cellular composition with a marginal row of square or upright cells and procumbent cells forming the body of the ray. Upright cells frequently occur in the biseriate portions however and included uniseriate portions are of upright cells. The fusiform rays containing ducts are up to 1 mm. high and 0·25 mm. across the widest part of the duct. Occasionally two ducts occur in the ray. The duct is surrounded by 2–3 layers of thin walled procumbent cells much narrower than those of the rest of the ray and with more oblique tangential walls. The cellular composition is otherwise similar to that of the smaller rays. Most of the cells in all types of rays are richly pitted and have dark contents and many show evidence of having contained crystals.

Comparison. The material on which the new species is based differs very little from the wood of *E. parviareolatum.* The vessels of the new species are a little wider and fewer per sq. mm.; the narrow rays are more commonly biseriate and on the whole not so high and are more widely spaced.

Such small variations in vessel size and number, and ray width and height are commonly found between different samples of a single living species in which case they may be the result of differences in the age or size of a tree, conditions of growth, relation to branches, and so on. The scarcity of biseriate rays in the younger wood of the new material accentuates the similarity, since the type specimen is obviously a young stem or branch while the new material consists for the most part of more mature wood.

The possibility that all the material belonged to a single natural species of Eocene times cannot be excluded. Nevertheless I have felt justified in giving the English specimen a new name, more particularly because the type species includes roots and stems and secondary phloem is present in both. The specific epithet has been chosen to stress the similarities between the new species and the type species.

AFFINITIES OF THE GENUS *EDENOXYLON*

Kruse (1954) placed Edenoxylon in the Anacardiaceae 'without too much confidence' since it could not be identified with any modern genus of the family. My own findings confirm this.

Two families of dicotyledons, the Anacardiaceae and Burseraceae, have wood structure similar to that of *Edenoxylon*. The similarity between the wood of these families is well known and has been put forward as evidence of their close relationship; the families had earlier been united in the Terebinthaceae even before the wood anatomy was well known. More recent studies of wood anatomy have suggested that the Anacardiaceae and Burseraceae should be considered along with the Meliaceae, Sapindaceae, Rutaceae, and Simarubaceae as a single phyletic complex (Heimsch 1942, Webber 1941).

In the Table below are set out some of the more important and variable characters of the wood of the five tribes of the Anacardiaceae and of the Burseraceae and *Edenoxylon*.

	Mangiferae	*Spondiae*	*Rhoideae*	*Semecarpeae*	*Dobineae*	*Burseraceae*	*Edenoxylon*
Vessel multiples	+ chains in few spp.	+ chains rare	+	+	seldom	+ chains in few spp.	+ chains
Banded parenchyma	+	—	rare	extended aliform	—	—	—
Scanty paratracheal parenchyma	few spp.	+	+	—	+	+	+
Radial ducts	+	+	+	1 genus	—	+	+
Septate fibres	1 genus	+	+	—	+	+	+
Opposite inter-vascular pitting	—	1 sp.	some genera	—	+	—	small areas
Unilaterally compound pitting	—	—	—	—	—	+	—

(Data chiefly from Heimsch 1942, Metcalfe and Chalk 1950, Webber 1941.)

+ commonly present in tribe or family; — not reported in tribe or family.

These signs denote presence or absence in *Edenoxylon*.

It will be seen that considering distribution of wood parenchyma and the occurrence of septate fibres and radial canals, *Edenoxylon* has most in common with the Spondiae and Rhoideae of the Anacardiaceae and with the Burseraceae. The Burseraceae however are usually readily distinguished by the unilaterally compound pits communicating between vessels and ray cells. Furthermore the presence of small areas of opposite intervascular

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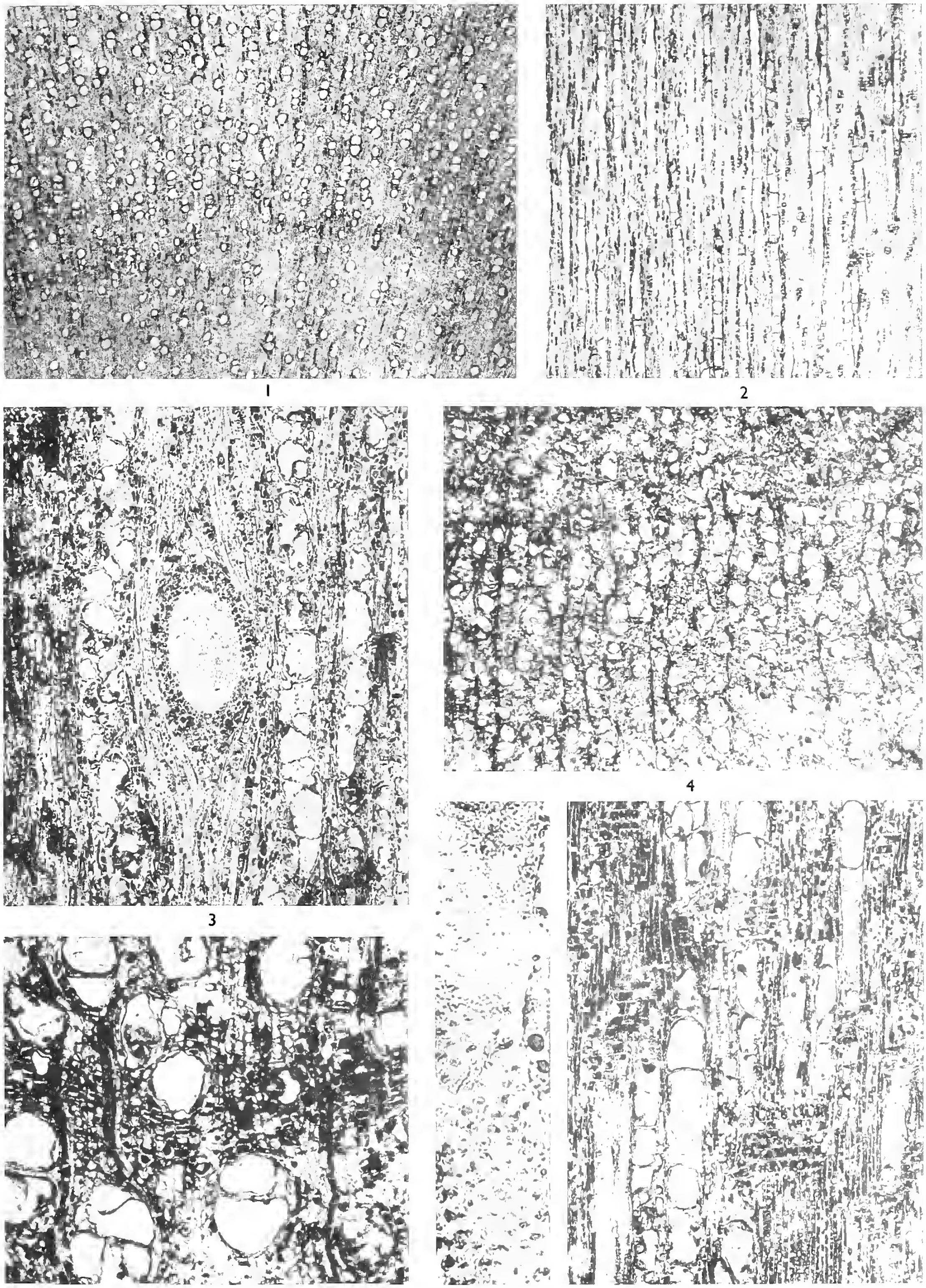
EXPLANATION OF PLATE 61

Figs. 1, 2. *E. parviareolatum*. 1, Transverse section of secondary wood of holotype; ×20. 2, Longitudinal section of same, mostly tangential, more or less radial to the right; ×20.

Figs. 3–7. *E. aemulum*. 3, Tangential section showing a large fusiform ray with duct; some narrower rays and vessels filled with tyloses are also shown; ×70. 4, Transverse section showing vessel multiples and numerous narrow rays, ×35. 5, The same at higher magnification showing 2- and 3-seriate rays and the uniform tissue, probably mainly septate fibres, between the large vessels; ×120. 6, Intervascular pitting on vessel wall; the arrangement is seen to be irregularly alternate; ×500. 7, Radial longitudinal section; ×70.



BRETT, Wood of Eocene Anacardiaceae

pitting in *Edenoxylon* is an additional feature linking the fossil genus with the Rhoideae and Spondiae.

The name '*parviareolatum*' was given to the type because the small intervascular pits (4–5 μ) present in this species 'are not characteristic of the family as a whole' (Kruse 1954). In the Rhoideae, however, small pitting is common and the larger intervascular pitting which is characteristic of the Mangiferae is rarely found. Intervascular pitting of about the same order of size as that of *Edenoxylon* is to be found in some species of *Rhus* (*R. toxicodendron* 6 μ, *R. thunbergii* 5 μ). and very small pitting is reported in *Faguetia* and *Trichoscypha* (Metcalfe and Chalk 1950), all three genera belonging to the Rhoideae.

DISCUSSION

Several fossil woods have been ascribed to the Anacardiaceae, and five organ-genera named. The first to be described, the genus *Rhoidium* Unger (1850), has been used by authors for fossil wood resembling the wood of *Rhus* spp. The genus *Anacardioxylon* Felix (1882, diagnosis 1894) was erected for fossil wood resembling wood of *Spondias*. Neither *Rhoidium* spp. nor *Anacardioxylon* spp. have radial ducts, with the exception of *Anacardioxylon mollii* Krausel which was subsequently called *Sumatroxylon* by den Berger because of doubt about its affinities (Edwards 1931). Radial ducts occur commonly throughout the family, in both *Rhus* and *Spondias*, and in the other three genera of fossil woods.

Glutoxylon Chowdhury (1934, diagnosis 1936) has been characterized so as to include wood of a type common to the living genera *Gluta* and *Melanorrhoea*. In addition to *Edenoxylon* another new organ genus, *Schinoxylon*, was described by Kruse (1954), and this is said to differ from the living *Schinus* only in the pattern of the vessels in transverse section.

Although not recorded previously from the lower beds of the English Tertiary (the wood described above has been noted in Brett 1960 and Chandler 1964) the Anacardiaceae are well represented among the fruits and seeds of the London Clay and the succeeding Lower Bagshot and Bournemouth Beds. Reid and Chandler (1933) described eleven fossil species. Only three living genera were recognized. Most of the remaining specimens were assigned to four new genera presumed to be extinct, and it seemed to these authors that some of the features characterizing the fossil genera have been recombined in the living genera (Reid and Chandler 1933, p. 299). All the fossils were, however, assigned to Spondiae. In addition to three species assigned to the Spondiae, the Lower Bagshot and Bournemouth Beds yielded four or five species of *Rhus* (Chandler 1962, 1963, 1964). Identifications of pollen grains from the London Clay (Sein 1961) and the Oligocene of the Isle of Wight (Pallot 1961) have also confirmed the presence in these floras of Spondiae and Rhoideae.

Of the few plants so far known from the Thanet Sands and Woolwich and Reading Beds several suggest a lowland tropical environment whilst others present a more temperate aspect. The situation is in fact similar to that of the London Clay flora and it is becoming clear that the vegetation of the Landenian probably differed very little, if at all, from that of the succeeding Ypresian (Chandler 1961, 1964: a full discussion of recent work is given in the latter). The character of the anacardiaceous wood *Edenoxylon* is essentially that of a tropical type with no strongly marked seasonal increments in its radial growth. In Wyoming *Edenoxylon* is found among other fossil woods of tropical or subtropical affinities including palm stems. Palm stems are also known from the Landenian of England, several having been found by collectors but none described.

The overall aspect of the vegetation of the Green River Formation, from which the Wyoming woods were derived, is warm temperate or subtropical. Like most large fossil floras the various remains (leaves, pollen, wood) probably include elements of a more extreme nature but, unlike the Lower Eocene floras of southern England, the Green River flora from Wyoming does not include any large assemblage of lowland rain forest types. Considering the present altitude of the Green River fossiliferous beds (5,000–10,000 ft.) it is not improbable that the area was already at some considerable height above sea level in Eocene times, although it has been concluded that the altitude could not have been above 3,000 ft. (Brown 1934).

Acknowledgements. I am indebted to the following for their help: the Director of the Royal Botanic Gardens, Kew, and Dr. C. R. Metcalfe, for access to the Kew collection of specimen slides and for permission to work in the Jodrell Laboratory; Dr. W. L. Stern, Curator of the Samuel James Record Memorial Collection, School of Forestry, Yale University for specimens of wood of Anacardiaceae; the Curator of the Palaeobotanical Collection of the University of Cincinnati, Ohio, for the loan of the type specimen of *Edenoxylon.*

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PARACHONETES, A NEW LOWER AND MIDDLE DEVONIAN BRACHIOPOD GENUS

by J. G. JOHNSON

ABSTRACT. *Parachonetes* is proposed as a new chonetid genus with *Chonetes macrostriata* Walcott from Nevada as its type species. It is thought to have been derived from the protochonetid genus *Eccentricosta*. Barrande's species *Chonetes verneuili* is assigned to *Parachonetes* as are two named species from south-eastern Australia. *Parachonetes* is absent in eastern North America, but is represented in Nevada, the Canadian Arctic, Novaya Zemlya, the Ural Mountains, Central Asia, south-eastern Asia, Czechoslovakia, and in south-eastern Australia.

IN the course of studies elucidating the Lower Devonian brachiopods of central Nevada (Johnson, in prep.) Walcott's species '*Chonetes*' *macrostriata* was studied through the preparation of internal moulds and found to be unassignable to any chonetid genus previously described. Further work on some excellent material of Barrande's species '*Chonetes*' *verneuili* from the Schary Collection at the Museum of Comparative Zoology, Harvard, showed that that species is congeneric. At the time these studies were in progress Talent (1963) published descriptions and illustrations of chonetids from the Lower Devonian of Victoria, Australia, which proved also to belong to the new genus. In addition silicified chonetids sent by Dr. Talent from the *Receptaculites* Limestone of New South Wales are illustrated herein and show the cardinalia very well.

SYSTEMATIC PALAEONTOLOGY

Superfamily CHONETACEA Bronn 1862
[*nom. transl.* Shrock and Twenhofel 1953 (*ex* Chonetidae Bronn 1862)]
Family CHONETIDAE Bronn 1862
Subfamily DEVONOCHONETINAE Muir-Wood 1962

Discussion. The two principal Silurian chonetid genera, *Protochonetes* and *Strophochonetes*, are much alike internally as a recent investigation of the interior of *Strophochonetes* has shown (Johnson, in prep.) and it seems likely that they shared a common ancestor. *Strophochonetes*, however, was assigned to a separate subfamily by Muir-Wood (1962, p. 40). *Parachonetes* gen. nov. is here assigned to the Devonochonetinae because of its close relation to *Eccentricosta* which must have been derived from *Protochonetes*, all of which suggest that a more critical appraisal needs to be made into the phylogenetic relations of *Protochonetes* and *Devonochonetes*. If the latter genus was indeed derived from the former, *Parachonetes* is a member of the Devonochonetinae although antipodal to the type genus *Devonochonetes*.

Genus PARACHONETES gen. nov.

Type species. *Chonetes macrostriata* Walcott 1884, p. 126.

Diagnosis. Protochonetids with low rounded costae originating along the hinge-line of some specimens. Brachial valve cardinalia characterized by a pair of posteriorly conjunct

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cardinal process lobes that develop an externally quadrilobate myophore and a more or less deep alveolus. Dorsal median septum present except on small specimens.

Discussion. Parachonetes is erected to include a group of chonetid species that were widespread geographically during most of Early Devonian and early Middle Devonian time. Medium and larger size shells are among the largest Lower Devonian chonetids and are deeply concavo-convex. In addition to the type species which is presently known only from Nevada, the genus includes *Chonetes verneuili* Barrande, which is widely reported in the Bohemian-Uralian faunal province in Czechoslovakia (Barrande 1879), Central Asia (Nikiforova 1937), the Ural Mountains (Rzhonsnitskaya 1960, p. 128), and as far north as Novaya Zemlya (Tscherkessowa 1960, p. 178). Topotype material of '*Chonetes*' *verneuili* was studied by the writer who was able to prepare internal moulds of both valves to confirm the generic assignment. These specimens are illustrated in figs. 4–8 on Plate 63. *Parachonetes verneuili* is a large species with much more regular ribbing than *P. macrostriatus* and in the brachial valve the alveolus of *P. verneuili* is shallower and broader. The writer has seen fragmentary remains of chonetids like *P. verneuili* from the upper Lower Devonian Stuart Bay Formation on Bathurst Island in the Canadian Arctic.

Chonetes kwangsiensis Wang (1956, p. 385, pl. 1, figs. D1–4) and *Strophomena carnica* Gortani (1915, p. 122, pl. 1, fig. 3) are species that resemble *Parachonetes* externally; however, their internal structures are unknown. The species *Plectambonites yenlacensis* Mansuy (1916, p. 49, pl. 7) probably is a *Parachonetes.* It has the typical shape and ribbing, a pair of lateral septa and a median septum in the brachial valve, and the posterior impression of the cardinal process is multilobate (Mansuy 1916, pl. 7, fig. 3*b*). Patte (1926, p. 62) suggested that several of the Indochinese chonetoids given different names by Mansuy, including *P. yenlacensis*, are no more than junior synonyms of *Chonetes zeili* Mansuy (1908, p. 36). It seems highly probable that this is true, but the figured specimens of Mansuy (1908, pl. 7, fig. 13) are insufficient for firm assignment to *Parachonetes.*

In addition to the North American and Eurasian occurrences of *Parachonetes*, the genus is represented by *Chonetes baragwanathi* Gill and by *Chonetes? suavis* Talent, both of which have recently been described and illustrated by Talent (1963) from the Lower Devonian of Victoria, Australia. *P. suavis* may prove to be synonymous with *P. baragwanathi* since the principal distinction of the former is its split dorsal septum, a feature that is evanescent in *P. macrostriatus.* There remains some uncertainty regarding generic affinities of *Chonetes? foedus* Talent (1963, pl. 37, 38).

Étienne Patte (1926, pp. 62, 63) first called attention to the resemblance between *P. verneuili*, *P. macrostriatus*, and several strongly concavo-convex coarse-ribbed species of Mansuy from Indochina. His astute evaluation, based wholly on considerations of external morphology, are borne out by the present investigation of the interior structures. Patte suggested further (1926, p. 63) that the Indochinese species '*C.*' *zeili* may be only a variety of *P. macrostriatus.*

Parachonetes macrostriatus and *P. verneuili* appear not to be threatened by senior synonyms, nor is there any basis to merge them together, and they may be usefully employed to split *Parachonetes* into two species groups, (1) the *macrostriatus* group with low, irregular, and commonly bifurcating costae and (2) the *verneuili* group, with even, more elevated costae that rarely bifurcate. On this basis group 1 comprises species from Nevada, south-east Asia, and Australia while group 2 is restricted to Bohemia, the Carnic Alps?, Central Asia, the Ural Mountains, Novaya Zemlya, and the Canadian Arctic.

Comparison. Eccentricosta is smaller and less strongly concavo-convex than *Parachonetes* and on this basis *Eccentricosta* and small *Parachonetes* are indistinguishable. Internally the cardinal process lobes of *Eccentricosta* are relatively smaller and more blade-like than the stout curved lobes of *Parachonetes* and the latter bears a well-defined alveolus. In addition, the elaborate posterior quadrilobation of the cardinal process of *Parachonetes* is not developed in *Eccentricosta* (Berdan 1963, text-fig. 1c; Bowen, in press, pl. 2, fig. 9) nor is there a dorsal median septum in *Eccentricosta* although this is a well-developed structure in *Parachonetes*.

Parachonetes macrostriatus (Walcott)

Plate 62, figs. 1–17; Plate 63, figs. 1–3

1884 *Chonetes macrostriata* Walcott, p. 126, pl. 2, fig. 13 (?); pl. 13, figs. 14, 14*a*, 14*b*, 14*c*.
1940 *Chonetes macrostriata* Merriam, p. 55, pl. 6, fig. 4.
1944 *Chonetes macrostriatus* Cooper, p. 345, pl. 134, fig. 16.
1962 *Longispina macrostriatus* Muir-Wood, p. 47.

Discussion. Muir-Wood (1962, p. 47) incorrectly assigned this species to *Longispina*, but she evidently had not seen interiors of either valve since they do not show any marked resemblance to the interiors of *Longispina* (cf. Muir-Wood 1962, p. 46, figs. 7 A, B).

Description. Exterior. The shells are transversely shield-shaped with the cardinal angles approximately equal to right angles in small shells. Large shells are commonly auriculate. The valves are concavo-convex in lateral profile, becoming strongly concavo-convex in large specimens. The hinge-line is long and straight and is the place of maximum width. Very small spine bases are commonly developed along the hinge-line, but spines are seldom seen. On one small shell measuring 8 mm. along the hinge-line there are six short tubular spines on either side diverging laterally from the hinge-line at varying angles from approximately 30 to 50 degrees. The spines are hollow and are filled with matrix like that of the enclosing rock. The ventral beak is small, inconspicuous, and strongly incurved. The interarea of the pedicle valve is orthocline to anacline, commonly orthocline laterally, but anacline near the middle. The interarea of the brachial valve is hypercline. The delthyrium is triangular and very broad at its base enclosing an angle of greater than 100 degrees; however, the teeth fill a large portion of the lateral part of the delthyrium at the hinge-line leaving an opening that is semicircular rather than triangular.

The ornament consists of irregular low radial costae emanating from the beak, and on large specimens also along the lateral portions of the hinge-line. Costae commonly and irregularly increase in number by bifurcation and there may be 5 to about 8 costae in a space of 5 mm., 10 mm. anterior to the beak.

Interior of pedicle valve. The hinge teeth are small and triangular in cross section and attach directly to the interior of the shell at the inner edges of the delthyrium. There is a low median septum developed slightly anterior to the apex of the beak and it may continue anteriorly, dividing the vascular trunks. The median septum may be slightly thickened or swollen at its posterior end. The diductor muscle scars are broad and flabellate, lightly impressed, and they blend with the interior of the shell imperceptibly along their anterior margin. The adductor scars are elongate and well defined. They are commonly fairly well impressed posteriorly and blend with the interior of the shell anteriorly. Laterally they may be deeply impressed or may be bounded by short, slightly arcuate, muscle bounding ridges. The vascular trunks are variably impressed anterior to the adductor scars. The internal surface of the valves is commonly pustulose due to the internal projection of the pseudopunctae and it is variably crenulated by the impress of the costae.

Interior of brachial valve. Broadly divergent sockets are widely set apart along the posterior edge of the shell and are bounded medially by low rounded socket plates. The socket plates join with a pair of posteriorly conjunct plates that form the cardinal process. The area between the cardinal process lobes is not only enclosed, but is depressed below the level of the surrounding shell material to form an approximately circular, broad, deep alveolus. On small shells the two cardinal process lobes are still partially separated medially at their posterior ends, but in larger specimens shell material is deposited around the plates, forming a more or less complete U-shaped structure, on the

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EXPLANATION OF PLATE 62

Figs. 1–17. *Parachonetes macrostriatus* (Walcott). '*Spirifer*' *pinyonensis* zone (Emsian), central Nevada. 1, Ventral view of the lectotype (×2), USNM 13809, Lone Mountain. Illustrated by Walcott (1884, pl. 13, fig. 14*b*). 2, Ventral view of a paratype (former cotype) (×1), USNM 13809A, Lone Mountain. Illustrated by Walcott (1884, pl. 13, fig. 14). 3, Ventral view (×3), USNM 140435, locality 10769, northern Roberts Mts. 4, Ventral view (×2), USNM 140436, locality 10709, Sulphur Spring Range. 5, Dorsal view of internal mould (×2), USNM 140437, locality 10762, northern Simpson Park Mts. 6, 7, Posterior view of middle part of hinge line (×5) and dorsal view (×1), USNM 140438, Lone Mountain. 8, Ventral view (×1), USNM 140439, locality 10788, Roberts Creek Mtn. 9, Rubber impression of internal mould of a small brachial valve (×5), impression of USNM 140440, locality 10729, McColley Canyon, Sulphur Spring Range. 10, 11, Internal mould of brachial valve and rubber impression (×3), USNM 140441, locality 10729, McColley Canyon, Sulphur Spring Range. 12, 13, Internal mould of brachial valve and rubber impression (×2), USNM 140442, locality 10729, McColley Canyon, Sulphur Spring Range. 14, Posterior view of internal mould of pedicle valve (×2), USNM 140443, locality 10705, northern Roberts Mts. 15, Internal mould of pedicle valve (×2), USNM 140444, locality 10729, McColley Canyon, Sulphur Spring Range. 16, 17, Posterior and ventral views of internal mould of pedicle valve (×1·5), USNM 140445, locality 10729, McColley Canyon, Sulphur Spring Range.

EXPLANATION OF PLATE 63

Figs. 1–3. *Parachonetes macrostriatus* (Walcott). Posterior, ventral, and anterior views of pedicle valve (×1), USNM 140446, locality 10705, '*Spirifer*' *pinyonensis* zone (Emsian), northern Roberts Mountains, central Nevada.

Figs. 4–8. *Parachonetes verneuili* (Barrande). Upper Koneprusy Limestone (lower Emsian), Czechoslovakia. 4, Posterior view of internal mould of pedicle valve (×2), USNM 140447. 5, 6, Posterior view (×2) and ventral view (×1) of internal mold of pedicle valve, Schary Collection, Museum Comparative Zoology, Harvard, 9441. 7, 8. Dorsal views (×1·5 and ×3) of internal mould, Schary Collection, Museum Comparative Zoology, Harvard, 9440.

Figs. 9–14. *Parachonetes* cf. *P. macrostriatus* (Walcott). *Receptaculites* Limestone, Taemas, N.S.W., Australia. 9, Dorsal view (×2), Geol. Surv. Victoria 61055. 10, Interior of brachial valve (×6), Geol. Surv. Victoria 61056. 11, Interior of pedicle valve (×3), Geol. Surv. Victoria 61054. 12, 13, Interior and posterior views of brachial valve (×6), Geol. Surv. Victoria 61058. 14, Interior of brachial valve (×3), Geol. Surv. Victoria 61057.


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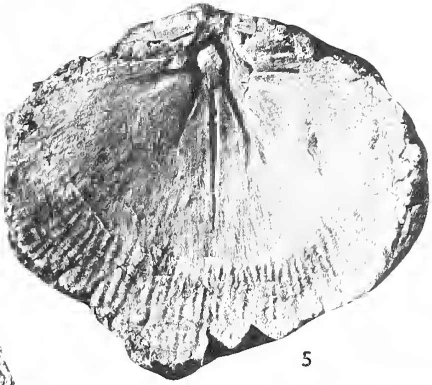
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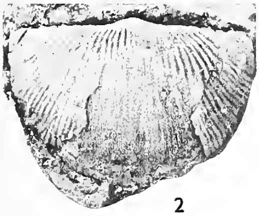
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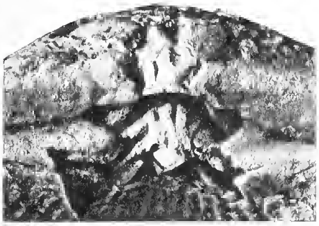
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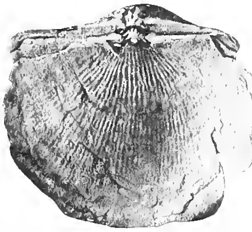
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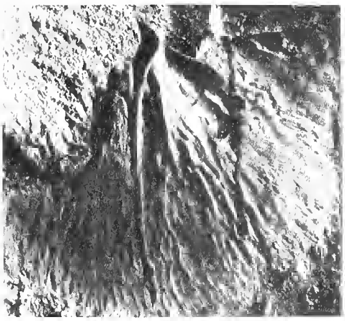
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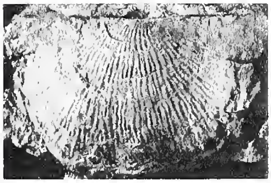
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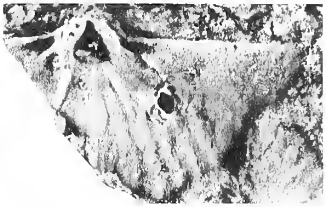
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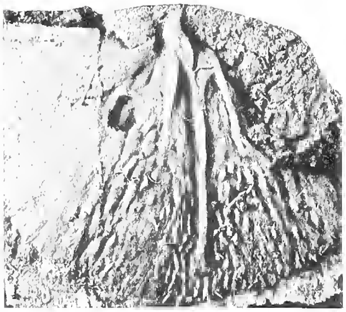
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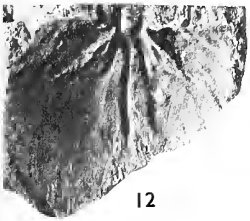
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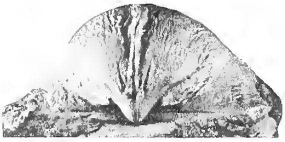
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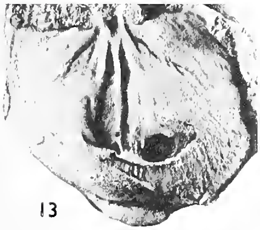
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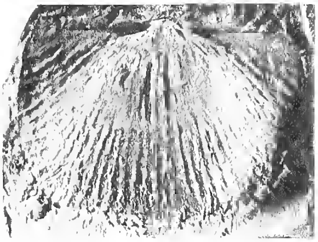
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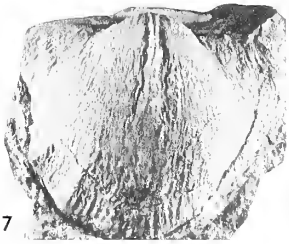
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JOHNSON, Devonian *Parachonetes* gen. nov.


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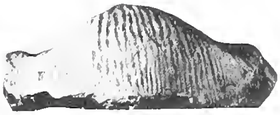
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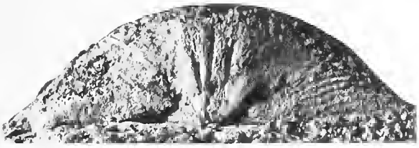
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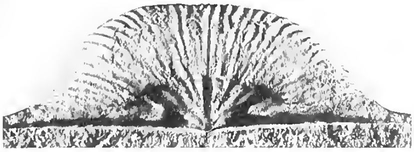
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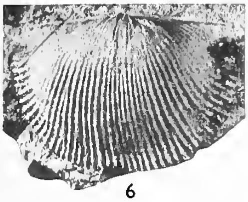
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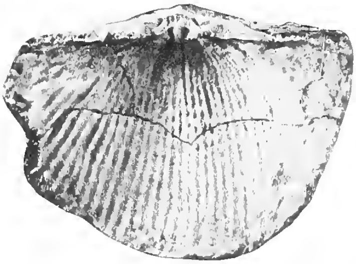
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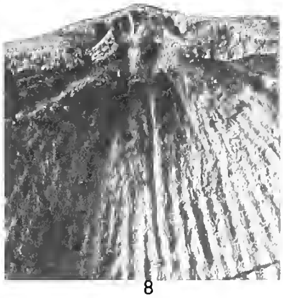
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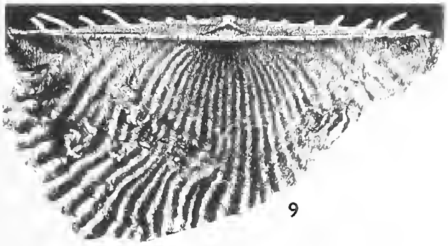
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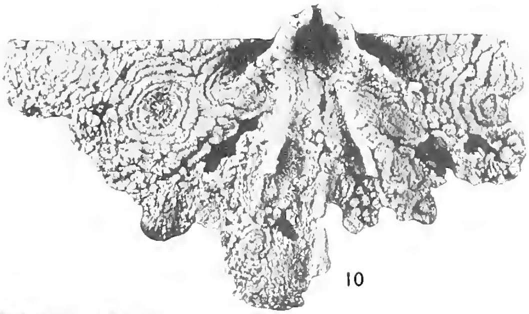
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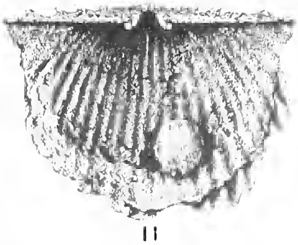
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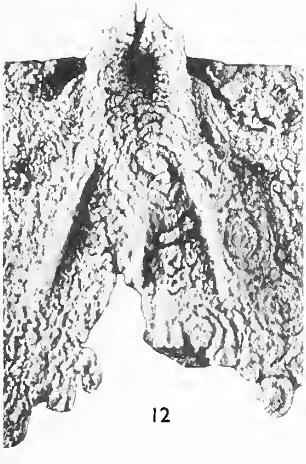
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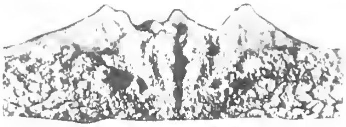
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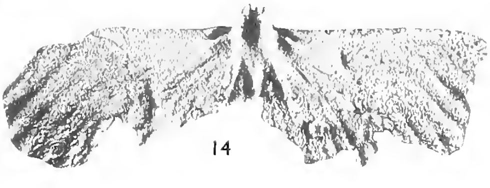
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JOHNSON, Devonian *Parachonetes* gen. nov.

posterior face of which four lobes of the cardinal process are developed. A broad flat median septum originates at the anterior edge of the alveolus and becomes narrow and strong anteriorly. The flat spatulate posterior end of the median septum tends to be split on some specimens and joins the inner edges of the cardinal process lobes. Adjacent to the point of origin of the median septum there is a pair of lateral septa that enclose the adductor scars. The lateral septa are short and diverge only slightly from one another. The shell is commonly thickened at the anterior edges of the socket plates forming irregularly triangular umbonal platforms. The interior of the valve is made pustulose by the pseudopunctae and may be more or less crenulate by the impression of the costae.

Comparison. Parachonetes macrostriatus from Nevada is very much like specimens from the *Receptaculites* Limestone in external form and ribbing. Internally as well the two bear considerable resemblance to one another. However, consistent differences may be seen in the thickness of the shell of the two species. The shell material of the Australian specimens is generally thinner than that of *P. macrostriatus* from Nevada so that the ribbing corrugates the interior surface rather strongly (Pl. 63, figs. 11 and 14). Specimens of the same size from Nevada have much thicker shells with the ribbing little impressed, or not at all, internally (Pl. 62, figs. 10–17), consequently their internal structures are generally a bit more well defined or strongly impressed so that the ventral vascular trunks and dorsal internal papillae are well displayed (Pl. 62, figs. 15–17, fig. 11).

Parachonetes macrostriatus differs from *P. verneuili* in having more irregular, more commonly bifurcating radial costae. In addition the ribbing of *P. verneuili* is relatively strongly impressed on the interior of the valves (Pl. 63, figs. 6, 7).

Occurrence. Parachonetes macrostriatus first appears in Nevada in the *Acrospirifer kobehana* zone (Emsian; see Johnson, 1962; 1965, fig. 4) on the north side of the Roberts Mountains. It is present in the '*Spirifer*' *pinyonensis* zone in the Sulphur Spring Range, in the Roberts Mountains, at Lone Mountain, and in the northern Simpson Park Range.

Cooper and others (1942, p. 1773) reported the presence of the '*Chonetes macrostriata*' fauna in the Muddy Mountains of southern Nevada. In order to investigate this occurrence the collections in question were borrowed from the U.S. National Museum. The material consists of two collections made by Dr. C. R. Longwell in 1926 and 1927. Both of these bear specimens of *Parachonetes macrostriatus* in a fauna that is indicative of the '*Spirifer*' *pinyonensis* zone, but the collection localities are from north of Las Vegas rather than from the Muddy Mountains and one of the two has a fairly detailed locality slip indicating that the collection was made near the east flank of the Spotted Range.

Figured specimens. The locality numbers cited in the plate legends are those of the U.S. National Museum. The cotypes, USNM 13809, come from Walcott's locality 555, Lone Mountain. Both specimens are refigured and the writer designates the specimen in figure 1 on plate 62 as the holotype. Walcott (1884, p. 127) lists several localities with *P. macrostriatus*, but Lone Mountain is not among them. However, the labels with Walcott's two best preserved illustrated specimens (pl. 13, figs. 14, 14*b*) examined on loan from the U.S. National Museum give Lone Mountain as their source locality and there is no doubt that the discrepancy is due to an error of omission in the text. The illustrated hypotype specimens include USNM nos. 140435–46.

Acknowledgements. The writer wishes to thank Dr. G. A. Cooper of the U.S. National Museum for the loan of Walcott's types of '*Chonetes*' *macrostriata* and for photographs of two specimens; Professor H. B. Whittington of the Museum of Comparative Zoology, Harvard, for loan of topotype specimens of *Parachonetes verneuili* from the Schary Collection; Dr. D. J. McLaren of the Geological Survey of Canada for the opportunity to examine collections from the Stuart Bay Formation of Bathurst Island; Professor A. J. Boucot of Pasadena for access to his collection of brachiopods from the upper Koneprus Limestone of the Barrandian. The writer is especially indebted to Dr. J. A. Talent of the Geological Survey of Victoria, Australia, for loan and permission to illustrate silicified specimens from the *Receptaculites* Limestone Taemas, N.S.W. Work on this project was supported by a grant from the National Science Foundation, number GP 2290.

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MORPHOLOGY AND STRATIGRAPHIC RANGE OF THE PHYLLOCARID CRUSTACEAN *CARYOCARIS* FROM ALASKA AND THE GREAT BASIN

by MICHAEL CHURKIN, JR.

Abstract. Exceptionally well-preserved specimens of *Caryocaris* from Alaska and the Great Basin show a peculiar shell enrolment; several other important skeletal details are described for the first time. In the light of this new material, Ruedemann's types that are the basis for his reconstructions of *Caryocaris* are re-examined. Finally, a review of the stratigraphic range of *Caryocaris* leads to the conclusion that none of its reported Silurian species are definitely *Caryocaris*. The range of the genus should therefore be restricted for the present to the Ordovician and probably to the lower half of the system.

Since Salter (1863) named *Caryocaris*, a pod-shaped crustacean from the Skiddaw Slates of the Lake District, England, it has been reported from Ordovician graptolitic shales in North America (Gurley 1896; Ruedemann 1921), South America (Bulman 1931), Australia (Chapman 1903), and Scandinavia (Størmer 1937), and new species of *Caryocaris* have been described from Silurian graptolitic shales in south-eastern Alaska (Ruedemann 1934) and Oklahoma (Ruedemann 1935). The flattened and crushed specimens hitherto described are difficult to interpret and have resulted in a number of different restorations.

The purpose of this paper is to describe exceptionally well-preserved specimens of *Caryocaris* from Alaska and Nevada that show for the first time a peculiar shell enrollment and several morphological details. In the light of this new material, Ruedemann's types that have served as the basis for his classical reconstructions are re-examined, and, finally, the stratigraphic range of *Caryocaris* is reviewed and greatly reduced.

Acknowledgements. This study is the result of the discovery of exceptionally well-preserved *Caryocaris* in mapping the Charley River (1:250,000) and Eagle D-1 (1:63,360) quadrangles in east-central Alaska (Brabb and Churkin 1964, 1965). I am indebted to Earl E. Brabb (U.S. Geological Survey) for his interest and numerous useful suggestions; to W. D. Ian Rolfe (Hunterian Museum, Glasgow) for critically reading the manuscript; to J. Wyatt Durham (University of California, Berkeley) for suggesting shell enrollment to explain the spirally coiled carapaces; to Copeland MacClintock (Peabody Museum of Natural History) for ideas concerning shell wall microstructure; to Robert A. Gulbrandsen (U.S. Geological Survey) for interpreting the X-ray patterns of *Caryocaris* shell material; to Charles W. Merriam (U.S. Geological Survey) for kindly furnishing his collections of *Caryocaris* from Nevada; to A. R. Palmer (U.S. Geological Survey) for arranging loans of type specimens from the U.S. National Museum; and to Donald W. Fisher and Clinton F. Kilfoyle (New York State Museum) for loaning type specimens in their care. Publication is authorized by the Director, U.S. Geological Survey.

CARYOCARIS IN EAST-CENTRAL ALASKA

Caryocaris occurs in several graptolitic shale horizons of Ordovician age in the Road River Formation (Ordovician and Silurian) of east-central Alaska and is especially

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abundant in chert at the base of the formation (Churkin and Brabb 1965). The best preserved specimens described below were obtained from loc. M1001-CO (see Appendix) near the Alaska–Canada border. Here abundant specimens of *Caryocaris* are preserved with the graptolites *Isograptus forcipiformis*, *Isograptus caduceus* cf. var. *maximodivergens*, and *Didymograptus* cf. *D. nitidus* in a greyish-black chert 5 to 8 feet stratigraphically above unnamed limestone containing Late Cambrian trilobites. Both *Caryocaris* and the graptolites are preserved in relief and are easily distinguished by their phosphate bloom, apparently a white phosphatic-weathering product (Pl. 64, figs. 1, 2). The graptolites associated with the *Caryocaris* indicate a latest Arenig or earliest Llanvirn age equivalent to graptolite Zone 5 of *Didymograptus hirundo* or Zone 6 of *Didymograptus bifidus* of Elles and Wood (1901–18). Conodonts found in chert directly below the *Caryocaris* locality were identified by John W. Huddle, of the U.S. Geological Survey, and suggest late Arenig. Thus, all of the Tremadoc and most of the Arenig seem to be absent in the less than 5-foot chert interval between the conodont locality, the lowest fauna in the Road River Formation, and the highest trilobite collection from the underlying Cambrian limestone. At loc. 63ACn 1533, about 3 miles east of loc. M1001-CO, *Caryocaris* is again very abundant in the basal Road River Formation, where it occurs in thin beds of chert pebble conglomerate and chert grit interstratified with and cemented by dark-grey chert. The poorly sorted angular grains, cross-laminae, and scour-and-fill structures suggest that the *Caryocaris* material, in places reaching coquinoid proportions, was laid down in a high energy environment as part of a basal deposit unconformably overstepping Cambrian limestone.

MORPHOLOGICAL FEATURES OF *CARYOCARIS* IN EAST-CENTRAL ALASKA

The Alaskan specimens of *Caryocaris* are unusual in that they have in various degrees their third dimension preserved in chert instead of appearing as completely flattened films in shale. Because the Alaskan specimens are not completely flattened, they reveal a peculiar spiral coiling of the carapace wall here described for the first time. In addition, other important skeletal features hitherto unknown or inadequately figured are described below, and lastly the microstructure and composition of the carapace wall are discussed. The terminology of the exoskeletal elements of *Caryocaris* has not been standardized, and therefore the nomenclature used in the following description is given in text-fig. 1.

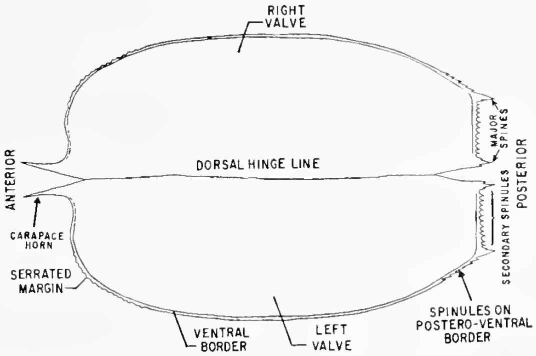
Carapace enrolment. Spirally coiled carapaces of *Caryocaris* appear in long view as cylindrically-shaped body walls tapering to blunt points at each end (Pl. 64, figs. 3, 4). All the larger specimens were partially broken, but several are still nearly 20 mm. long. Their corresponding diameters are about 2 mm.; and width to length ratio is about 1:10 as contrasted with about 1:4 in associated flattened specimens.

In a number of specimens transverse breaks show in cross-section the internal spiral coiling of the carapace wall (Pl. 64, figs. 5, 6). The fragile carapace walls, nearly black in colour, are supported by microcrystalline white quartz deposited between each whorl. In thin sections random profiles through coiled carapaces reveal a number of differently appearing patterns of the shell wall (Pl. 64, fig. 7) of which the shapes of the longitudinal (Pl. 64, fig. 8) and nearly transverse profiles (Pl. 65, fig. 1) are highly characteristic.

Apparently each coiled piece is a single valve that is the result of separation, perhaps by moulting, along the dorsal hinge line followed by in-curling of the valve wall starting from the ventral margin.

Spined posterior margin. Ruedemann (1921) originally described several features of *Caryocaris* from graptolitic shale here referred to the Road River Formation at the Alaska–Yukon boundary, but the coiled and three-dimensional specimens preserved in chert from the base of the formation apparently were not available to him.

'The Alaska–Yukon material', Ruedemann wrote, 'which is not obscured by an imperfect cleavage leaves no doubt that the posterior margin of the carapace was indeed furnished with a fine comb of uniform bristles or teeth.' As Ruedemann pointed out, the posterior margins of the Alaska–Yukon species certainly have a row of 'bristles or teeth' (here referred to as spines and spinules to divorce these structures of unproved function from a genetic connotation) and are not a product of structural deformation. These spines, however, are not of equal size as Ruedemann claimed. The spine at each end of the posterior margin is several times larger than the 13 intervening spinules (Pl. 65, fig. 3). In addition, the ventral margin in its posterior portion, has a row of 5 and possibly more posteriorly directed spinules (Pl. 64, fig. 3 and Pl. 65, fig. 3) which have not been previously recorded anywhere and are rarely preserved even in the best Alaskan specimens.



TEXT-FIG. 1. Orientation and terminology of *Caryocaris* used in this paper.

Carapace horn. The Alaskan *Caryocaris* certainly has a horn-like projection at the anterior end of its dorsal margin (Pl. 65, fig. 2) but it is simply a prolongation of the carapace wall instead of a 'distinct plate' or true rostrum as Ruedemann (1921, p. 96, figs. 45, 51; p. 99) indicated.

Segmentation and appendages. Although the Alaskan collections consist of several hundred specimens, none of the carapaces has either an abdomen or telson attached as Ruedemann (1921) showed in figs. 46, 48, and 51. Several fragments that resemble 'abdomina' and 'telsons', were found but these segmented structures, though they are well preserved, are completely detached from any carapace and their biological affinities to *Caryocaris* can only be conjectured. An examination of the original specimens in the New York State Museum from which Ruedemann's figs. 46, 48, and 49 were drawn has also failed to show any justification for the segmentation or appendages shown in his drawings.

Ventral margin. The ventral margins of the Alaskan *Caryocaris* have a thickened border that is more or less well preserved. In flattened specimens this border is frequently impressed in various positions on the opposite valve wall, thus suggesting that the carapace walls were in these cases enrolled before flattening.

Carapace surface ornamentation and wall microstructure. The surface of the *Caryocaris* exoskeleton has the iridescent lustre common to other phosphatic shells and appears smooth except in flattened specimens from shale, where it is generally finely wrinkled. Under the microscope, however, the exterior of the carapace is seen to be distinctly corrugated into very fine furrows and ridges that form a slightly sinuous pattern.

The microstructure of the carapace wall in thin section consists of three distinct layers (Pl. 64, fig. 7; Pl. 65, fig. 1). The outer and inner layers range in colour from pale yellowish-orange to shades of yellowish-brown and are separated from each other by a much thinner middle layer that is dark brown. Frequently the edges or centre of this middle layer of the carapace wall serve as a plane along which the inner layer separates from the outer layer. A very faint fibrous structure (possibly representing in part very fine canals) normal to the carapace wall can be seen in the inner and outer layers, but the middle layer instead seems to have a faint lamination or parting, especially along its centre, that parallels the carapace layering. Several specimens seem to have a very narrow hollow space where two carapace walls come to a point. Presumably this is the union of two valves along the hinge line.

In thin sections the shells have the faint birefringence of microcrystalline apatite that probably represents very nearly the original chitino-phosphatic material of the exoskeleton. The mineralogical composition of *Caryocaris* shell material separated out from Coll. 63ACn 1533 gave the X-ray pattern of carbonate-fluorapatite.

Involute phosphatic shells similar to those described above but only one-third normal

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EXPLANATION OF PLATE 64

Fig. 1. Crushed carapaces of *Caryocaris curvilata* associated with *Isograptus caduceus* cf. var. *maximodivergens*. The phosphatic fossils weather greyish-white and stand out clearly against the greyish-black chert matrix; USNM 147441, loc. M1001-CO, Road River Formation, east-central Alaska. ×2.

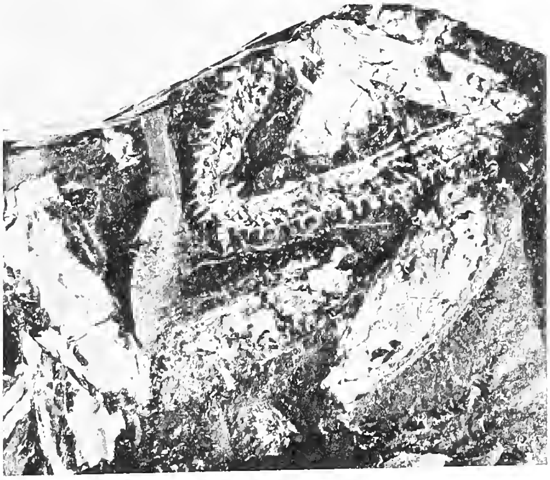
Fig. 2. Right valve view of *Caryocaris curvilata* associated in the same chert fragment with *Isograptus forcipiformis*; USNM 147442, loc. M1001-CO, Road River Formation, east-central Alaska. ×2.

Fig. 3. Enrolled valve of *Caryocaris* (lower centre) next to two partially flattened valves. The valve in the upper left corner shows the spined posterior margin characteristic of *Caryocaris curvilata* and the rarely preserved fine spinules along the postero-ventral border; USNM 147443, loc. M1001-CO, Road River Formation, east-central Alaska. ×3. Photographed with ammonium chloride coating.

Fig. 4. Enrolled *Caryocaris* reflecting light from its phosphatic carapace that has an iridescent lustre; USNM 147444, loc. M1006-CO, Road River Formation, east-central Alaska. ×2.

Figs. 5, 6. Enrolled *Caryocaris* showing transverse views of the spiral coiling of the very thin and dark carapace wall. The delicate spiral structure is supported by white microcrystalline quartz filling the space between each whorl; 5, USNM 147445; 6, USNM 147446; loc. M1001-CO, Road River Formation, east-central Alaska. ×6.

Figs. 7, 8. Photomicrographs of a thin section through coiled carapaces of *Caryocaris*; 7, random cross-section across a partially crushed specimen showing a complicated pattern of carapace wall folding and the characteristic three-layered microstructure of the carapace wall, ×114; 8, longitudinal profile, ×45; USNM 147447, loc. 63ACn 1533, Road River Formation, east-central Alaska.



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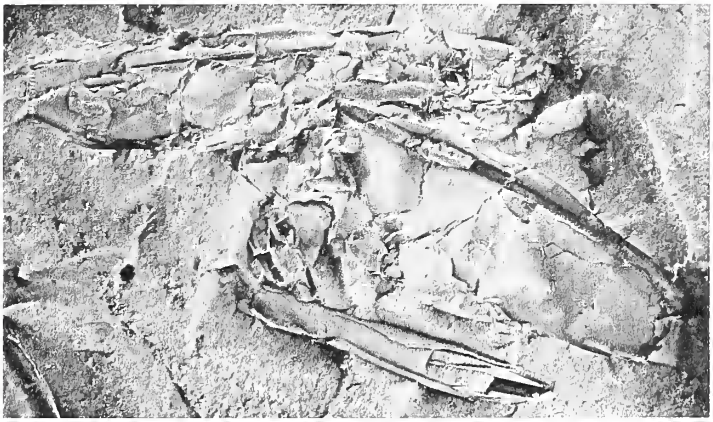

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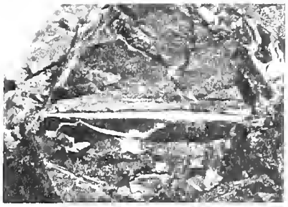

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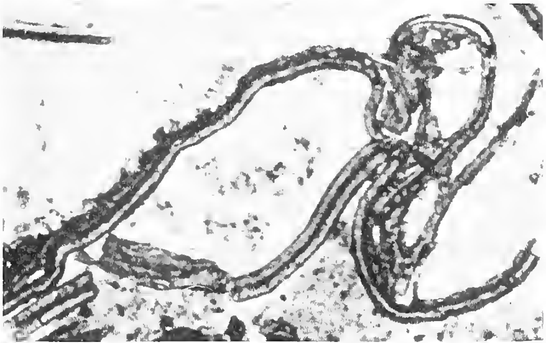

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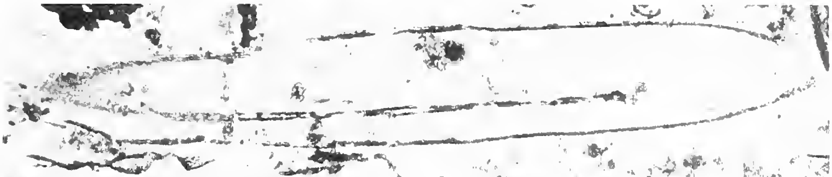

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CHURKIN, Phyllocarid crustacean *Caryocaris*

size (Pl. 65, figs. 4–6) were found in chert grit layers of the basal Road River Formation near the Yukon River (loc. 63ABa 3181B). Fig. 6 shows that the shell wall has the same three-layered microstructure as in *Caryocaris.* In the heart-shaped cross-sections there is a very narrow but definite break in the shell microstructure where the shell wall comes to a point, and this suture probably represents the dorsal hinge line. The shell walls coiled into a double spiral can then be interpreted as two connected valves curled in along their ventral margins. In some cross-sections the incurled valves on either side of the supposed dorsal hinge line have shell walls of variable and unequal thickness but this is largely due to splitting of the layered walls, as in the feather edge of the outer whorl in fig. 6, rather than because of any original difference between the two valves.

Mertie (1930, pl. 9) illustrated involute shells from cherty grit in the same area. Edwin Kirk (*in* Mertie 1930, p. 83) wrote that 'the zoological affinities of these curious fossils are doubtful' and assigned them to the Pteropoda 'mainly by a process of elimination'. These involute fossils reported by Mertie appear in thin section identical to those in Plate 65, figs. 4–6, and in both cases are similar in outline and have the same shell wall microstructure as those of *Caryocaris* described above.

MORPHOLOGICAL FEATURES OF *CARYOCARIS* FROM NEVADA AND IDAHO

Gurley (1896) described *Caryocaris wrightii* Salter and named a new species, *C. curvilatus*, from Summit, Nevada (this locality lies in what is known today as Garden Pass). In a large collection of *Caryocaris*, made by C. W. Merriam from the same graptolitic shale at Summit, Nevada, I found several specimens of *C. curvilata* with a well-developed carapace horn not originally recognized by Gurley. In these specimens the posterior border, where preserved, is lined with a row of spinules. The larger spines at each end of the posterior border, although generally incompletely preserved in the Summit specimens, were recognized and figured by Gurley (pl. 5, fig. 3) but were not mentioned by Ruedemann (1921) in his subsequent description of *C. curvilata* from the Alaska–Yukon boundary. The type species of *Caryocaris* may lack the posterior spines and carapace horn so characteristic of the western North American species discussed in this paper, and as W. D. Ian Rolfe pointed out (*in* Theokritoff 1964, p. 183), *Caryocaris curvilata* and other species of *Caryocaris* in America may belong to *Rhinopterocaris* Chapman, a Lower Ordovician genus from Australia that has been synonymized with *Caryocaris* but perhaps is generically distinct.

The major differences in shell width as well as the 'complicated foldings and refoldings of the marginal filaments' reported by Gurley (1896, p. 87) along the ventral margin are probably a result of carapace enrollment before flattening as noted above in the Alaskan material. Now that specimens of *Caryocaris curvilata* from its type locality are known to have a carapace horn and a distinctively spined posterior margin, it may be concluded that the better-preserved Alaskan specimens are more certainly conspecific with *C. curvilata* from Summit, Nevada. The Alaskan specimens provide details not preserved in the type material from Nevada.

Several tridentate fossil parts resembling caudal appendages of various phyllocarids (Jones and Woodward 1888–99, pl. 10, figs. 10, 11; Ruedemann 1934, pl. 22, fig. 7) occur with *Caryocaris curvilata* at the Summit locality but in every case are detached from any carapace. In this and in all collections of *Caryocaris* studied no single appendage was found attached to a carapace, nor was there evidence of body segmentation. Ruedemann (1921, p. 96, fig. 51) in a restoration of the *Caryocaris curvilata* from the Alaska–Yukon boundary connected a segmented 'abdomen' to a spined posterior margin and then attached a tridentate 'telson' to the end of the 'abdomen'. Later Ruedemann (1934, p. 92, pl. 22, figs. 8, 9) illustrated a specimen of *C. curvilata* from Trail Creek, Idaho, that he implied showed 'both the abdomen and the telson in place' for the first time. A re-examination of Ruedemann's plesiotypes indicated that his figs. 8 and 9 are actually a highly inferential reconstruction and that none of the specimens in the USNM type collection no. 90858 from Trail Creek loc. 1367 has a telson-like structure attached to the posterior end of a carapace as Ruedemann's figures show. According to W. D. Ian Rolfe, of the Hunterian Museum, Glasgow (written communication, May 1965), the original specimen from which Ruedemann's figs. 8 and 9 were made lacks the anterior part of the carapace including any 'articulated rostrum', and has a telson near the posterior end of the carapace, but definitely detached from it. Unfortunately, this specimen has been recently damaged and the posterior end of the carapace has been chipped off and lost, further obscuring any connexion between the carapace and the associated telson. Another and more completely preserved specimen (text-fig. 2*a*) on the same shale slab as the type for Ruedemann's figs. 8 and 9, has a tridentate structure that is probably part of another specimen adjoining its dorsal margin instead of being attached to the posterior end, and also lacks any definite articulated rostrum or segmented abdominal parts as indicated by Ruedemann.

In shales *Caryocaris* is generally preserved with either the right or left valve showing. Rarely are both valves found connected. Ruedemann (1934, pl. 22, fig. 5) illustrated such a specimen from Trail Creek, Idaho, and noticed 'prominent spines on the inner point of the posterior margins on both sides of the dorsal hinge'. He failed to mention, however, a correspondingly large spine at the opposite (ventral) end of the posterior margin of the left valve (see text-fig. 2*b*, a camera lucida drawing of Ruedemann's figured specimen). In the same collection from Trail Creek a specimen of *C. curvilata*

EXPLANATION OF PLATE 65

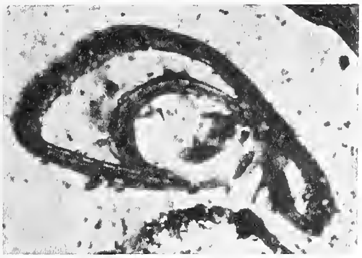
Fig. 1. Photomicrograph of nearly transverse cross-section through coiled valve of *Caryocaris*; USNM 147448, loc. 63ACn 1533, Road River Formation, east-central Alaska. ×86.

Fig. 2. Right valve view of small *Caryocaris* with part of its carapace horn still intact; USNM 147449, loc. M1001-CO, Road River Formation, east-central Alaska. ×5. Photographed with ammonium chloride coating.

Fig. 3. Close-up of the posterior portion of *Caryocaris curvilata* shown on Pl. 64, fig. 2. The two spines at each end of the posterior margin are separated from each other by 13 intervening spinules. The row of 5 posteriorly directed spinules along the postero-ventral margin is also preserved; USNM 147442, loc. M1001-CO, Road River Formation, east-central Alaska. ×10. Photographed with ammonium chloride coating.

Figs. 4–6. Photomicrographs of cross-sections of very small involute shells resembling *Caryocaris*. In the heart-shaped cross-sections there is a break in the shell wall where it comes to a point. 4, ×35; 5, ×70; 6, ×114. All in thin section USNM 147450, loc. 63ABa 3181B, Road River Formation, east-central Alaska.

Figs. 7–9. *Caryocaris curvilata* from shale at Ninemile Canyon, east-central Nevada; 7, left valve view of flattened specimen, USNM 147451, ×3; 8, anterior portion of carapace with the entire carapace horn intact, USNM 147452, ×3; 9, spined posterior margin, USNM 147453, ×10.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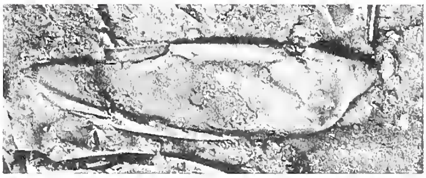
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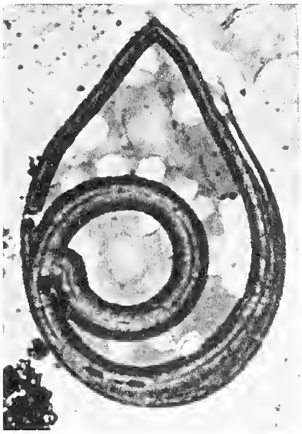
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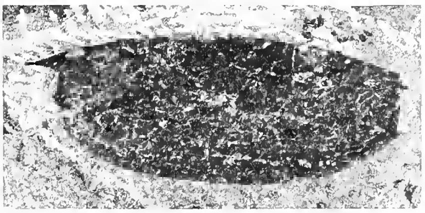
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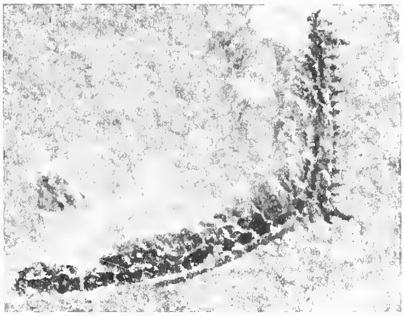
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CHURKIN, Phyllocarid crustacean *Caryocaris*

shows both pairs of prominent spines apparently at the posterior tips of each valve (text-fig. 2*c*).

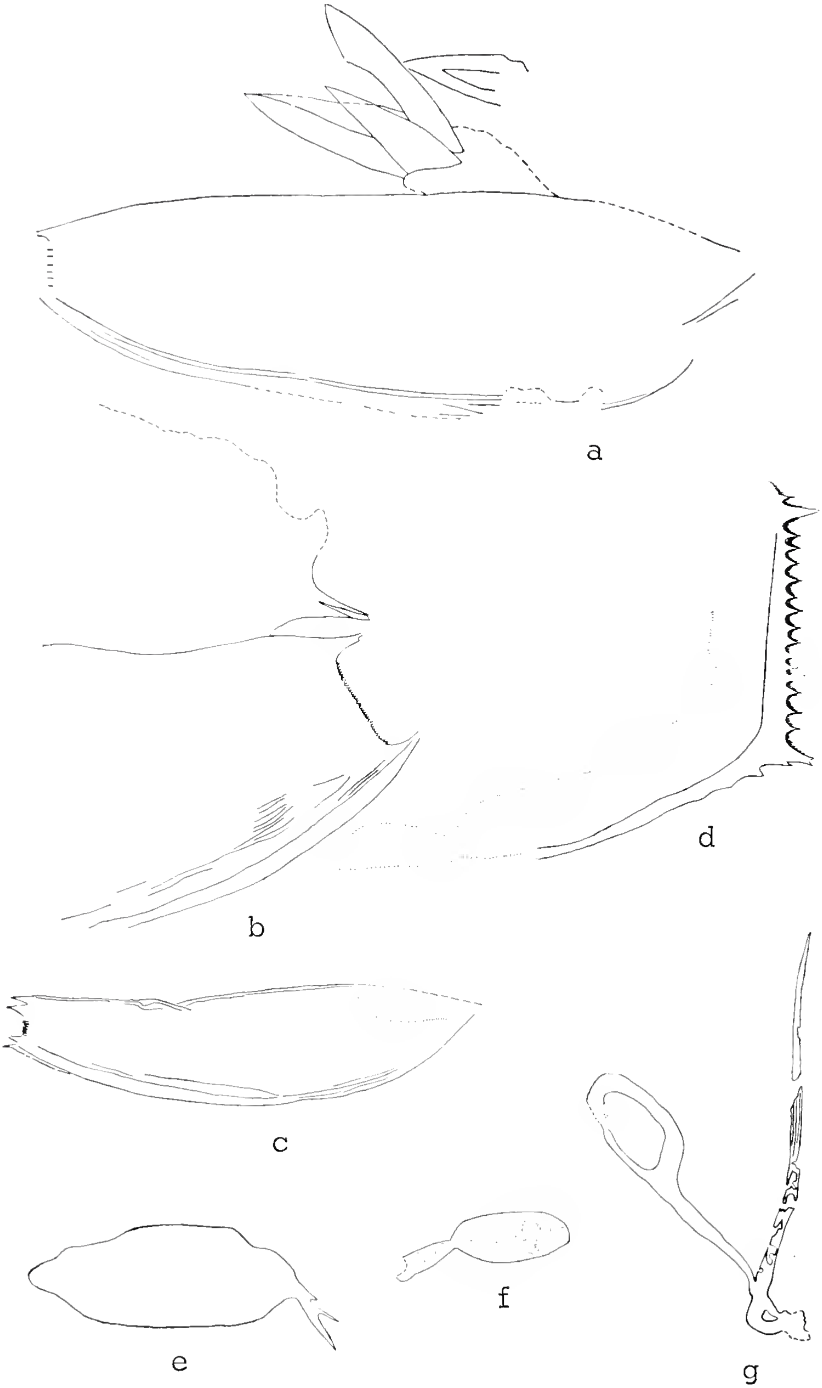
In Ninemile Canyon at the north end of the Antelope Range, east-central Nevada, abundant and exceptionally well-preserved specimens of *Caryocaris* occur in a grey shale devoid of graptolites (Nolan *et al.* 1956; Merriam 1963). Numerous specimens have carapace horns and spined posterior margins particularly well preserved in a collection made by C. W. Merriam from the Ninemile locality (Pl. 65, figs. 7–9). In addition, the very rarely preserved spinules along the posterior portion of the ventral margin are preserved on several specimens. An exceptionally well-preserved posterior margin shows for the first time that the flanks of the major posterior spines, and the flanks of the intervening spinules themselves bear a uniform set of microscopic spinules parallel to the larger spines (Pl. 65, fig. 9, and text-fig. 2*d*). Another specimen has along the antero-ventral portion of the valve a serrated margin (see text-fig. 1) probably originally present but not preserved in other specimens.

STRATIGRAPHIC RANGE OF *CARYOCARIS* IN ALASKA AND THE WESTERN UNITED STATES

Although *Caryocaris* has been reported from Ordovician and Silurian shales in western North America it seems more likely from the evidence given below that *Caryocaris* is restricted to the Ordovician and probably only to the lower half of the Ordovician.

Ordovician. The oldest record of *Caryocaris* in western North America may be from the grey shale provisionally included as the uppermost division of the Windfall Formation of Late Cambrian age (Nolan *et al.* 1956, p. 21) or as the basal member of the overlying Goodwin Limestone of Early Ordovician age (Merriam 1963, pp. 14–18, 21). This 150-foot *Caryocaris*-bearing shale at Ninemile Canyon, Nevada, is overlain, however, by limestone bearing the Early Ordovician *Kainella* trilobite fauna according to Nolan *et al.*, and thus may be itself Early Ordovician. Elsewhere in the Great Basin and Alaska, *Caryocaris* is associated with graptolites that generally permit an accurate age assignment. *Caryocaris* was found in the following graptolite zones of the Road River Formation in Alaska (Churkin and Brabb 1965): uppermost Arenig Zone 5 of *Didymograptus hirundo* or lower Llanvirn Zone 6 of *Didymograptus bifidus* (locality M1001-CO); upper Llanvirn Zone 7 of *Didymograptus murchisoni* (locality M1003-CO); and lowest Caradoc Zone 9 of *Nemagraptus gracilis* (locality M1019-CO). At Summit, Nevada, *Caryocaris curvilata* is associated with graptolites of the Llandeilo Zone 8 of *Glyptograptus teretiusculus.* The best specimens of *Caryocaris curvilata* in the graptolitic shale sequence at Trail Creek, Idaho, occur in Zone 4 of *Didymograptus extensus.*

Silurian. The range of *Caryocaris* was extended from the 'lowest Ordovician to the Silurian' by Ruedemann (1934) when he described the new species *Caryocaris silurica* (p. 95, 96, pl. 22, figs. 15–20) from Silurian graptolitic shale at Klakas Inlet, Prince of Wales Island, south-eastern Alaska. The types of *C. silurica* in the U.S. National Museum were re-examined and are considered as not identifiable to genus or even to phylum with certainty because of poor preservation. The original illustrations of *C. silurica* given in pl. 22, figs. 15 and 16 are highly interpretive, and the general shape, 'eye', and



TEXT-FIG. 2

apparent segmentation of Ruedemann's types seem to reflect more the pattern of exfoliation of fossil material than the true outline and structures of the original fossils. Text-figs. 2*e*, *f*, prepared from the original specimens, show only a general agreement in broad outline with Ruedemann's illustrations, but I could not positively identify any of the internal segmentation or the 'eye'. In the field season of 1964 I made large collections of Silurian graptolitic shale from Klakas Inlet, the type locality for *C. silurica*, but no phyllocarids were found.

Besides *C. silurica* the only other Silurian record of *Caryocaris* was made by Ruedemann (1935), when he named two new species, *C. magnus* and *C. oklahomensis*, from the Henryhouse Shale of Oklahoma. An examination of Ruedemann's type specimens indicates that *C. magnus* is simply a pod-shaped depression in the rock and probably not a fossil. *C. oklahomensis*, on the other hand, seems to have a branched structure (text-fig. 2*g*) instead of the segmented abdomen that Ruedemann's figs. 2 and 3 indicate. Thus the general outline of *C. oklahomensis* is unlike any phyllocarid, and its identification as to phylum is uncertain. It may even be a plant.

None of the three species of *Caryocaris* reported from the Silurian can definitely be identified as *Caryocaris*, and the stratigraphic range of the genus should therefore be restricted to the Ordovician.

APPENDIX

Geographic position of *Caryocaris* collections in the basal part of the Road River Formation of east-central Alaska

Collection numbers are those of the U.S. Geological Survey.

M1001–CO. From greyish-black chert at the base of the Road River Formation and 5 to 8 feet stratigraphically above limestone containing Late Cambrian trilobites. On the ridge crest in NE. ¼, SW. ¼, Sec. 28, T. 2 N., R. 33 E., Eagle D-1 quad. (1:63,360), lat. 64° 58·3′ N., long. 141° 2·4′ W.

63ABa 3181B. From pale yellowish-brown and greyish-black laminated chert about 6 feet above the base of the Road River formation. South flank of BM2814 (Crow) at elevation 2600′, NE. ¼, SW. ¼, Sec. 26, T. 2 N., R. 32 E., Eagle D-1 quad. (1:63,360), lat. 64° 58·3′ N., long. 141° 10·9′ W.

EXPLANATION OF TEXT-FIG. 2

a–c, *Caryocaris curvilata* from Lower Ordovician graptolitic shale near Trail Creek, Idaho (USGS Coll. 1367-SD): *a*, one of the most complete specimens in collection. Ruedemann's plesiotype (1934, pl. 22, figs. 8, 9) in the U.S. National Museum (USNM 90858A), that according to Ruedemann has 'both the abdomen and the telson in place' lies on the same slab of shale; ×5. *b*, Ruedemann's figured specimen (1934, pl. 22. fig. 5; USNM 90858B), showing the spined posterior portions of both valves still connected along the dorsal hinge line; ×5. *c*, nearly complete right valve and posterior portion of left valve showing both pairs of prominent spines at the posterior tips of each valve; USNM 90858C, ×5.

d, Posterior margin of *Caryocaris curvilata* showing that the flanks of the major posterior spines and the flank of the intervening spinules themselves bear a uniform set of microscopic spinules, ×14; USNM 147454; Ninemile Canyon, east-central Nevada.

e, *f*, Type specimens of *Caryocaris silurica* Ruedemann from Silurian graptolitic shale at Klakas Inlet, Prince of Wales Island, south-eastern Alaska (USGS loc. 1037); *e*, Ruedemann's figured specimen (1934, pl. 22, fig. 15), USNM 90857A, ×5; *f*, 'small specimen' (Ruedemann 1934, pl. 22, fig. 16), USNM 90857B, ×5.

g, *Caryocaris oklahomensis* Ruedemann (1935, fig. 2), holotype, USNM 114534, ×5. Henryhouse Shale, Silurian, Oklahoma.

All camera lucida drawings.

63ACn 1533. From chert grit interbedded with greyish-black laminated chert and shale. In Yukon Territory, Canada, about 0·4 mile north-east of McCann Hill (International boundary monument 105), lat. 64° 55·5′ N., long. 140° 59·5′ W.

63ACn 1713. From small isolated outcrop of dark-grey, thin-bedded chert and shale. North side of Hard Luck Creek valley SW. $\frac{1}{4}$, SW. $\frac{1}{4}$, Sec. 6, T. 4 N., R. 32 E., Charley River A-1 quad. (1:63,360), lat. 65° 11·8′ N., long. 141° 19·5′ W.

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DEVONIAN SCHIZOPHORIID BRACHIOPODS FROM WESTERN EUROPE

by YVONNE P. POCOCK

ABSTRACT. Six species and one subspecies of the genus *Schizophoria* are described from the Devonian of western Europe, with their stratigraphical ranges and postulated phylogeny. All taxa are shown to be externally and internally distinct. Neotypes are proposed for *Schizophoria provulvaria* (Maurer) and *S. strigosa* (Sowerby).

SPECIMENS of *Schizophoria* have been studied in this work from the Lower to Upper Devonian of the southern border of the Dinant basin, the Upper Devonian of Boulonnais; the Lower Devonian of the Rheinischen Schiefergebirge, and the Middle Devonian of the Eifel. The stratigraphical succession of the Dinant basin is given by Maillieux (1922, 1941), together with stratigraphical correlations with the Rheinischen Schiefergebirge (1922). The succession of the Boulonnais inlier is presented by Pruvost (1924), and that of the Eifel by Struve (1963).

The stratigraphical distribution of the species studied from these regions is shown on text-fig. 1.

Abbreviations. In the following descriptions, relevant museum collections listed are as follows: BC—Bedford College, University of London; BM—British Museum (Natural History); GSM—Geological Survey Museum (London); GMUS—Geology Museum, University of Saskatchewan; HMUG—Hunterian Museum, University of Glasgow; IRSN—Institut royal des sciences naturelles de Belgique; MNB—Museum für Naturkunde, Berlin (Haupt-Sammlung); SMF—Senckenberg Museum, Frankfurt.

In each text-fig. of serial sections, the numbers represent distances in millimetres measured anteriorly from the umbones. Muscle field patterns and vascular markings are also illustrated on figures of internal moulds, since moulds, rather than discrete valves, are the common form of preservation.

SYSTEMATIC DESCRIPTIONS

Suborder DALMANELLOIDEA Moore 1952
Family SCHIZOPHORIIDAE Schuchert and Le Vene 1929
Subfamily SCHIZOPHORIINAE Schuchert and Le Vene 1929
Genus SCHIZOPHORIA King 1850

Type species. Conchyliolithus Anomites resupinatus Martin 1809.

Outline transversely rectangular to elliptical, quadrate to rounded, ventribiconvex to biconvex to dorsibiconvex, the dorsal valve generally deeper in adult forms. Ventral valve convex umbonally, flattening laterally, depressed medially. Dorsal valve evenly convex longitudinally, or greatest convexity umbonally, flattening laterally and anteriorly. Hinge-line straight, submegathyrid; cardinal angles rounded. Beaks small, pointed, incurved; brachial beak more incurved. Interareas curved to beaks, pedicle interarea higher; delthyrium and notothyrium open. Anterior commissure varying from

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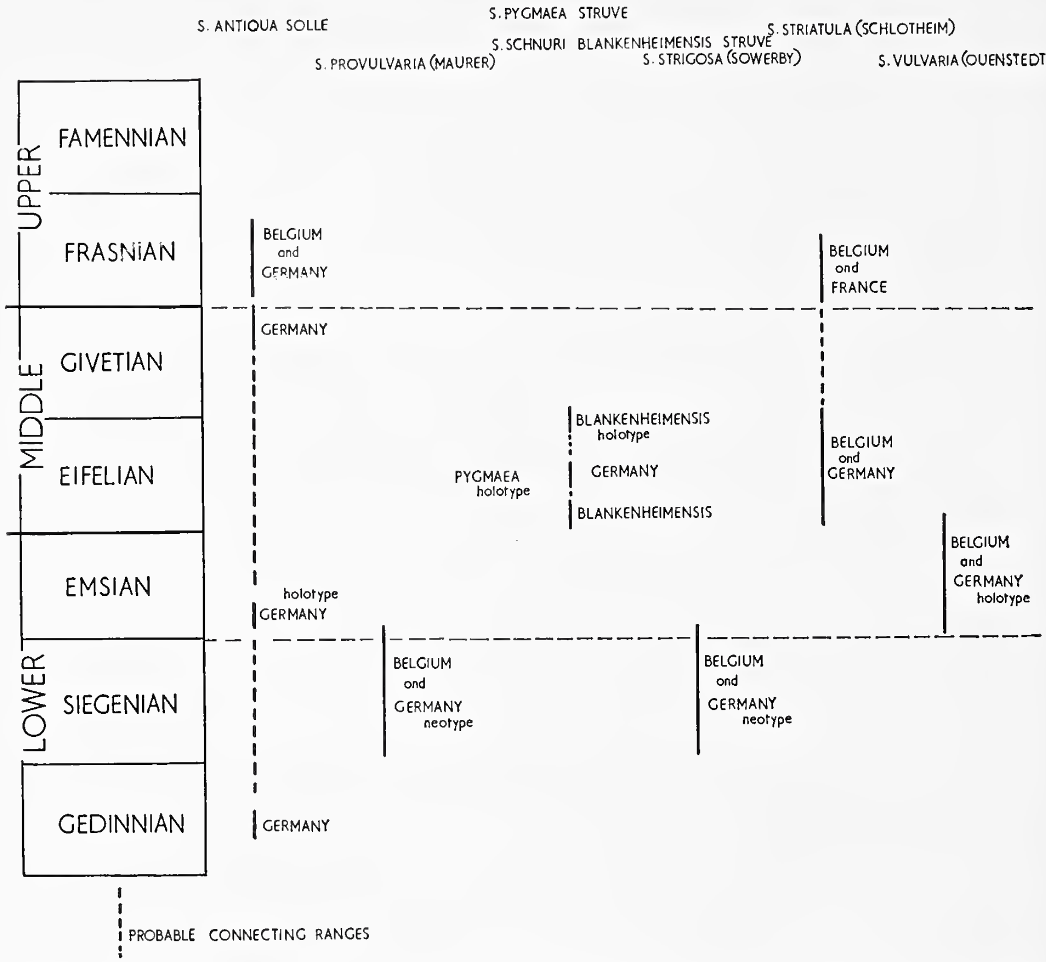
rectimarginate to uniplicate, unisulcate, sulciplicate, biplicate. Dorsibiconvexity and height of anterior plication increase with age. Ventral sulcus frequently developed; dorsal fold occasionally developed adjacent to anterior commissure. Shell costellate, rugate, punctate. Costellae separated by narrower, more angular striae, costellae increasing by bifurcation and intercalation. Growth rugae variably developed with age, and between species, concentrated anteriorly and laterally. Puncta subrounded, concentrated along striae on shell surface, concentrated along costellae in lower shell layers, evenly distributed in inner shell layers.



TEXT-FIG. 1. Stratigraphical range of species of *Schizophoria* from Belgium, NE. France, and Germany.

Ventral muscle field parallel-sided or flabellate, bounded posteriorly by dental lamellae supporting compound teeth, laterally and anteriorly by ridge-like extensions of lamellae. Ridges decreasing in height anteriorly, reflexed, uniting with end of median septum generally to form anterior re-entrant. Diductor muscle field longitudinally divided by median septum, originating near apex of delthyrial cavity. Adductor muscles attached to median septum. Two subparallel vascula media originating from anterior of muscle field. Genital markings developed laterally and postero-laterally. Shell partially filling delthyrial cavity, decreasing in thickness and disappearing anteriorly.

Dorsal valve with simple or compound serrated myophore. Compound form consisting of central ridge bounded by two to four shorter, narrower ridges (one or two either side). Myophore bounded by divergent or curved brachiophore plates supporting stubby brachiopores. Shell partially filling notothyrial cavity, decreasing in thickness and disappearing anteriorly. Ventral teeth articulating with dorsal sockets. Sockets oval in transverse section, bounded internally by smaller, shallower accessory sockets, and externally by larger, irregularly shaped accessory cavities. Dorsal muscle field generally one-third to one-half valve length, quadripartite, bounded posteriorly by brachiophores, brachiophore plates, laterally and anteriorly by accessory ridges. Ridges decreasing in height anteriorly, reflexed to form anterior re-entrant, uniting with median septum. Median septum originating at base of notothyrial cavity. Minor septum frequently dividing each half of adductor muscle field into pyriform anterior scar and digitate or tripartite posterior scar. Four subparallel vascula media originating from anterior of muscle field. Two vascula myaria occasionally developed laterally to vascula media from ends of minor septa. Genital markings developed laterally and postero-laterally.

Schizophoria antiqua Solle

Plate 66, figs. 1*a*, *b*; text-figs. 2–5

1907 Orthis (*Schizophoria*) *striatula* Schlotheim; Walther, p. 279, pl. 13, fig. 9.
1910 *Orthis striatula* Schlotheim; Assman, p. 161, pl. 9, figs. 1, 2.
1916 *Orthis striatula* Schlotheim; Viétor, p. 452, pl. 18, fig. 10.
1936 *Schizophoria antiqua* Solle, p. 208, figs. 14, 15.

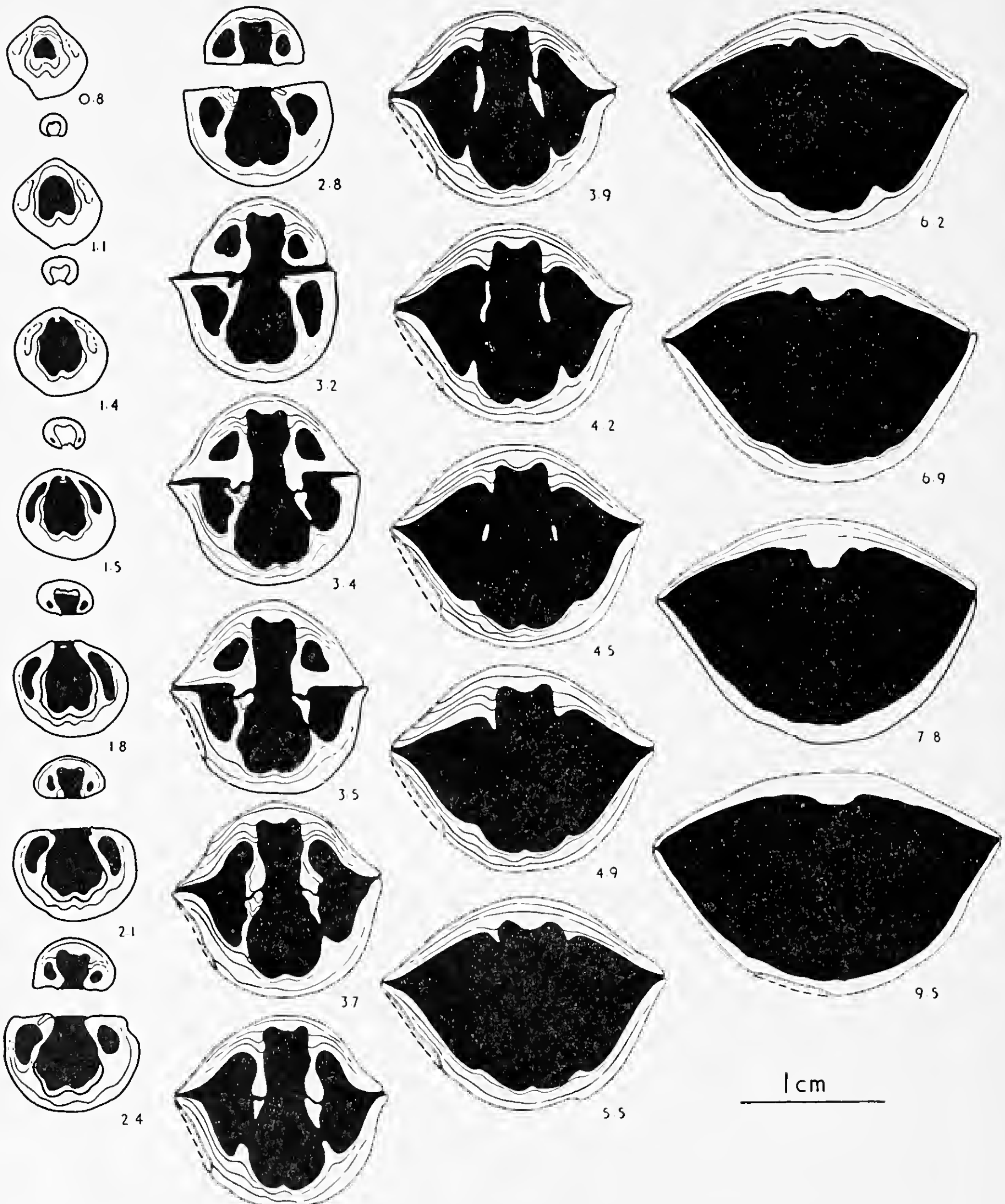
Type. The holotype, Nr. XVII 533*a*, and specimen Nr. XVII 533*b* are deposited in the Senckenberg Museum, Frankfurt.

Diagnosis. Medium to small, rectangular to elliptical, rugate shell, dorsibiconvex in adult form. Ventral muscle field strongly incised, flabellate, with broad, rounded median septum. Dorsal muscle field longitudinally elliptical, bounded posteriorly by curved brachiophore plates.

Description. Shell medium to small, ventribiconvex to dorsibiconvex, rectangular to elliptical, with greatest shell width at mid-length. Ventral sulcus ill-defined, originating near anterior border. Low, broad, subrounded anterior uniplication. Costellae coarse, 4 to 5 in 1 mm. at 10 mm. from beaks. Prominent growth rugae.

Teeth compound, supported by anteriorly divergent ventrally subparallel to divergent dental lamellae (text-fig. 2, sections 1.8–3.8). Ventral muscle field (text-fig. 3*a*) one-third to one-half valve length, flabellate, strongly incised. Deep, broad, rounded anterior re-entrant. Median septum generally prominent, rounded, broadening and increasing in height, and becoming flat-topped anteriorly (text-fig. 2, sections 1.1–9.5). Two slightly divergent vascula media. Genital markings developed postero-laterally (text-fig. 3*a*).

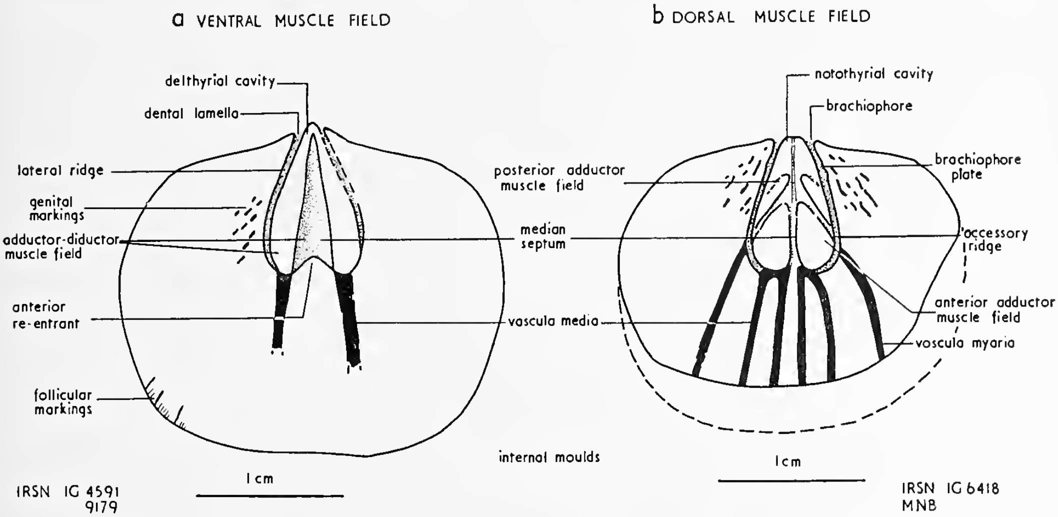
Myophore small, simple or rudimentarily compound, with central ridge bordered by two lateral ridges. Stubby brachiophores fused to strong, curved brachiophore plates (text-fig. 2, sections 1.4–3.8). Dental sockets oval, articulating with ventral teeth (text-fig. 2, sections 3.4, 3.5). Dorsal muscle field (text-fig. 3*b*) moderately incised,



TEXT-FIG. 2. *Schizophoria antiqua* Solle. Transverse serial sections (IRSN IG6154).

longitudinally elliptical, with greatest width anteriorly, one-third to one-half valve length. Accessory ridges continuous with brachiophore plates, smoothly reflexed anteriorly. Median septum angular, increasing in height and broadening very slightly anteriorly (text-fig. 2, sections 0.8–5.5). Anterior adductor muscle scar pyriform; posterior muscle scar possibly digitate. Four weakly divergent vascula media, and pair of divergent vascula myaria (text-fig. 3*b*). Genital markings developed postero-laterally.

Dimensions. External dimensions and muscle field dimensions are plotted on text-fig. 4.



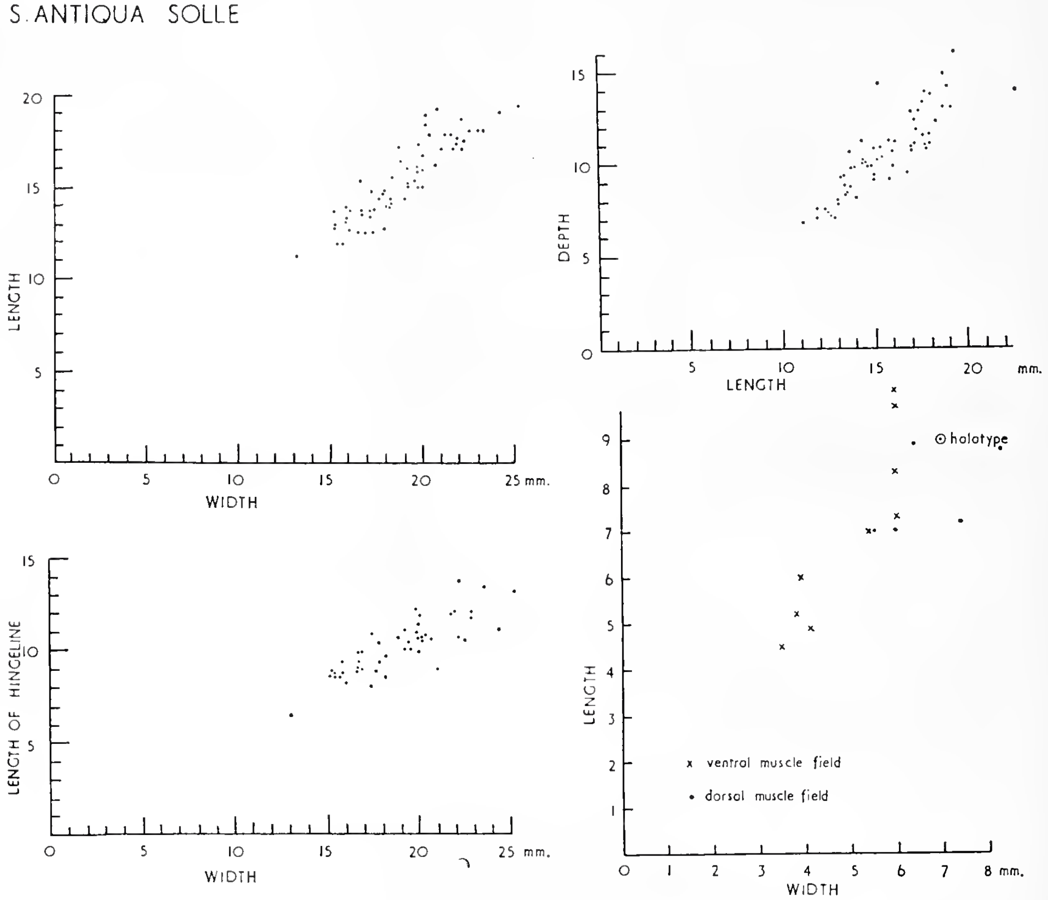
TEXT-FIG. 3. *Schizophoria antiqua* Solle. Ventral and dorsal muscle fields.

Remarks. Although Solle described *Schizophoria antiqua* from the Lower Devonian (Emsian) of Germany, the bulk of the material examined is deposited in the Institut royal des sciences naturelles de Belgique, and was collected from the Frasnian of the Dinant Basin. Two additional specimens from the Museum für Naturkunde, Berlin, collected from the Gedinnian of the Taunus region, extends the range of the species. This medium to small, tumid, rugate form of *Schizophoria* is distinct from other Devonian species (text-fig. 5).

Schizophoria antiqua closely resembles *S. woodi* Bond of the Carboniferous in outline, tumidity, prominent growth rugae, curved brachiophore plates, and flabellate pedicle muscle field. There is a closer resemblance in size with the smaller form of *S. woodi* from the Treak Cliff, Cracoe, and Craven areas of reef limestone. But *S. antiqua* is more coarsely costellate, lacks spine bases, and the brachial muscle field is more elliptical in outline.

Youthful forms of *S. antiqua* resemble *S. connivens* (Phillips) of the Carboniferous, in rectangular outline and coarse costellae, but internally there are distinct differences. The flabellate ventral muscle field, and broad median septum, contrast with the less flabellate, elliptical form and narrower septum of *S. connivens.* The elliptical dorsal muscle field, curved brachiophore plates, and six pallial sinus trunks of *S. antiqua* contrast with the elliptical to rounded muscle field, divergent brachiophore plates, and four pallial sinus trunks of *S. connivens.*

Material. Belgium: Frasnian, Assise de Frasnes (F2)-F2d (IRSN IG5911, 6154, 8439, 9179), F2h (IRSN IG4591, 6418), F2i (IRSN IG8701), Dinant basin. Germany: Gedinnian, Hobrächer Schichten (MNB), Taunus; Lower Emsian (MNB), Villmar. Middle Devonian (MNB), Boppard; Lower Frasnian (BC B1–9), Paffrather Syncline, near Cologne; Upper Middle Devonian (SMF), Villmar.



TEXT-FIG. 4. Dimensions of *Schizophoria antiqua* Solle.

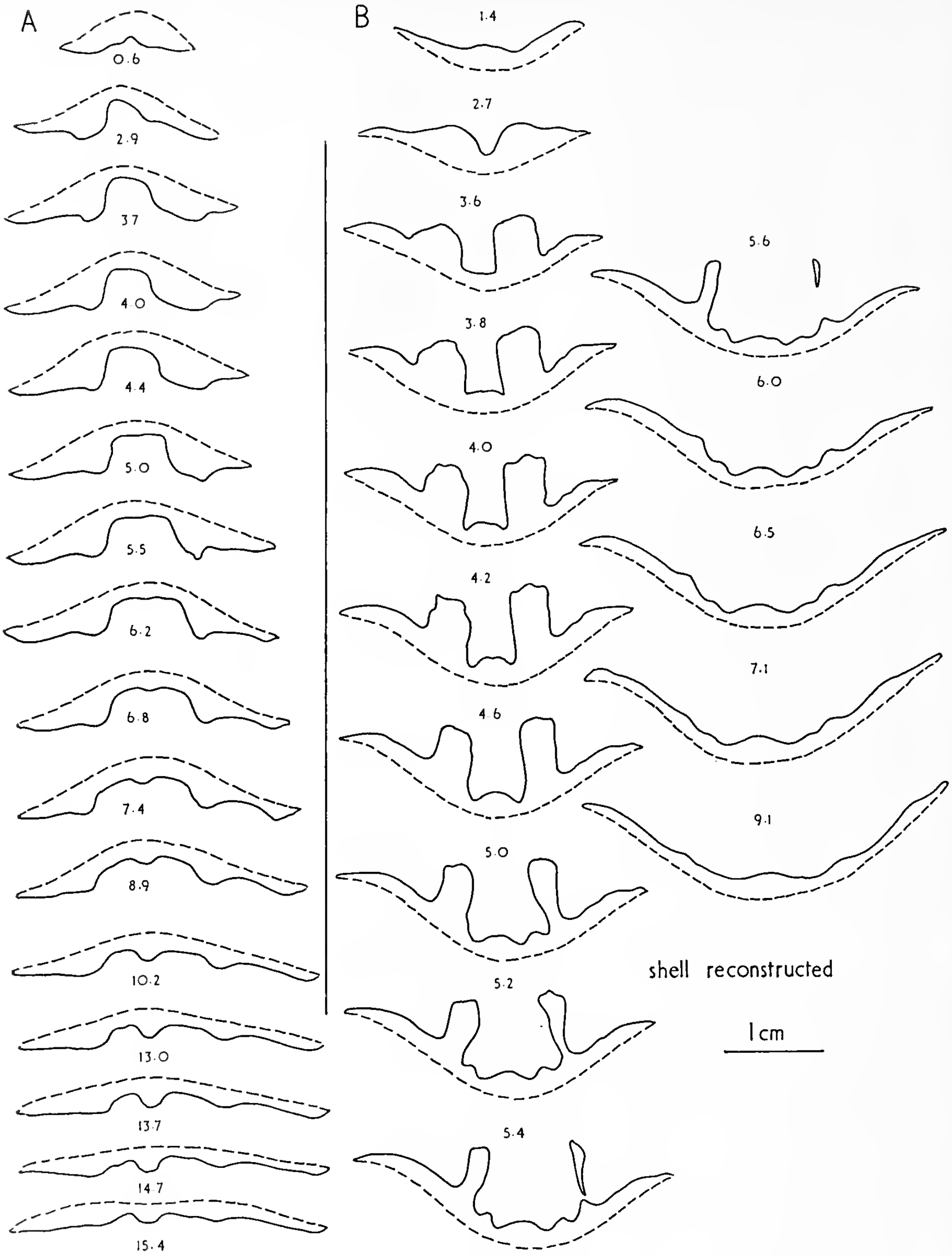
Schizophoria provulvaria Maurer

Plate 66, figs. 2, 3, 10; text-figs. 6–9

1864–5 *Orthis hipparionix* Vanuxem (?); Davidson, p. 90, pl. 17, figs. 9, 10? *non* 8, 11.
1886 *Orthis provulvaria* Maurer, p. 21.
1890 *Orthis personata* Zeiler; Kayser, pl. 12, fig. 3.
1893 *Orthis provulvaria* Maurer; Maurer, p. 7, pl. 3, figs. 1–4.
1904 *Orthis* (*Schizophoria*) *provulvaria* Maurer; Drevermann, p. 267, pl. 30, figs. 29? 30; pl. 31, figs. 11–19 (11? 16? 18?).
1936 *Schizophoria provulvaria* Maurer; Termier and Termier, p. 1126, pl. 3, figs. 3, 4: 1950, pl. 71, figs. 10, 11?; pl. 72, figs. 12? 13?
1938 *Schizophoria provulvaria* (Maurer); Shirley, p. 465, pl. 4, figs. 10–13.
1942 *Schizophoria provulvaria* (Maurer); Gill, p. 36, pl. 6, fig. 1.

	SIZE	OUTLINE	CONVEXITY	ORNAMENT	DENTAL LAMELLAE	VENTRAL MUSCLE FIELD	BRACHIOPHORES BRACHIOPHORE PLATES	DORSAL MUSCLE FIELD
Schizophoria antiqua Solle	medium small	rectangular elliptical	dorsibiconvex tumid	costellae coarse rugae prominent	ventrally subparallel to divergent	broad flabellate strongly incised	stubby brachiophores curved brachiophore plates	elongate oval moderately incised
Schizophoria provulvaria (Maurer)	large	elliptical	dorsibiconvex	—	ventrally subparallel to convergent	broad flabellate strongly incised	stubby brachiophores strong subparallel brachiophore plates	rectangular elliptical moderately incised digitate posterior adductor scars
Schizophoria pygmaea Struve	small	rectangular elliptical	weakly dorsibiconvex generally thin form	costellae fine rugae weak	ventrally divergent	broad flabellate strongly incised	stubby brachiophores curved brachiophore plates	rectangular rounded moderately incised
Schizophoria schnuri blankenheimensis Struve	large	rectangular elliptical	weakly dorsibiconvex generally thin form	costellae fine rugae weak	ventrally divergent	broad flabellate strongly incised	stubby brachiophores curved brachiophore plates	rectangular rounded moderately incised digitate posterior adductor scars
Schizophoria striatula (Schlotheim)	medium large	quadrate elliptical	dorsibiconvex	costellae coarse rugae prominent	ventrally subparallel to divergent	elongate oval flabellate strongly incised	stubby brachiophores strong divergent brachiophore plates	quadrate rounded moderately incised digitate posterior adductor scars
Schizophoria strigosa (Sowerby)	medium large	quadrate elliptical	dorsibiconvex	—	—	broad elongate oval flabellate strongly incised	—	quadrate rounded moderately incised digitate posterior adductor scars
Schizophoria vulvaria (Quenstedt)	large	quadrate rectangular elliptical	dorsibiconvex	—	ventrally convergent	elongate oval flabellate strongly incised	stubby brachiophores strong divergent brachiophore plates	quadrate rounded moderately incised digitate tripartite posterior adductor scars

TEXT-FIG. 5. Comparisons of Devonian species of *Schizophoria*.

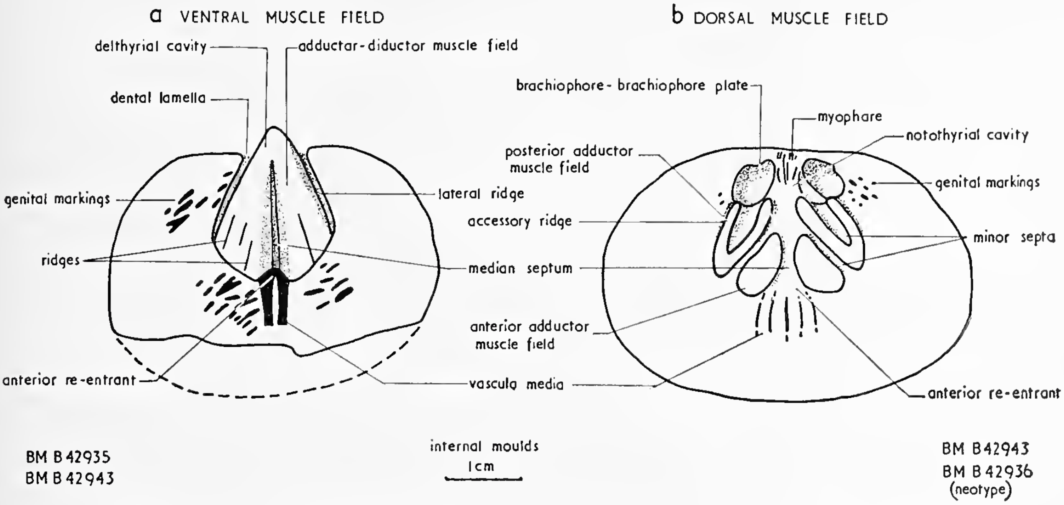


TEXT-FIG. 6. *Schizophoria provulvaria* (Maurer). Transverse serial sections of plaster internal moulds. A—ventral valve (HMUG L5345/2), B—dorsal valve (HMUG L5341/2).

Type. Maurer's specimens (1886, 1893) cannot be traced. These were collected from the Lower Devonian of Seifen, Germany. A neotype has been selected, BM B42943, a dorsal internal mould. This was also collected from the Lower Devonian of Seifen, Dierdorf.

Diagnosis. Shell large, elliptical. Ventral muscle field broad, flabellate, strongly incised, with broad, rounded median septum. Brachiophores-brachiophore plates thick, sub-subparallel to divergent. Short peripheral follicular markings.

Description. Shell mould large, dorsibiconvex, elliptical in outline, with greatest width at or slightly anterior to midlength. Anterior commissure rounded uniplicate.



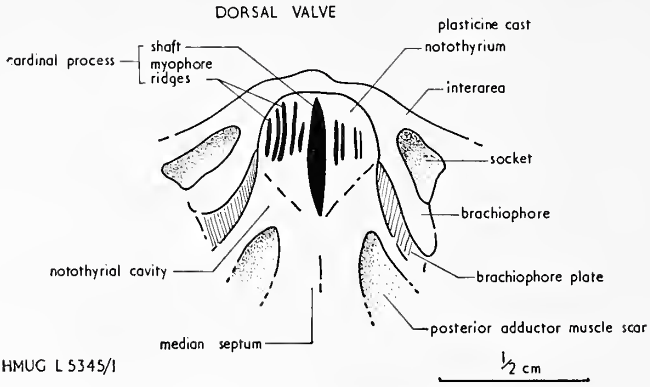
TEXT-FIG. 7. *Schizophoria provulvaria* (Maurer). Ventral and dorsal muscle fields.

Ventral muscle field (text-fig. 7*a*) one-half to two-thirds valve length, broad, flabellate, strongly incised. Subrounded anterior re-entrant. Median septum narrow, rounded, rapidly broadening and increasing in height anteriorly (text-fig. 6*a*, sections 6.2–15.4). Two parallel vascula media originating in anterior re-entrant of muscle field. Genital markings developed laterally and postero-laterally (text-fig. 7*a*).

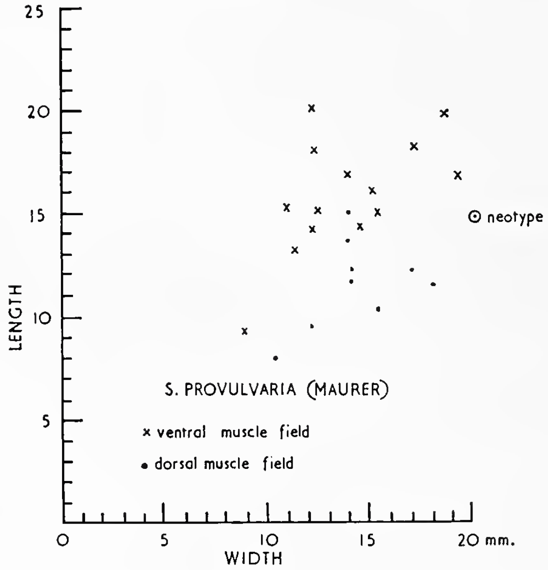
Prominent cardinal process; broad, compound myophore, narrow shaft (text-fig. 8). Stubby brachiophores fused to strong, thick, subparallel to divergent brachiophore plates (text-fig. 6*b*, sections 3.6–5.6). Dorsal muscle field (text-fig. 7*b*) moderately incised, transversely rectangular to elliptical, one-half valve length. Low accessory ridges smoothly reflexed anteriorly to form shallow, sub-rounded anterior re-entrant. Median septum low, broad, rounded, narrowing anteriorly (text-fig. 6*b*, sections 3.8–7.1). Anterior adductor muscle scar pyriform; posterior muscle scar more incised, digitate, with slightly longer inner lobe (text-fig. 7*b*). Two vascula media, each bifurcating (text-fig. 7*b*). Short follicular markings developed peripherally.

Dimensions. Dimensions of available muscle fields are plotted on text-fig. 9.

Remarks. Apart from a few doubtful specimens assigned to *S. provulvaria* preserved as fragmentary external moulds and illustrating a coarsely costellate shell, all specimens are preserved as fragmentary internal moulds. Serial sections of plaster internal moulds



TEXT-FIG. 8. *Schizophoria provulvaria* (Maurer). Cardinalia.



TEXT-FIG. 9. Dimensions of muscle fields of *Schizophoria provulvaria* (Maurer).

EXPLANATION OF PLATE 66

Fig. 1. *Schizophoria antiqua* Solle. 1 *a*, *b*, Ventral and dorsal views of internal mould, MNB (× 1½).

Figs. 2, 3, 10. *Schizophoria provulvaria* (Maurer). 2, Internal mould of dorsal valve, neotype, BM B42936 (× 1). 3, 10, Internal moulds of dorsal valves, MNB (× 1).

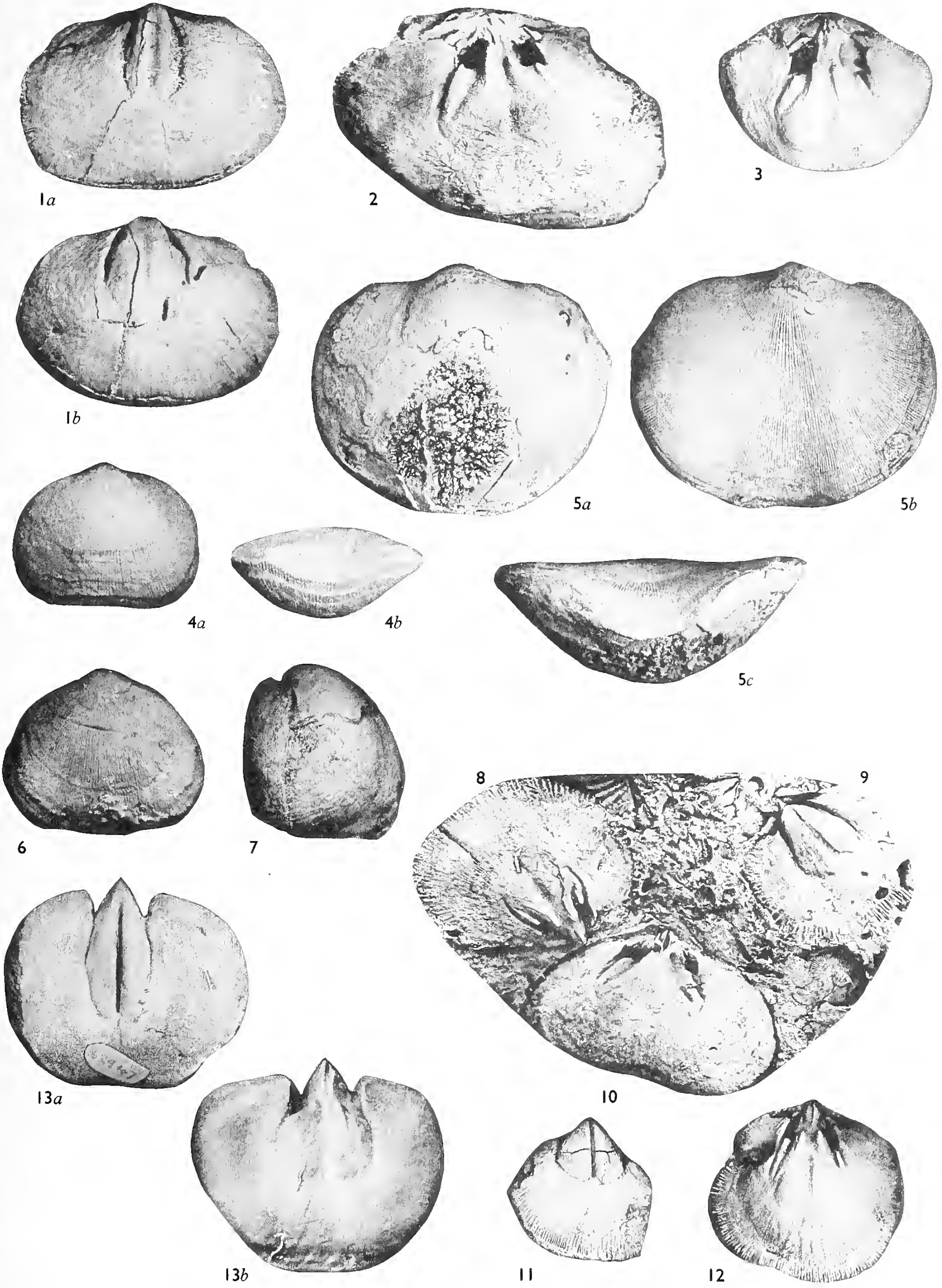
Fig. 4. *Schizophoria pygmaea* Struve. 4 *a*, *b*, Dorsal and anterior views, BC B55 (× 2).

Fig. 5. *Schizophoria schnuri blankenheimensis*. 5 *a–c*, Dorsal, ventral, and lateral views, BC B68 (× 1).

Figs. 6, 7. *Schizophoria striatula* (Schlotheim). 6, Ventral view, BC B90 (× 1). 7, Lateral view, BC B108 (× 1).

Figs. 8, 9, 11, 12. *Schizophoria strigosa* (Sowerby). 8, Internal mould of dorsal valve, neotype, MNB B102.1 (× 1). 9, 11, Internal moulds of dorsal valves, MNB (× 1). 12, Internal mould of dorsal valve, IRSN IG8219 (× 1).

Fig. 13. *Schizophoria vulvaria* (Quenstedt). 13 *a*, *b*, Ventral and dorsal views of internal mould, BM B62947 (× 1).



POCOCK, Devonian schizophoriid brachiopods

(Stanley, 1964) show the general appearance of internal structures. Only discrete valves were available, showing no ventral–dorsal valve relationship (text-fig. 6).

S. provulvaria (Maurer) superficially resembles *S. strigosa* (Sowerby). Comparisons are listed under *S. strigosa* (see text-fig. 5). *S. provulvaria* is distinguished externally from *S. vulvaria* (Quenstedt) by its wider outline. Internally, the flabellate ventral muscle field, broad median septum, and deep anterior re-entrant, contrast with the longer, lanceolate to weakly flabellate muscle field, narrow septum, and shallow, or lack of re-entrant of *S. vulvaria.* The moderately incised, rectangular dorsal muscle field, thick brachiophores and parallel-to-divergent brachiophore plates, and bipartite posterior adductor muscle scars of *S. provulvaria* contrast with the more quadrate, strongly incised muscle field, thinner brachiophores and divergent brachiophore plates, and commonly tripartite posterior muscle scar of *S. vulvaria.*

Davidson's use of *Orthis hipparionix* (1864–5 p. 90) for his specimens resembling *S. provulvaria* is invalid. He did state that his large internal moulds resembled *Orthis hipparionyx* of American authors, but could not be certain as to their identification. The genus *Hipparionyx* was established by Vanuxem in 1842, and is synonymous with the genus *Streptorhynchus* King. In 1853, Schnur, working in the Eifel, discovered specimens with a similar flabellate ventral muscle field, which he considered belonged to the genus *Orthis*, and changed Vanuxen's nomenclature to *Orthis hipparionyx*. But Schnur's specimens are orthotetid brachiopods. Davidson (1864–5) presumably recognized the flabellate ventral muscle field of his specimens and listed them in synonymy with Schnur's *Orthis hipparionyx.*

Material. Belgium, Dinant Basin: Siegenien, Grès d'Anor, Sg 2 (IRSN IG12533); Grauwacke de Saint-Michel, Sg 3 (IRSN IG5382, 5746, 8219); Grauwacke Inférieur de Laroche, Sg 3III (IRSN IG9382). Quartzophyllades de Saint-Vith, Sg 5III (IRSN IG8633); Emsien Inférieur, Grauwacke de Pesche, Em 1a (IRSN IG8791); Grès de Mormont, Em 1g (IRSN IG8390). Germany: Lower Devonian (BM B24563, B24565, B42935, 6, B42942, 3, B42945, 6, B49,920, HMUG L5341/4), Seifen, Dierdorf. Siegener Schichten (HMUG L5345/1, 2, SMF), Seifen. Siegener Schichten, Rauhflaserschichten (MNB), Seifen. South-west England: Lower Devonian (GSM 49692), New Drive above Hope's Nose, Torquay.

Schizophoria pygmaea Struve

Plate 66, figs. 4*a*, *b*; text-figs. 10, 12, 15

1963*a* *Schizophoria pygmaea* Struve, p. 251, pl. 39, 40.

(See Struve for synonymy.)

Schizophoria schnuri blankenheimensis Struve 1965

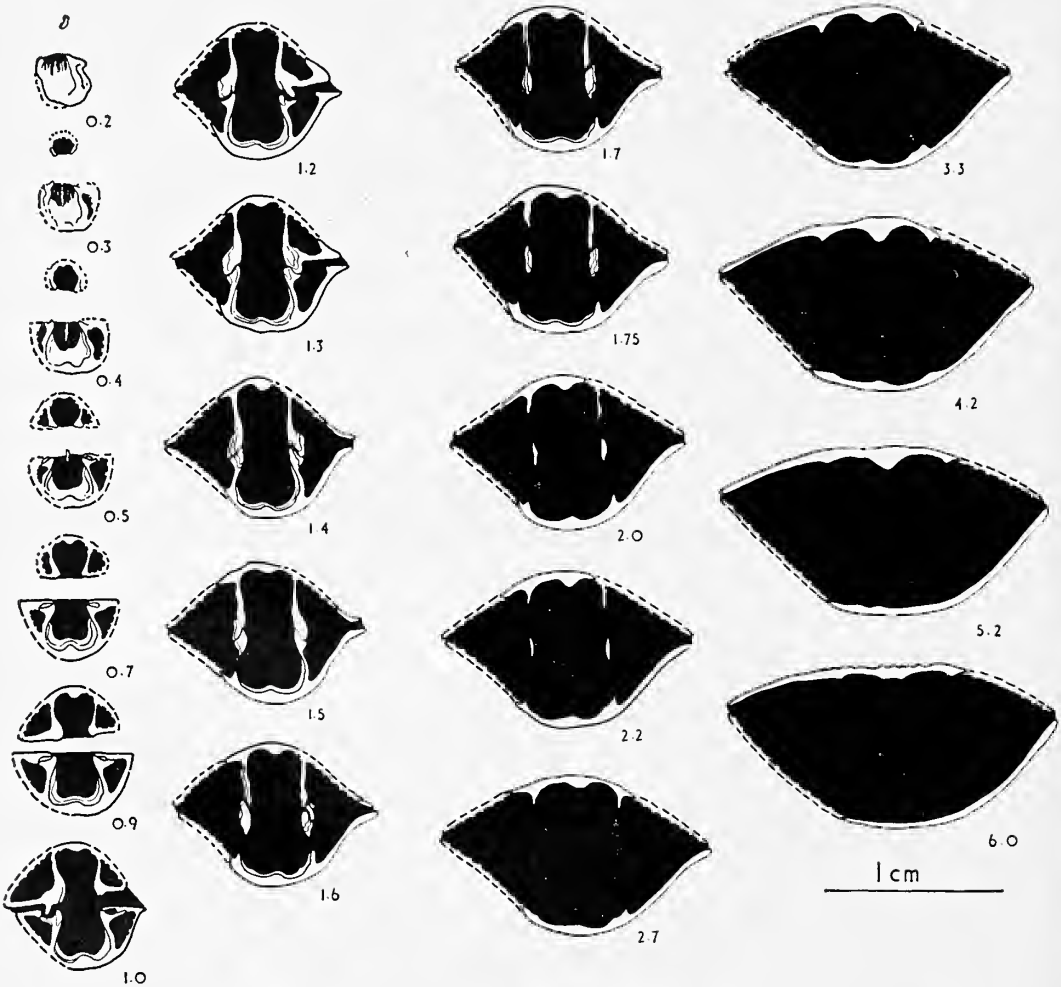
Plate 66, figs. 5*a–c*; text-figs. 11, 13–15

1853 *Orthis striatula* d'Orbigny; Schnur, pl. 38, fig. 1*e–g*?
1942 *Schizophoria excisa* (Quenstedt); Spriesterbach, p. 182, pl. 5, figs. 9–14.

Types. Struve (1963*a*) deposited the holotype, SMF 17298, and paratypes of *Schizophoria pygmaea* in the Senckenberg Museum, Frankfurt. The holotype of *Schizophoria schnuri blankenheimensis*, SMF 19559, and paratypes, are also deposited in the Senckenberg Museum.

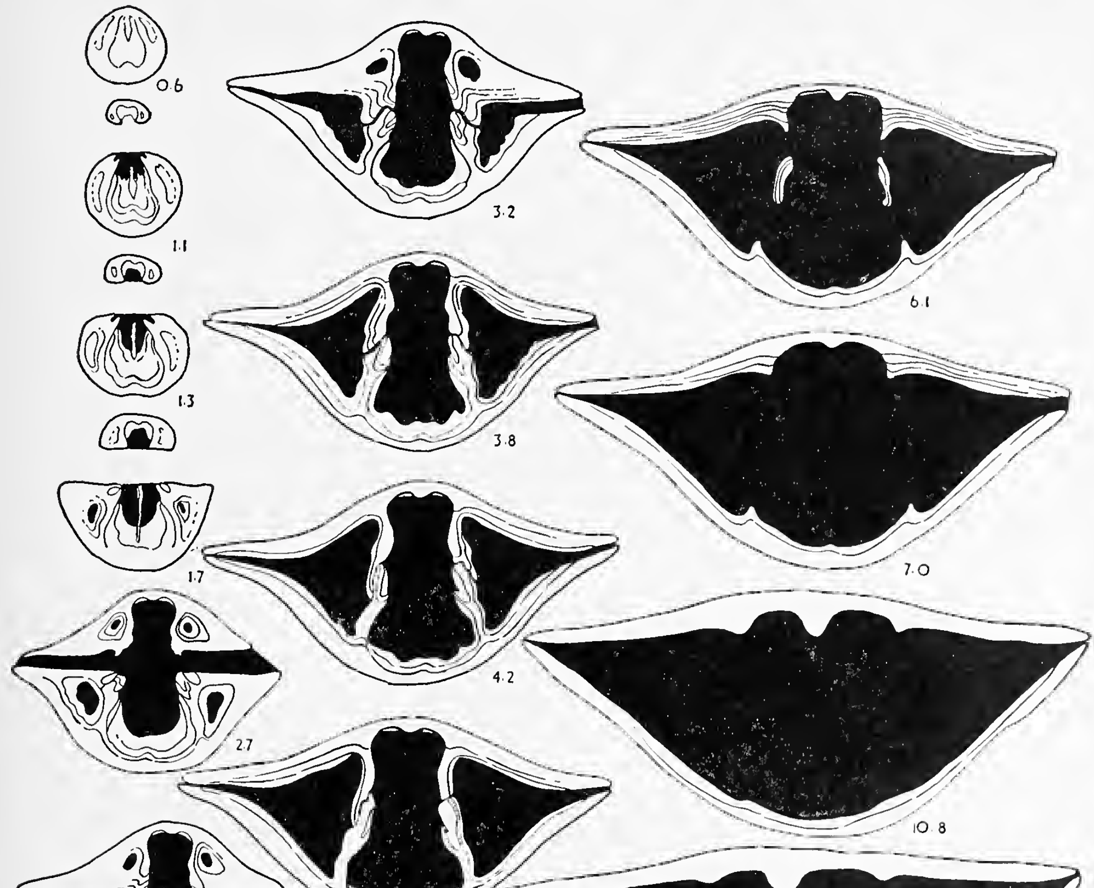
Diagnosis. Shell small (*S. pygmaea*) to large (*S. schnuri blankenheimensis*) rectangular to elliptical, weakly dorsibiconvex, with prominent ventral sulcus. Ventral muscle field flabellate, strongly incised, with broad, rounded median septum. Strong, curved brachiophore plates.

Description. Shell small to large, weakly dorsibiconvex, thin, rectangular to elliptical, with greatest width at or anterior to mid-length. Ventral sulcus well defined, originating below umbo, flaring and deepening anteriorly. Gentle dorsal fold developed in older specimens. Anterior commissure rounded uniplicate. Costellae fine, 5 to 6 in 1 mm. at 10 mm. from beaks. Spine bases developed at anterior ends of scattered costellae. Growth rugae developed on older specimens.



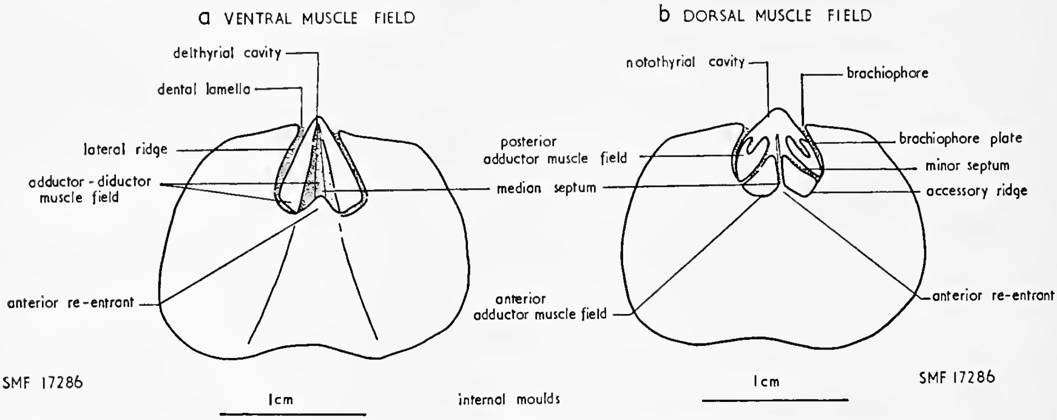
TEXT-FIG. 10. *Schizophoria pygmaea* Struve. Transverse serial sections (BC B58).

Teeth prominent, compound, supported by anteriorly and ventrally divergent dental lamellae (text-figs. 10, sections 0.4–1.75; 11, sections 2.2–5.0). Articulation supplemented by interlocking ends of brachiophores and dental lamellae (text-fig. 10, sections

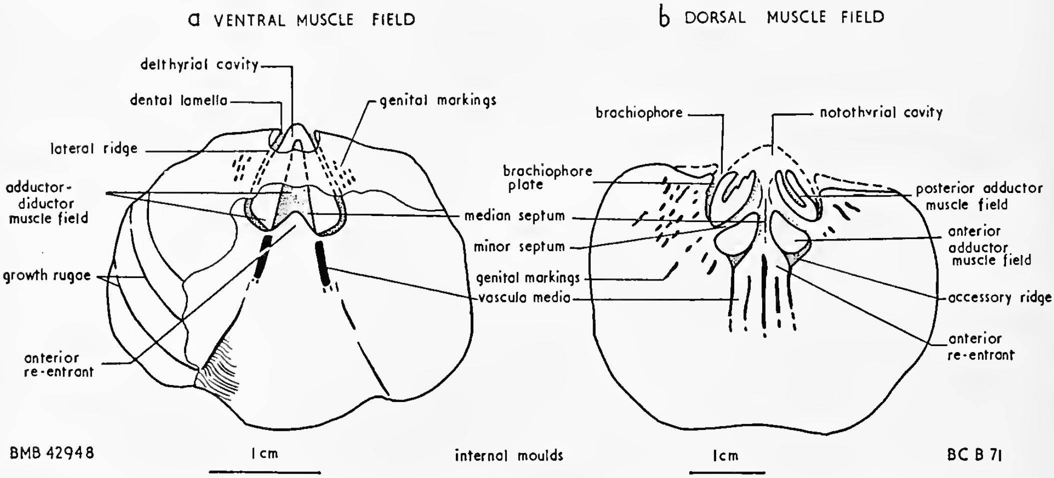


TEXT-FIG. 11. *Schizophoria schnuri blankenheimensis*. Transverse serial sections (BC B70).

1.4–1.6). Ventral muscle field (text-figs. 12, 13) one-third to one-half valve length, flabellate, strongly incised. Deep, subrounded anterior re-entrant. Median septum rounded, broadening and increasing in height, and becoming flat-topped anteriorly (text-figs. 10, sections 0.4–6.0; 11, sections 1.1–13.0). Two vascula media; genital markings developed postero-laterally (text-fig. 13).

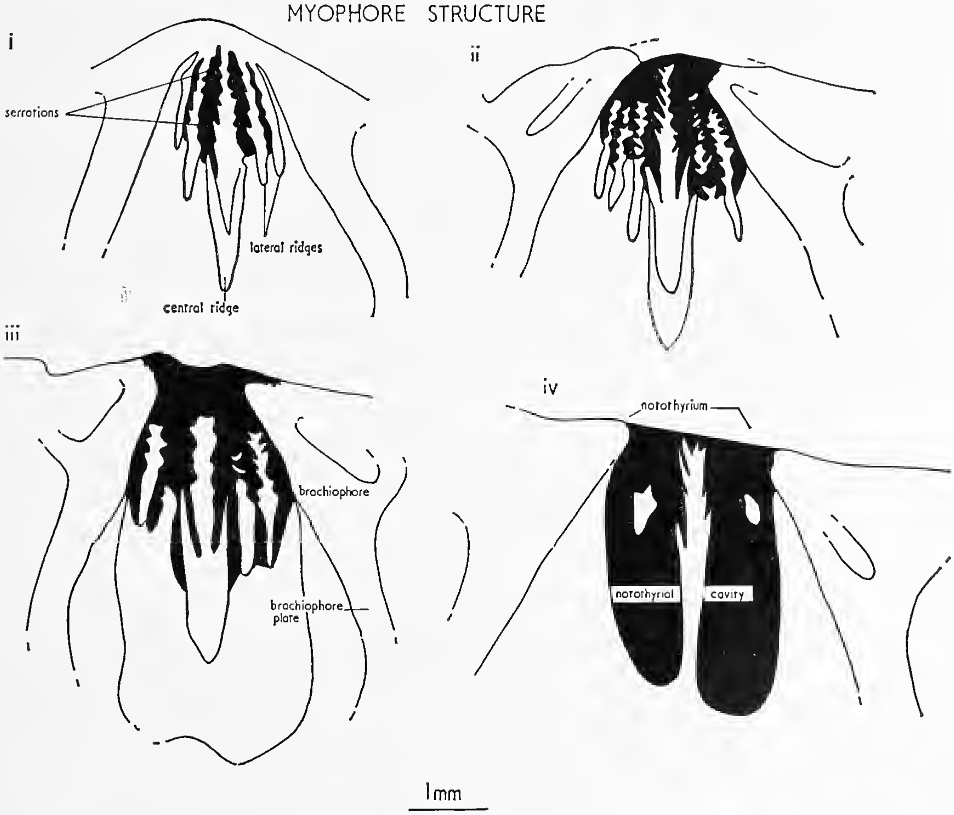


TEXT-FIG. 12. *Schizophoria pygmaea* Struve. Ventral and dorsal muscle fields.



TEXT-FIG. 13. *Schizophoria schnuri blankenheimensis*. Ventral and dorsal muscle fields.

Myophore prominent, compound, average width 2·3 mm., with central ridge bordered by four lateral ridges, all finely serrated (text-fig. 14). Stubby brachiophores fused to strong curved brachiophore plates (text-figs. 10, sections 0.4–1.5; 11, sections 1.1–5.3). Brachiophore plates thickened posteriorly by shell filling notothyrial cavity (text-figs. 10, sections 0.5–1.5; 11, sections 2.2–4.2). Deep, oval dental sockets articulating with ventral teeth (text-figs. 10, sections 1.0–1.3; 11, sections 2.8–3.8). Dorsal muscle field (text-figs. 12, 13) moderately incised, rectangular to rounded. Accessory ridges smoothly reflexed anteriorly to form deep subrounded re-entrant. Median septum rounded, decreasing in width and becoming sharp-crested anteriorly (text-figs. 10, sections 0.4–5.2; 11, sections 1.1–7.0). Anterior adductor muscle scar pyriform, posterior muscle scar digitate, both parts of similar length (text-figs. 12, 13). Two parallel vascula media, both bifurcating. Genital markings developed laterally and postero-laterally (text-fig. 13).

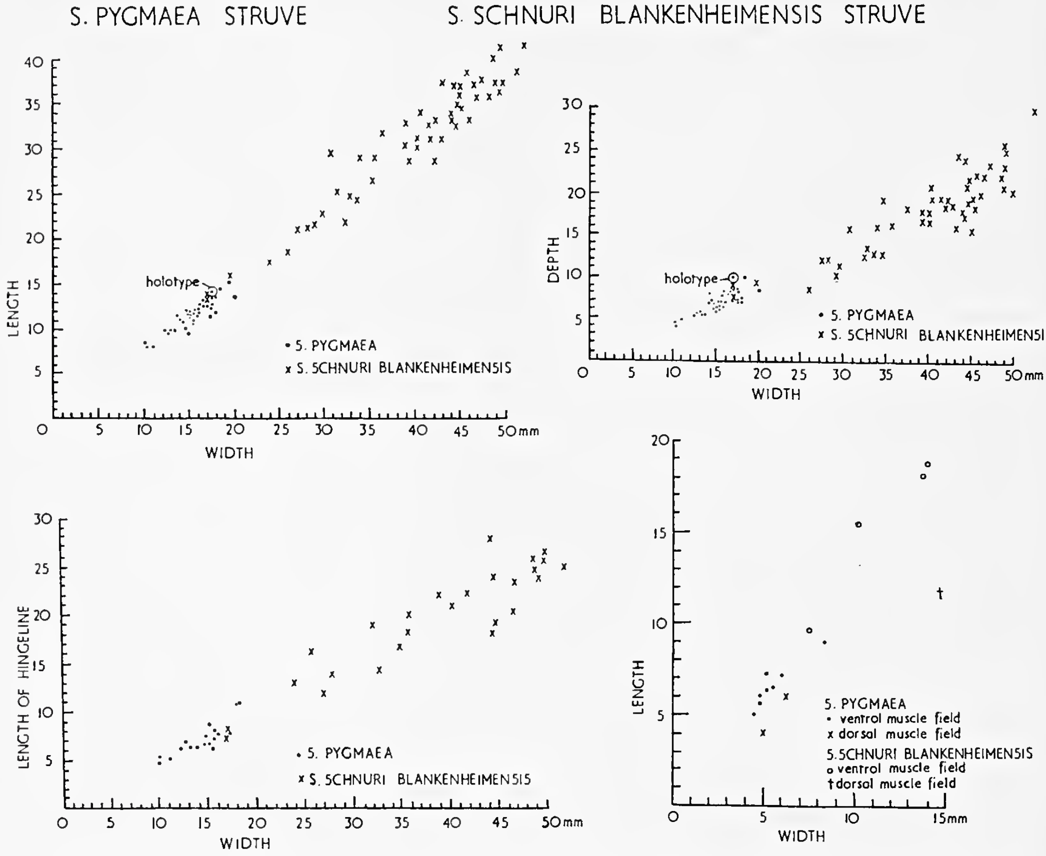


TEXT-FIG. 14. *Schizophoria schnuri blankenheimensis.* Myophore structure.

Dimensions. External dimensions and dimensions of muscle fields are plotted on text-fig. 15.

Remarks. Struve (1963*a*, p. 251) described and illustrated a small, relatively thin form of *Schizophoria*, *S. pygmaea*, from the Eifelian Hundsdell, Bildstock, and Flesten Horizons of the Eifel region. Spriesterbach (1942, p. 182) previously described and illustrated a large, relatively thin form of *Schizophoria* from the Middle Devonian of the Blankenheim region, also in the Eifel, which he listed in synonymy with *S. excisa* (Quenstedt). But *S. excisa* (Quenstedt), (Quenstedt 1868–71, p. 561, pl. 55, figs. 138–46) is a separate, distinct form and is synonymous with another species, *S. striatula* (Schlotheim 1813, p. 8, pl. 1, fig. 6; 1820, p. 254, pl. 5, fig. 4). Struve recognized the similarity between *S. pygmaea* and the specimens illustrated by Spriesterbach (1942 pl. 5, figs. 9–14), since he listed the specimen of figure 14 in synonymy with his species. But he made no reference at that time to the larger specimens illustrated on this plate. Figure 14 is probably a more youthful, smaller specimen of the form illustrated by Spriesterbach.

Struve (1965 p. 204) has since described these large specimens under a new subspecies, *S. schnuri blankenheimensis*. His new species, *S. schnuri*, is here considered to be a large form of *S. striatula*, and *S. schnuri blankenheimensis* is considered to be closely related to *S. pygmaea* Struve. *S. pygmaea* appears to be a dwarf form of *S. schnuri blankenheimensis*. Size is the only distinction. The largest (adult) specimens of *S. pygmaea* are comparable with some of the smallest (youthful) specimens of *S. schnuri blankenheimensis* (text-fig. 15). The two forms are similar externally and internally (cf. text-figs. 10, 11 and 12, 13).



TEXT-FIG. 15. Dimensions of *Schizophoria pygmaea* Struve, and *S. schnuri blankenheimensis*.

The dwarf species, *S. pygmaea*, occurs in the Hundsdell, Bildstock, and Flesten Horizons, where other brachiopods are smaller than normal. This dwarf form is preceded and succeeded stratigraphically by the larger form of *S. schnuri blankenheimensis*. Struve (1965) makes no reference to the similarity between *S. pygmaea* and *S. schnuri blankenheimensis*.

Schizophoria schnuri blankenheimensis superficially resembles *S. provulvaria* (Maurer) in the flabellate ventral muscle field and strong median septum, and the dorsal muscle field and four parallel vascula media. However, externally, *S. schnuri blankenheimensis* is generally less convex, and has a well-defined ventral sulcus. Specimen BC B64, from the lowermost Middle Devonian (Wolfenbach Horizon) is more convex, but when sectioned, illustrated the characteristic internal structures of *S. schnuri blankenheimensis*. *S. pygmaea* resembles *S. provulvaria* in the same manner, but is much smaller in size.

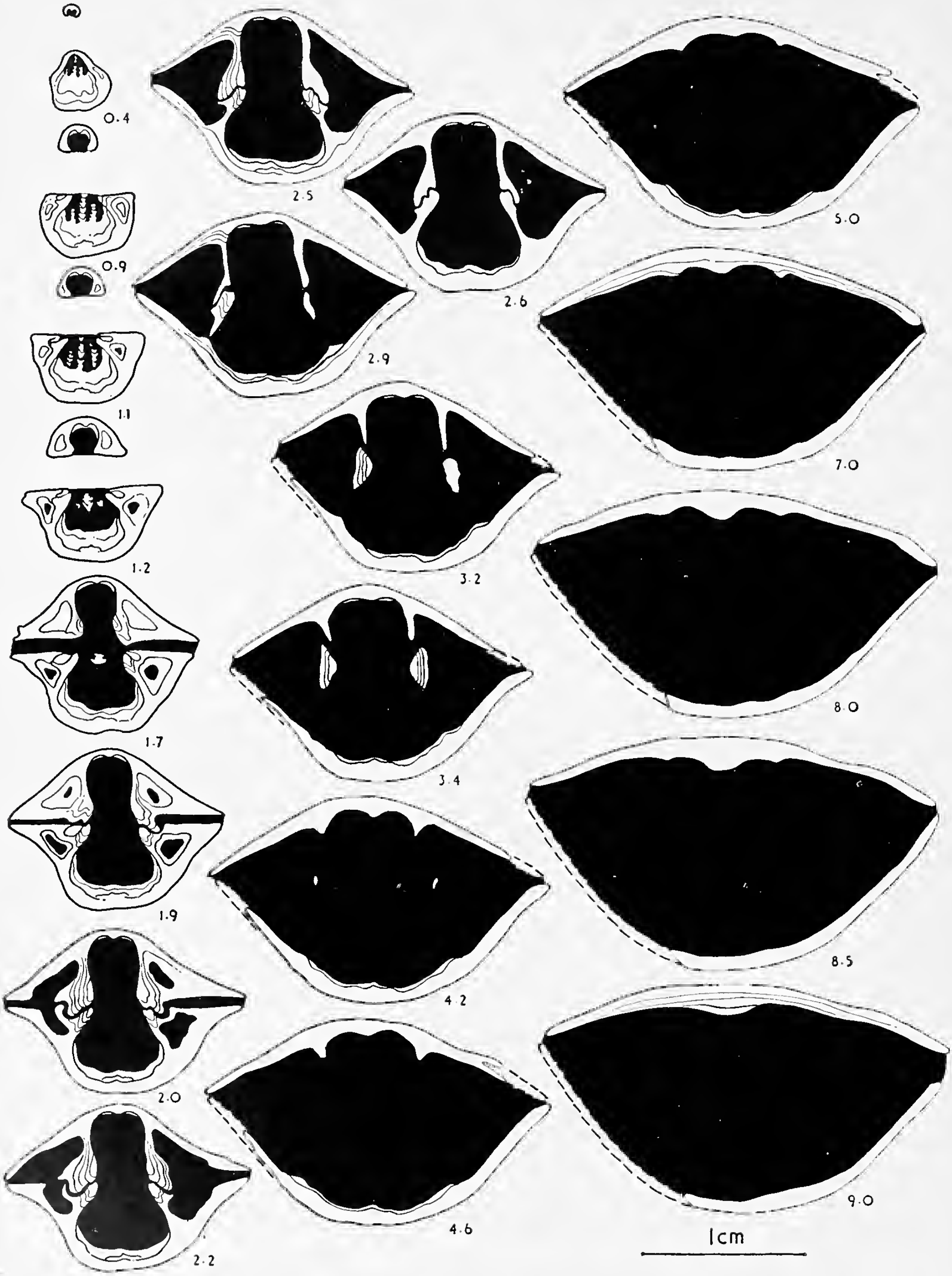
Schizophoria schnuri blankenheimensis is distinguished from *S. striatula* (Schlotheim) by its more rectangular outline and weaker convexity. *Schizophoria striatula* is generally more quadrate to rounded, with greatest shell width situated anteriorly. Internally there are muscle field differences (text-figs. 13, 17). The strongly flabellate ventral muscle field, deep re-entrant, broad median septum, and widely separated, slightly divergent vascula media of *S. schnuri blankenheimensis* contrast with the less flabellate to elongate elliptical muscle field, narrower re-entrant and median septum, and closely spaced, parallel vascula media of *S. striatula* from the Middle Devonian. In the dorsal valve, *S. striatula* has a longer inner portion to the posterior adductor muscle scar, divergent pallial sinus trunks, and shorter genital markings. The divergent brachiophore plates also contrast with the curved plates of *S. schnuri blankenheimensis*.

Material. Germany, Eifel region: Eifelian, *S. pygmaea*—Ahrdorf Beds, Bildstock Horizon, MTB Dollendorf (BC B10). Same stratigraphical level, MTB Dollendorf (BC B11). Ahrdorf Beds, Flesten Horizon, MTB Dollendorf (BC B12, 13). Same stratigraphical level, MTB Dollendorf (BC B14, 15). Same stratigraphical level, Ahrdorf Syncline, MTB Dollendorf (BC B16–59). Ahrdorf Beds, MTB Mechernich (BC B60–63). Nohn–Ahrdorf Beds, Hundsdell–Bildstock Horizon, Sötenicher Syncline, MTB Mechernich (SMF 17267). Schwirzheim Horizon, Gerolstein (SMF 17278). Ahrdorf Beds, Bildstock Horizon, Hillesheimer Syncline, MTB Dollendorf (SMF 17286). *S. schnuri blankenheimensis* —Lauch Beds, Wolfenbach Horizon, MTB Dollendorf (BC B64). Junkerberg Beds, Blankenheim Railway Cutting (BC B65–67, 69–71). Same stratigraphical level, MTB Blankenheim (BC B72–82). Middle Devonian, Gerolstein (BM B42948). Upper Junkerberg Beds, Blankenheim Railway Cutting (GMUS Eu DE 77(5). Lower and Upper Middle Devonian, Blankenheim (MNB). Middle Devonian, Gerolstein (MNB).

Schizophoria striatula (Schlotheim)

Plate 66, figs. 6–7; text-figs. 16–20

1777 *Terebratulae minutissime striatae*; Schröter, p. 390, pl. 4, fig. 24.
1813 *Anomia terebratulites striatulus* Schlotheim; Leonhard, p. 8, pl. 1, fig. 6.
1820 *Terebratulites striatulus*; Schlotheim, p. 254, pl. 15, fig. 4.
1841 *Orthis resupinata*; Phillips, pl. 27, fig. 115.
1842–4 *Orthis striatula*; De Koninck, p. 224, pl. 13^2, fig. 6; *non*. pl. 13, fig. 11.
1850–6 *Orthis striatula*; Sandberger and Sandberger, p. 355, pl. 34, fig. 4.
1851–5 *Orthis striatula*, Schlotheim; Davidson, pl. 7, figs. 128–33.
1853 *Spirifer striatulus* Schlotheim sp.; Geinitz, p. 61, pl. 15, figs. 10–12.
1853 *Orthis striatula* d'Orbigny; Schnur, p. 215, pl. 38, fig. 1 *a–d*, *h–i*; *e–g*?
1860 *Orthis striatula* Schlotheim; Grünewaldt, p. 87, pl. 2, fig. 6.
1864–5 *Orthis striatula* Schlotheim; Davidson, p. 87, pl. 17, figs. 4–7.
1868–71 *Orthis excisa*; Quenstedt, p. 561, pl. 55, figs. 138–45.
1908 *Orthis* (*Sch*) *striatula* (Schlotheim); Cowper-Reed, p. 79, pl. 13, figs. 19–24.
1922 *Orthis* (*Schl*) *striatula* (Schlotheim); Cowper-Reed, p. 34, pl. 6, figs. 12, 13.
1930 *Orthis* (*Schizophoria*) *resupinata* var. *striatula* (Schloth.); Paeckelmann, p. 158, pl. 9, figs. 3–10.
1959 *Schizophoria striatula* (Schlotheim); Biernat, p. 54, pls. 7–9; pl. 10, fig. 3.
non 1907 *Orthis* (*Schizophoria*) *striatula* Schlotheim; Walther, p. 279, pl. 13, fig. 9.
non 1916 *Orthis striatula* Schl; Viétor, p. 452, pl. 18, fig. 10.
non 1932 *Schizophoria* aff. *striatula* (Schlotheim); Schuchert and Cooper, pl. 23, figs. 22–25.

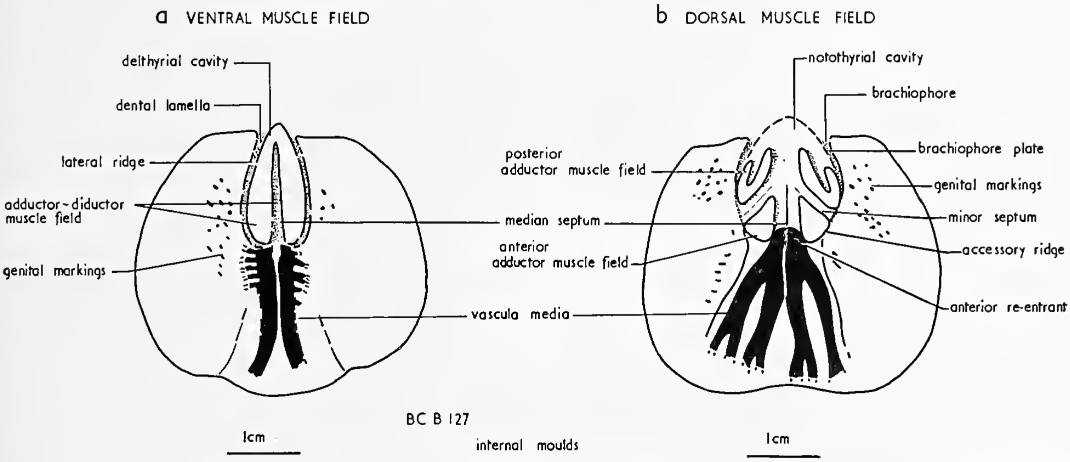


TEXT-FIG. 16. *Schizophoria striatula* (Schlotheim). Transverse serial sections (BC B94).

Type. Schlotheim's holotype is deposited in the Museum für Naturkunde, Berlin.

Diagnosis. Shell medium to large, elliptical to quadrate, with prominent anterior dorsal fold in older specimens. Ventral muscle field oval to flabellate. Strong divergent brachiophore plates.

Description. Shell medium to large, dorsibiconvex, quadrate to elliptical, with greatest shell width generally anterior to mid-length. Ventral sulcus originating half way along valve, broadening and deepening anteriorly. Dorsal fold developed in older specimens. Anterior commissure rounded uniplicate. Costellae moderately coarse, 4 to 5 in 1 mm. at 10 mm. from beaks. Growth rugae prominent on older specimens.



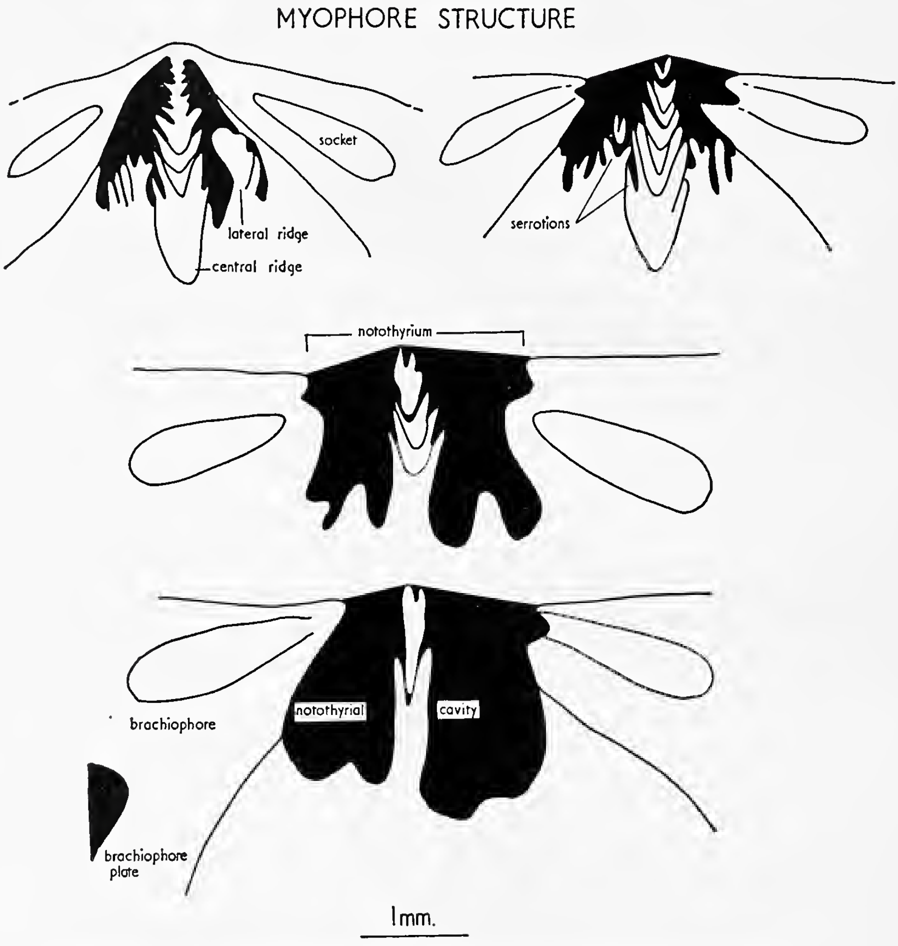
TEXT-FIG. 17. *Schizophoria striatula* (Schlotheim). Ventral and dorsal muscle fields.

Teeth prominent, compound, supported by anteriorly divergent, ventrally parallel to divergent dental lamellae (text-fig. 16, sections 1.7–3.2). Articulation supplemented by interlocking ends of brachiophores and dental lamellae. Shell partially filling delthyrial cavity (text-fig. 16, sections 0.9–3.4). Ventral muscle field (text-fig. 17*a*) one-third to one-half valve length, elliptical to flabellate, strongly incised. Rounded anterior re-entrant, or re-entrant absent. Median septum rounded, broadening and increasing in height anteriorly (text-fig. 16, sections 0.4–9.0). Two parallel vascula media, divergent anteriorly. Genital markings developed postero-laterally (text-fig. 17*a*).

Myophore prominent, compound, average width 3 mm., with central ridge generally bordered by two lateral ridges, all coarsely serrated (text-fig. 18). Stubby brachiophores fused to strong divergent brachiophore plates (text-fig. 16, sections 1.1–3.4). Deep dental sockets articulating with ventral teeth (text-fig. 16, sections 1.9–2.2). Dorsal muscle field incised, quadrate to rounded, one-third to one-half valve length. Accessory ridges smoothly reflexed anteriorly to form moderately deep, rounded re-entrant. Median septum angular to subrounded, broadening and increasing in height, then narrowing anteriorly (text-fig. 16, sections 0.9–7.0). Anterior adductor muscle scar pyriform, with acute apex; posterior muscle scar digitate, with longer inner lobe (text-fig. 17*b*). Two divergent vascula media, each bifurcating. Two narrower vascula myaria with lateral markings apparently developed, one either side main trunks. Genital markings developed postero-laterally (text-fig. 17*b*).

Dimensions. External dimensions and dimensions of muscle fields are plotted on text-fig. 19.

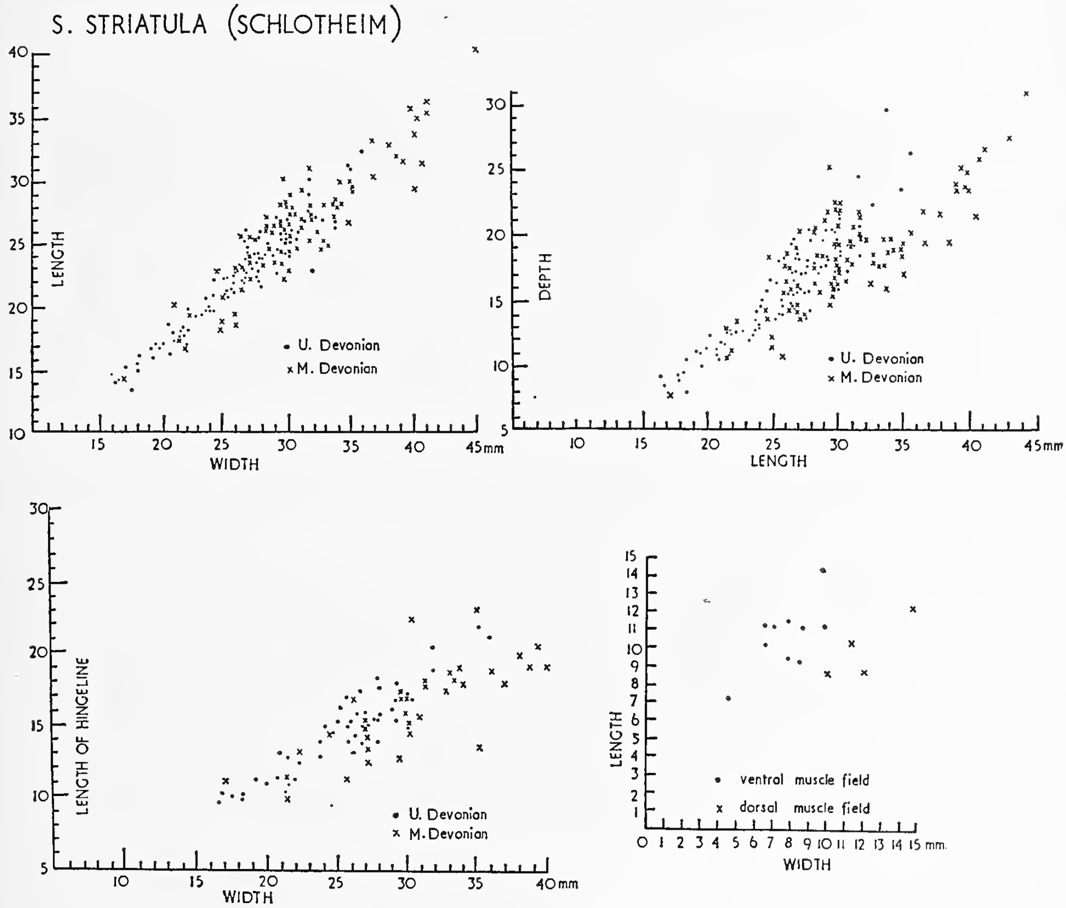
Remarks. Variation in the form of the ventral muscle field is shown on text-fig. 20.



TEXT-FIG. 18. *Schizophoria striatula* (Schlotheim). Myophore structure.

Schizophoria striatula (Schlotheim) is a long-ranging species (Eifelian–Frasnian), and shows little variation in morphology, except in size. Although specimens from the Middle and Upper Devonian have been differentiated on text-fig. 19, they have comparable dimensions. But many Upper Devonian specimens lack the characteristic dorsal anterior fold of the Middle Devonian forms, and have their greatest shell width at the mid-length. Internally, the ventral muscle field of many Upper Devonian specimens is more flabellate, with a broader septum. However, specimen BC B131 collected from the Middle Devonian, although representing a minority, has a flabellate muscle field, and specimen GSM 34/20, an Upper Devonian form, is an exception, with an elliptical muscle field (text-fig. 20).

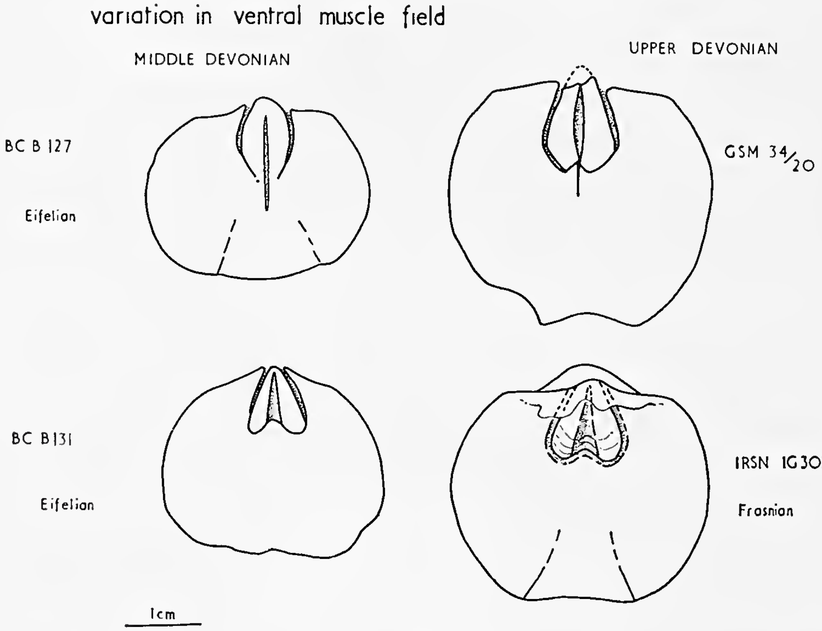
Specimens of *Schizophoria striatula* from the Geisdorf Horizon (Eifelian) of the Eifel region are much larger. Other members of fauna at this level are also larger. Struve (1965, p. 202) described a new species, *Schizophoria schnuri*, from the Middle Devonian of the Eifel, which also appears to be a large form of *S. striatula*. At the same time, he established the subspecies *S. schnuri schnuri*, *subexcisa*, *junkerbergiana*, and *biscissa*. There are no illustrations of internal structures, and externally the subspecies could represent variation within *S. striatula*.



TEXT-FIG. 19. Dimensions of *Schizophoria striatula* (Schlotheim).

Schizophoria striatula superficially resembles *S. resupinata* (Martin) of the Carboniferous in general outline and muscle fields. Early workers frequently considered them as one species. But *S. striatula* is generally smaller, more quadrate, lacks a dorsal sulcus, has a higher anterior plication, and lacks spine bases. *Schizophoria resupinata* is frequently larger, rectangular to elliptical, with a rectimarginate to uniplicate to unisulcate to sulciplicate anterior commissure, and is frequently covered in spine bases. The elliptical to weakly flabellate ventral muscle field of *S. striatula* superficially resembles that of *S. resupinata*, and the dorsal muscle fields are comparable.

Material. France, Boulonnais: Lower Frasnian, NE. end Carrière Parisienne (BC B83–89); Devonian, Ferques (BM B19213, B82765, B82778); Devonian (BM B26,209). Belgium, Dinant Basin: Couvinien Supérieur (CO 2)—CO 2a (IRSN IG4916, 6887, 8663), CO 2c (IRSN IG4761, 4916, 5127, 9694); Frasnien Moyen (F2)—F2a (IRSN IG3031, 5911, 8254, 11.349), F2b (IRSN IG3349), F2e (IRSN IG4591), F2i (IRSN IG3031, 2731, 4761, 5408). Germany, Eifel region: Eifelian–Lower Nohn beds, Weilersbach Horizon, Hillesheimer Syncline, MTB Dollendorf (BC B90–92); Lower Nohn Beds, low Schleit Horizon, MTB Dollendorf (BC B93, 94); Upper Junkerberg Beds, Geisdorf Horizon, MTB Gerolstein (BC B95); same stratigraphical level, Prüm Syncline (BC B96–98); same stratigraphical level, MTB Mechernich (BC B99). Upper Junkerberg Beds to Upper Freilingen Beds, MTB Gerolstein (BC B100–12); Lower Freilingen Beds, MTB Mechernich (BC B113–17); same stratigraphical level, MTB Münstereifel (BC B118–28). Freilingen Beds, MTB Dollendorf (BC B129); Freilingen Beds, Eilenberg Horizon, MTB Dollendorf (BC B130, 131); Givetian, Loogh Beds, Rech Horizon, Hillesheimer Syncline (BC B132, 133); Middle Devonian, Gerolstein (BM B39562, 3); Middle Devonian (BM B62946, B86023); Mitteldevon, *ostiolatus* Horizon, Geisdorf (SMF); Mitteldevon, Gerolstein (SMF). Southwest England: Upper Devonian (probably Petherwin Beds, Gatehouse Quarry), Petherwin (GSM 34/20).



TEXT-FIG. 20. *Schizophoria striatula* (Schlotheim). Variation in ventral muscle field.

Schizophoria strigosa (Sowerby)

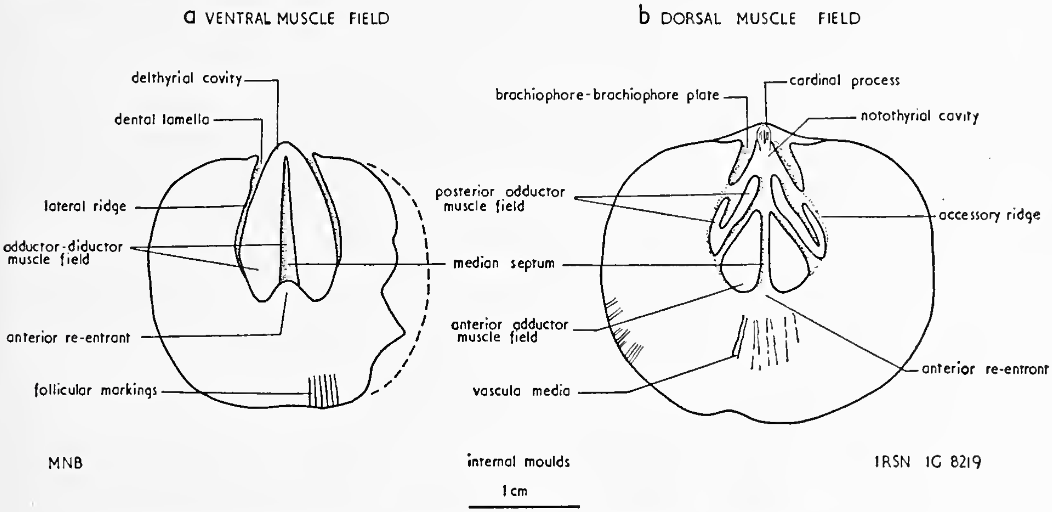
Plate 66, figs. 8, 9, 11, 12; text-figs. 21, 22

1842 *Orthis? strigosa*, Sowerby, p. 409, pl. 38, fig. 7.
1886 *Orthis*; Maurer, p. 18.
1887 *Orthis strigosa* Sowerby; Béclard, p. 88, pl. 4, figs. 15, 16.
1893 *Orthis occulta* Maurer, p. 9, pl. 3, figs. 5–9.

non 1871 *Orthis strigosa* Quenstedt, pl. 56, figs. 55, 56.
non 1890 *Orthis personata* Zeiler; Kayser, pl. 2, figs. 3–6.

Type. Sowerby's specimen (1842) cannot be traced. This was collected from Devonian rocks of the Dill synclinorium. A neotype, a dorsal internal mould, has been selected from the Museum für Naturkunde, Berlin. This was collected from the Lower Devonian, Rauhflaserschichten, at Seifen.

Diagnosis. Shell medium to large, quadrate to elliptical. Ventral muscle field moderately long, flabellate, strongly incised, with narrow to broad, rounded median septum. Moderately thin brachiophores and brachiophore plates. Long peripheral follicular markings.



TEXT-FIG. 21. *Schizophoria strigosa* (Sowerby). Ventral and dorsal muscle fields.

Description. All specimens examined are preserved as internal moulds. Internal mould medium to large, dorsibinconvex, quadrate to elliptical, with greatest width at mid-length. Anterior commissure rounded uniplicate.

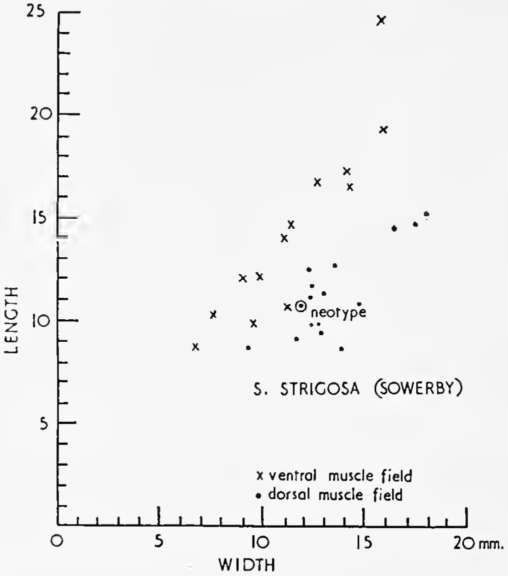
Ventral muscle field (text-fig. 21*a*) one-half to two-thirds valve length, flabellate, strongly incised. Shallow anterior re-entrant, or re-entrant absent (text-fig. 21*a*). Median septum varying in width, rounded, broadening, and increasing in height anteriorly.

Cardinal process differentiated into oval myophore supported by narrower shaft. Myophore compound, with up to twelve lateral ridges. Dorsal muscle field (text-fig. 21*b*) incised, quadrate to rounded. Accessory ridges smoothly reflexed anteriorly to form shallow, sub-rounded anterior re-entrant. Median septum narrow, subangular, narrowing and decreasing in height anteriorly. Anterior adductor muscle scar pyriform; posterior adductor muscle scar bipartite, with longer inner lobe. Long follicular markings developed peripherally.

Dimensions. Dimensions of available muscle fields are plotted on text-fig. 22.

Remarks. Sowerby (1842, pl. 38, fig. 7) illustrated a fragmentary ventral internal mould, under *Orthis*? *strigosa*, from the Silurian of Haiger Sülbach (Dillenburg) in the German Rhineland. More recent work has shown that Devonian rocks outcrop in the Dill synclinorium, and not Silurian rocks as previously supposed. Other German and Belgian material of this species is Lower Devonian in age. Béclard (1887, pl. 4, fig. 17) illustrated a similar ventral internal mould under *Orthis strigosa* Sowerby, from the Dinant Basin, Belgium.

Detailed and accurately localized collections from the Lower Devonian of Belgium (deposited in the Institut royal des sciences naturelles) include forms closely resembling Sowerby's, Béclard's, and Maurer's illustrations. These have been listed under *S. strigosa* (Sowerby). The dorsal muscle fields of these specimens (text-fig. 21*b*) closely resemble Maurer's illustrations. But the ventral muscle field is often less flabellate, and the median septum narrower, as shown by Sowerby.



TEXT-FIG. 22. Dimensions of muscle fields of *Schizophoria strigosa* (Sowerby).

The ventral field occasionally resembles that of *Schizophoria vulvaria* (Quenstedt) in outline and narrow median septum. These variations have previously been illustrated by authors with specimens under *S. vulvaria* (eg. Oehlert 1887, pl. 5, figs. 1, 5) and *S. provulvaria* (Drevermann 1904, pl. 30, fig. 20). These could possibly belong to *S. strigosa*. The specimens of *S. vulvaria* illustrated by Oehlert (1887) have also been listed by Maillieux (1936, p. 53) under *S. provulvaria*, indicating further the presence of specimens with close similarities with both *S. provulvaria* and *S. vulvaria*.

The specimens illustrated by Drevermann (1904, pl. 31, figs. 16–18) under *S. provulvaria* have long follicular markings, characteristic of *S. strigosa*. Those of *S. provulvaria* are shorter.

Schizophoria strigosa appears in the Siegenian, and ranges into the lower Emsian, where it is succeeded by *S. vulvaria*.

Maurer (1893, p. 10, pl. 3, figs. 5–9) described and illustrated another species, *Schizophoria occulta*, which is here considered synonymous with *S. strigosa*. The ventral muscle fields and follicular markings are similar. Maurer also illustrated a dorsal internal mould, not shown by Béclard or Sowerby. Maurer recognized *S. occulta* (i.e. *S. strigosa*) as distinct from the contemporaneous species *S. provulvaria.* The ventral muscle field of *S. occulta* is strongly incised, flabellate, with a rounded median septum, while that of *S. provulvaria* is much more strongly incised, protuberant in profile, and often with a broader median septum.

There are distinct differences in the dorsal muscle fields of *S. occulta* (*S. strigosa*) and *S. provulvaria.* The more slender brachiophores and brachiophore plates, and longer inner lobe of the digitate posterior adductor muscle scar, contrast with the strong brachiophores and brachiophore plates and more equal lobes of *S. provulvaria.*

Material. Belgium, Dinant Basin: Siegenien, Grauwacke de Petigny, Sg 3b (Hersdorferschichten), (IRSN IG8254); Grauwacke de Petigny, Sg 4 (IRSN IG8190); Grauwacke de Saint-Michel, Sg 3 (IRSN IG8219); Emsien Inférieur, Grauwacke de Pesche, Em 1a (IRSN IG8791). Germany: Siegener Schichten (MNB.B102.1—neotype), Rauhflaserschichten (MNB), Seifen, Lower Coblenzian (SMF).

Schizophoria vulvaria (Quenstedt) 1867

Plate 66, figs. 13*a*, *b*; text-figs. 23–25

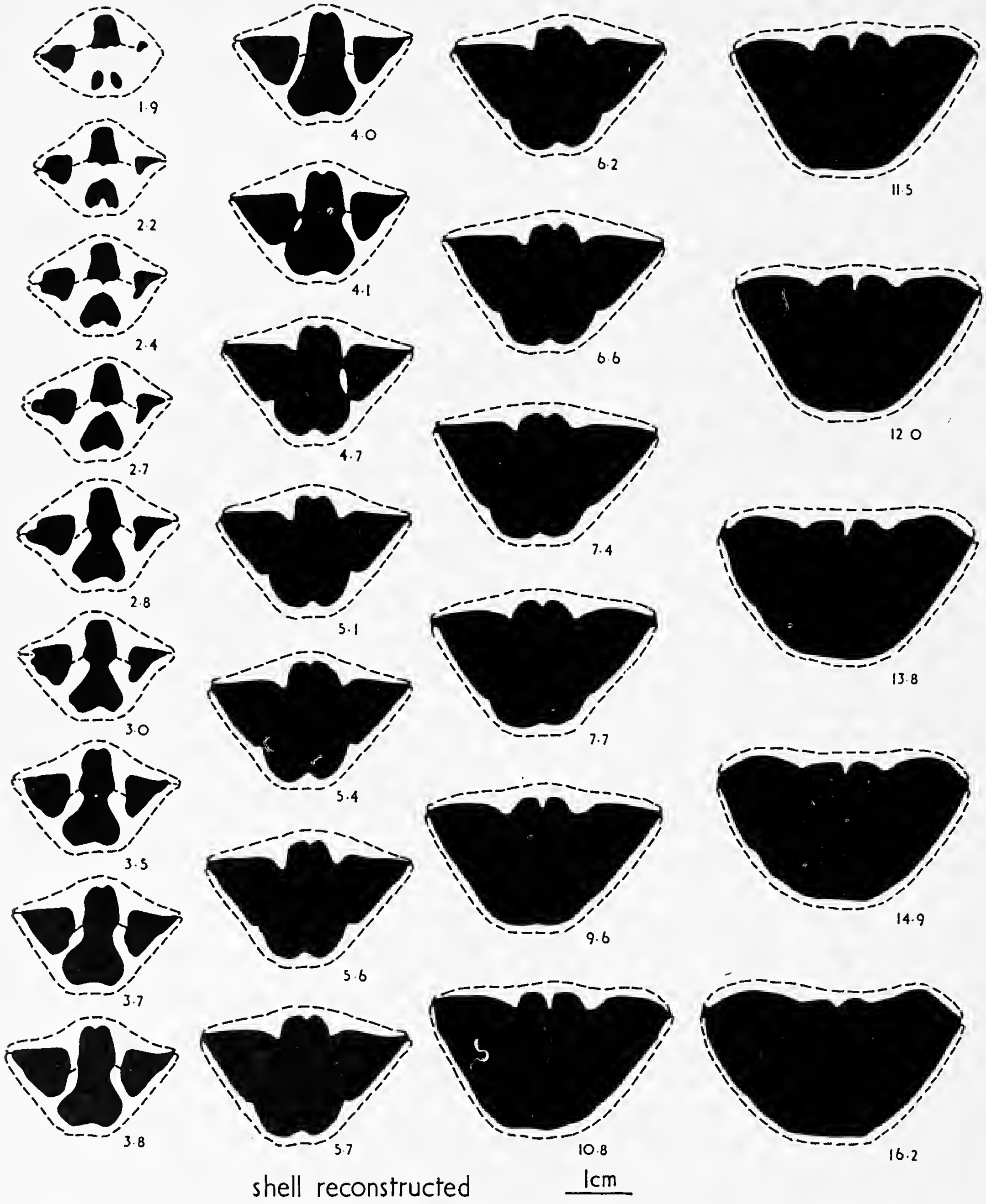
1655 *Hysterolithos*; Worm, p. 83, text-fig. on same page.
1719 *Hysterolithus*; Wolfart, pl. 3, figs. 3, 5, *non* 4.
1763–4 *Hysterolites vulva marina*; Baumer, p. 327, fig. 28.
1768 *Hysterolites*; Walch, p. 90, pl. B4, figs. 5, 6.
1820 *Hysterolites vulvarius* Schlotheim, p. 247, pl. 29, fig. 26? *non* 2*a*, 3.
1853 *Orth. Beaumonti* de Verneuil; Schnur, p. 215, pl. 37, fig. 9.
1867 *Hysterolithes vulvarius* Quenstedt, p. 577, pl. 49, fig. 2.
1868–71 *Hysterolithus vulvarius*; Quenstedt, p. 565, pl. 56, figs. 2–6.
1882 *Hysterolithes vulvarius*; Quenstedt, p. 737, fig. 252.
1885 *Hysterolithes vulvarius*; Quenstedt, pl. 57, fig. 13.
1887 *Orthis* (*Hysterolithes*) *vulvarius* Schlotheim sp.; Oehlert, p. 53, pl. 5, figs. 1–9.
1889 *Orthis hysterita* Gmelin; Kayser, p. 53, figs. 1, 7–9.
1893 *Orthis vulvaria* Quenstedt; Maurer, pl. 4, figs. 1, 2.
non 1753 *Hysterolithus*; Tessin, p. 90, pl. 5, fig. 2.
non 1850 *Orthis Beaumonti* de Verneuil, p. 180, pl. 4, fig. 8.
non 1938 *Schizophoria vulvaria* (Schlotheim); Compte, p. 13, pl. 1, figs. 2, 3.

Type. Schlotheim's specimens (1820, pl. 29, figs. 2*a*, 3, and possibly 2*b*) were probably spiriferids (see '*Remarks*'). Quenstedt (1867, 1868–71, 1882, 1885) is apparently the first author to describe and illustrate *Schizophoria vulvaria* proper. These specimens are deposited in the Geological Museum, Tübingen.

Diagnosis. Shell large, quadrate to rectangular. Ventral muscle field long, lanceolate to weakly flabellate, strongly incised, divided by narrow, subrounded median septum. Strong divergent brachiophore plates. Each posterior adductor muscle scar tripartite or quadripartite.

Description. Internal mould large, dorsibiconvex, quadrate to rectangular, with greatest width at or slightly anterior to mid-length. Anterior commissure rounded uniplicate.

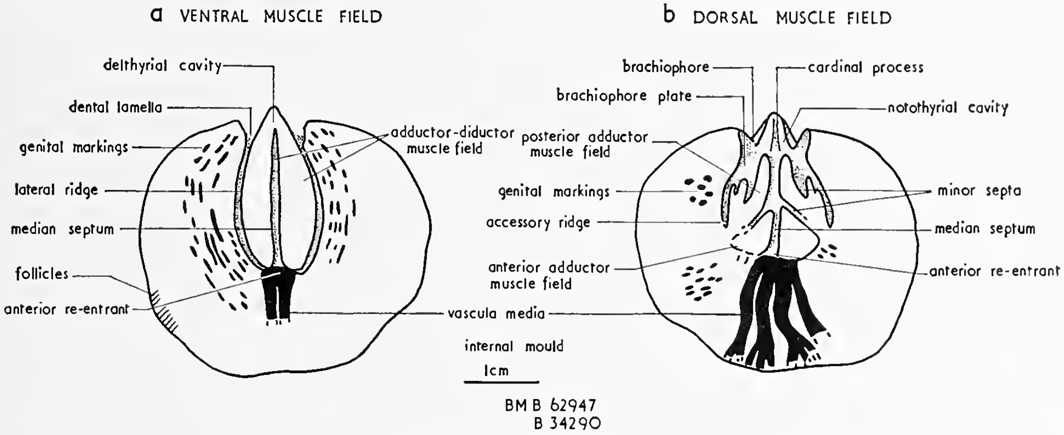
Ventral muscle field (text-fig. 24*a*) long, one-half to two-thirds valve length, lanceolate to weakly flabellate, strongly incised. Dental lamellae ventrally convergent anteriorly divergent. Shallow, subangular re-entrant, or re-entrant absent (text-fig. 24*a*). Median septum narrow, subrounded, broadening slightly anteriorly, first increasing, then decreasing in height (text-fig. 23, sections 3.5–16.2). Two sub-parallel vascula media, with lateral branches, originating from diductor muscle field or anterior re-entrant. Genital



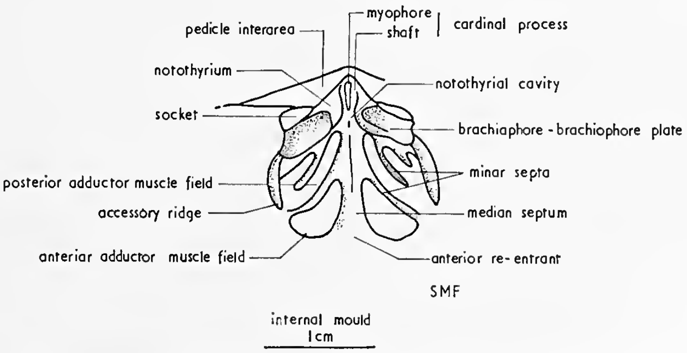
TEXT-FIG. 23. *Schizophoria vulvaria* (Quenstedt). Transverse serial sections of plaster internal mould (BM B23179).

markings arranged concentrically, developed laterally and postero-laterally (text-fig. 24*a*).

Cardinal process prominent, broad myophore supported by narrower shaft (text-fig. 24*c*). Myophore compound, with up to six lateral ridges. Stubby brachiophores fused to strong, divergent brachiophore plates (text-fig. 23, sections 2.2–4.1). Dental sockets deep, oval.



c DORSAL MUSCLE FIELD ENLARGED



TEXT-FIG. 24. *Schizophoria vulvaria* (Quenstedt). Ventral and dorsal muscle fields.

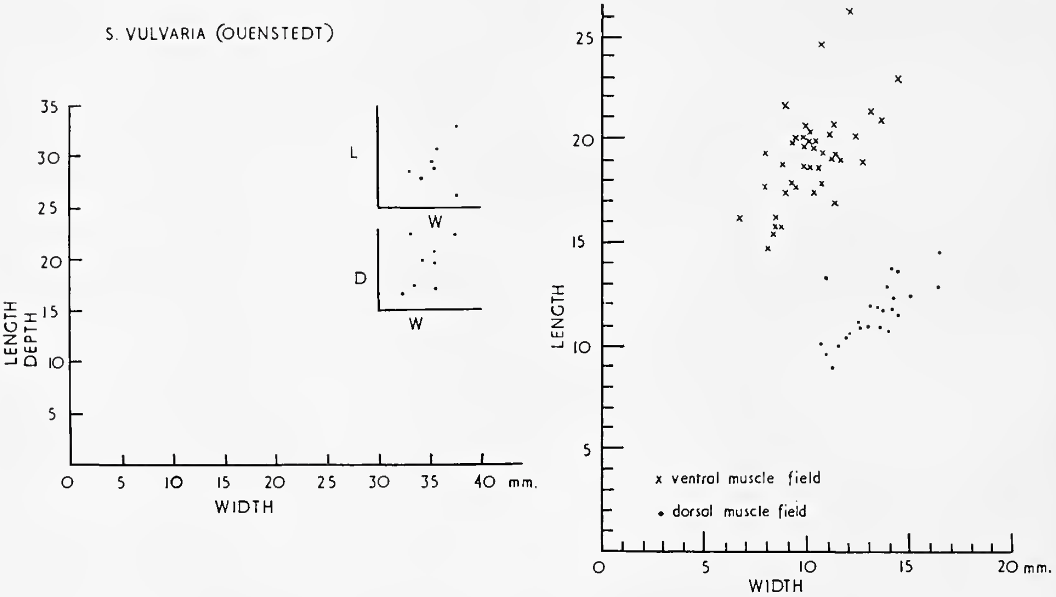
Dorsal muscle field (text-fig. 24*b*, *c*) quadrate to rounded, length and width approximately equal. Accessory ridges smoothly reflexed to form shallow, subrounded anterior re-entrant. Median septum low, broad, rounded, decreasing in height and narrowing anteriorly (text-fig. 23, sections 2.2–9.6). Anterior adductor muscle scar pyriform; posterior muscle scar generally tripartite or quadripartite, with longer inner lobe, shorter middle lobe(s), short outer lobe (text-fig. 24*b*, *c*). Two main divergent vascula media, each bifurcating, branching peripherally; two lateral vascula myaria occasionally developed from anterior adductor scars. Genital markings developed laterally and postero-laterally (text-fig. 24*b*). Short peripheral follicular markings (text-fig. 24*a*).

Dimensions. External dimensions and dimensions of available muscle fields are plotted on text-fig. 25.

Remarks. All the specimens examined are preserved as internal moulds.

Comparisons with *Schizophoria strigosa* (Sowerby), *S. provulvaria* (Maurer), and *S. striatula* (Schlotheim) are made under these species. *Schizophoria strigosa* and *S. provulvaria* range from the Sigenian to Lower Emsian. *Schizophoria vulvaria* appears higher in the Emsian, ranging into the Lower Eifelian, when it is succeeded by *S. striatula.*

Maillieux (1932, p. 24) presented a long synonymy of *S. vulvaria*, and discussed the naming of the species, with reference to authors of the seventeenth century. The name *S. vulvaria* is synonymous with *Hysterolites*. Gmelin (1790, p. 3345) very briefly described a form under *Anomia hysterita*, which has been included under *S. vulvaria* by later authors. However, this description is not specific.



TEXT-FIG. 25. Dimensions of *Schizophoria vulvaria* (Quenstedt).

Schlotheim (1820, p. 247, pl. 29, figs. 2, 3), the stated author of the species by Quenstedt and later authors, described and illustrated some specimens grouped under *Hysterolites vulvarius*, which have the transverse outline and long hinge-line characteristic of a spiriferid. His figure 2*b* has a lanceolate ventral muscle field characteristic of *S. vulvaria*, but the hinge-line is curved, obscuring its length. The mould outline and muscle form of figure 2*b* also probably represents a spiriferid.

Later authors have apparently misinterpreted Schlotheim's work as actually representing the schizophoriid species *S. vulvaria*, mainly on the basis of the ventral muscle field in his figure 2*b*.

Quenstedt (1868–71 p. 565) stated that Schlotheim (1820, pl. 29, figs. 2*a*, 3) incorrectly described and figured specimens under *S. vulvaria*, and that only figure 2*b* could possibly represent the ventral valve of *S. vulvaria*. However, Schlotheim makes no reference to the genus *Schizophoria* (then *Orthis*) in his description, and was probably describing a new spiriferid, since *Hysterolithes* is an old group term for spiriferids. He described the specimens under *Hysteroliten*.

The ventral muscle field of Schlotheim (1820, pl. 29, fig. 2*b*) has confused later authors, who incorrectly recognized Schlotheim as author of the schizophoriid species *S. vulvaria*. Quenstedt (1867, 1868–71, 1882, 1885) was the first author to describe and illustrate *S. vulvaria* as such. Quenstedt is hereby listed as the author of *S. vulvaria*.

De Verneuil (1850, p. 180, pl. 4, figs. 8*a–d*) described and illustrated a new species *Orthis Beaumonti* from the Devonian of northern Spain, which resembles *S. vulvaria* in shell outline, and elongate form of the ventral muscle field. But the ventral valve pallial sinus and genital markings of *O. Beaumonti* are radially arranged, in contrast to the concentric arrangement in *S. vulvaria*. In the dorsal valve of *O. Beaumonti*, the anterior adductor muscle scars are very small, the posterior scars apparently non-digitate, and only two parallel vascula media originate from the anterior of the muscle field. In *S. vulvaria*, the anterior muscle scar is larger, the posterior scar tripartite or quadripartite, and four to six trunks diverge from the muscle field.

Compte (1938 p. 13, pl. 1, figs. 2, 3) described and illustrated specimens from the Lower and Middle Devonian of northern Spain under *S. vulvaria*, with *Orthis Beaumonti* de Verneuil listed in synonymy. Compte's specimens resemble those of Verneuil, and were collected from the Upper Siegenian, Emsian, and Lower Eifelian stages. *Schizophoria vulvaria* from Belgium and Germany is restricted to the Emsian and Lower Eifelian stages.

Although resembling and probably related to *S. vulvaria*, *Orthis Beaumonti* has not been listed in synonymy with *S. vulvaria*, but is here considered a separate form, based on its dorsal muscle field and pallial sinus markings.

Material. Belgium, Dinant Basin; Lower Devonian (BM B15708). Emsien Supérieur, Grauwacke de Hierges, Em 3 (IRSN IG4916, 5391, 5746, 5910, 5911, 8254, 8284, 8573); Couvinien Inférieur, Assise de Bure (CO 1)–CO 1a (IRSN IG12409), CO 1b (IRSN IG5746); Germany, Lower Devonian (BM B19002) Lahnstein; (BM B23179, B34290, B49920, B39450) Eifel; (BM B39435) Coblenz; (BM B86626, 7), mouth of River Lahn; Ober Coblenzian (HMUG L2031) Daleiden; Coblenzian (HMUG L5344) Grimbach; Ober Ems (SMF) Prüm.

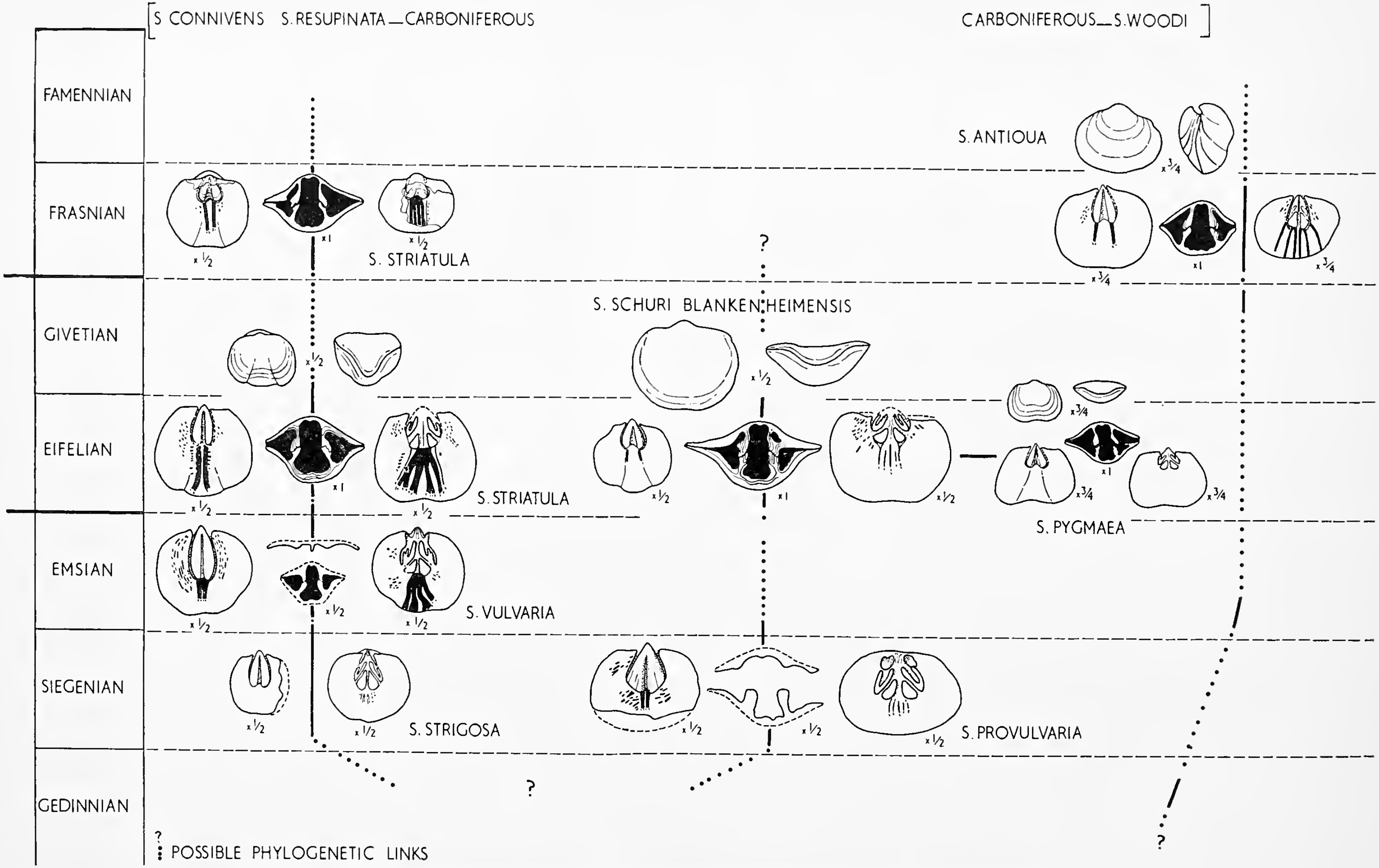
PHYLOGENY

The postulated phylogeny of Devonian species of *Schizophoria* studied, and possible links with the Carboniferous, is shown on text-fig. 26. This chart is based solely on material examined, and could conceivably represent only a part of the true picture of descent.

The relationship of species has been based externally on outline, and internally on muscle field patterns and form of the brachiophore plates, correlated with stratigraphical occurrence. External and internal features are illustrated on text-fig. 26.

The species appear to have been derived from two, perhaps three, root stocks. *Schizophoria antiqua* (Gedinnian–Frasnian) is the first species to appear in Europe. Morphologically, *S. antiqua* bears little relationship to other Devonian species, but resembles more closely *S. woodi* from the Carboniferous. *Schizophoria antiqua* is represented as a separate line of development.

Other Devonian species could have been derived from the *S. provulvaria* (Siegenian–Emsian) and *S. strigosa* (Siegenian–Emsian) stocks. *Schizophoria provulvaria* appears to have given rise to *S. pygmaea* and *S. schnuri blankenheimensis* (Eifelian). There are close resemblances in external outline and muscle field patterns. Although *S. pygmaea* is



TEXT-FIG. 26. Postulated phylogeny of *Schizophoria* from the Devonian of western Europe.

much smaller than *S. provulvaria*, *S. pygmaea* is a dwarf form of *S. schnuri blankenheimensis*. The subspecies *blankenheimensis* and *S. provulvaria* are comparable in size.

Schizophoria strigosa is replaced by *S. vulvaria* in the Emsian. The two species have comparable outline and muscle field patterns.

Schizophoria striatula (Eifelian–Frasnian) shows both external and internal affinities with *S. vulvaria*, and is considered to have been derived from this line of development.

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THE MICROMETRIC FORMULA AND THE CLASSIFICATION OF FENESTRATE CRYPTOSTOMES

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ABSTRACT. A critical assessment of the use of the micrometric formula in classifying fenestrate cryptostomes shows that although the device may be of some use as an aid to description and as a means of indexing species, it is an ineffective basis for structural comparisons. The method employed in making such comparisons is also unsound. Nevertheless, taxonomic conclusions are commonly drawn from them, and a result of this is an unreasonable increase in the number of recognized species. It is suggested that the micrometric formula should be discarded for comparative purposes and its place taken by one of the orthodox biometrical tests of significance. Such tests afford a simple and objective way of comparing sets of data. Samples for comparison should consist of groups of specimen means: owing to the colonial nature of the organisms, data from a single colony are inadequate for the purpose. A procedure for comparing samples is outlined, and an example given.

SINCE colonies of fenestrate bryozoa were first examined in detail it has been evident that the pattern of structural elements in a zoarium offers the basis for a numerical means of discriminating between species. M'Coy (1844) and his contemporaries incorporated measurements of these features in systematic descriptions with a view to their use in comparison, and at a later date Shrubsole (1881, p. 189) presented similar data in tabular form with the same end in view. With the passage of time a desire for greater refinement led to the inclusion of increasing numbers of measurements in descriptions, particularly by Russian authors. These became so numerous that Nekhoroshev (1926) introduced the practice of extracting those that seemed most critical and presenting them separately in the form now known as the 'meshwork formula' (Condra and Elias 1944, pp. 56–57), or the 'micrometric formula' (Miller 1961, p. 224). These figures were intended to convey the essential structural characteristics of the forms described. They were based on measurements of four kinds: the number of branches in 10 mm., measured perpendicular to the axis of growth; the number of fenestrules in the same distance, measured along the branch length; the number of zooecial apertures in a single row in 5 mm., and the number of carinal nodes, also in 5 mm. The formula stated the frequency or (more often) the observed range of each feature.

This procedure was made known to western workers by Condra and Elias in the paper mentioned above, in which they also proposed a standard method for making the required measurements. These authors strongly advocated the use of the formula in descriptive work and also used it as a basis for taxonomic comparisons. Since that time it has been accepted into general use and become a principal means of discriminating between the numerous species of fenestrate cryptostomes.

For descriptive purposes the micrometric formula has much in its favour. It is readily obtained even from small specimens, and provides a convenient shorthand expression of important structural characteristics of colonies. Because these formulae are now available in the literature for almost all adequately described species they also provide a useful basis for indexing (Miller 1961, p. 224), a valuable asset in a genus like *Fenestella* with more than 500 named species. As a basis for taxonomic discrimination, however, the formula has less to commend it and the purpose of this paper is to examine its

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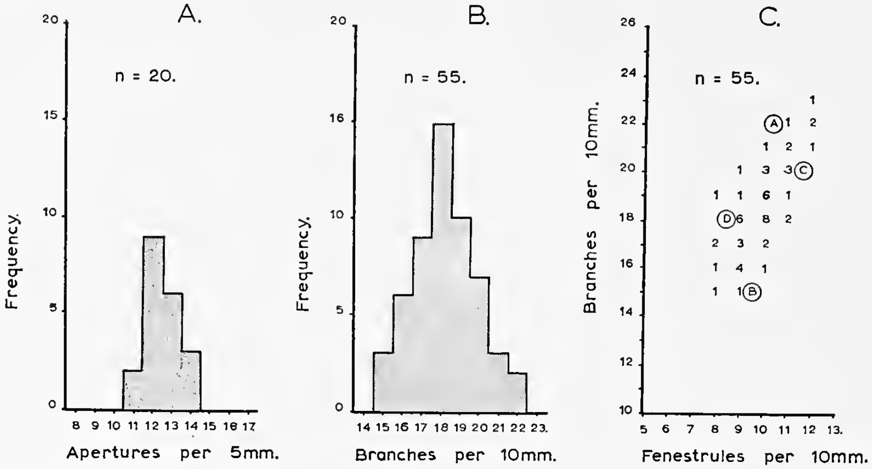
function in this respect and to suggest improvements. Before doing so it is helpful to consider certain structural characteristics of fenestrate colonies, and also the nature of the information that the formula contains.

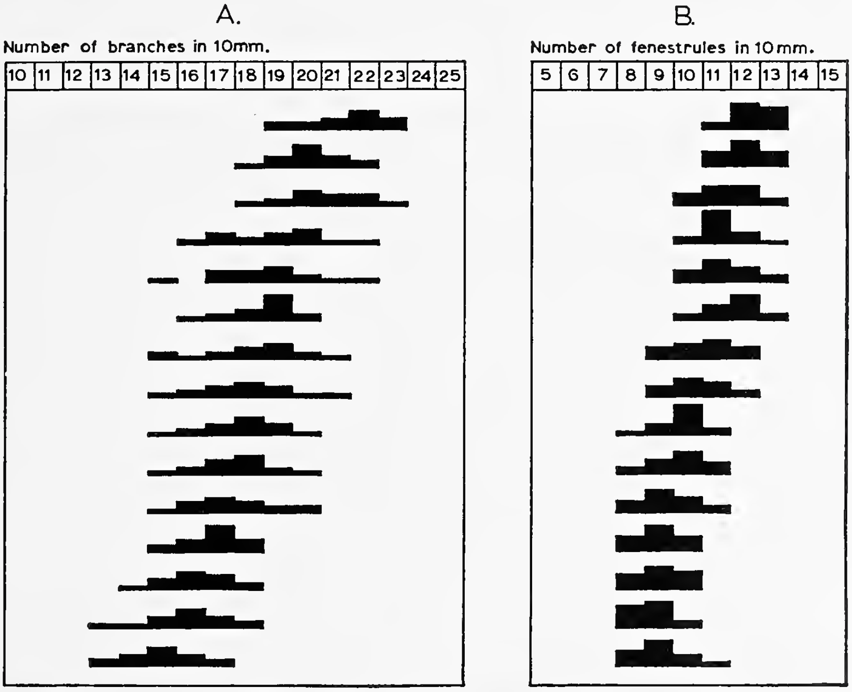
Structural variation in fenestrate colonies. The tendency towards structural variation within a species is a widely recognised characteristic of fenestrate cryptostomes and one that has been commented on by many authors (e.g. Foerste 1887, p. 84; Condra and Elias 1944, p. 56). This variation takes two main forms: that within a colony, and that between colonies. If a number of readings from a colony are represented graphically they form an approximately normal distribution (text-fig. 1*a*). Each variable is distributed in this way, occurring between certain observable limits, and it is therefore possible to construct a micrometric formula for a single zoarium, or even a fragment. It is important to remember, however, that a zoarium is a clone, that is, an association of asexually produced individuals that are genetically alike, and the range of variation within it will not, therefore, be of direct use in classification.



TEXT-FIG. 1. *a*. Graph of measurements made on a single colony (a homeotype of *Fenestella hemispherica* M'Coy, Sedgwick Museum specimen E 17841); *b*. Distribution of the modes of 55 colonies of *Ptilofenestella carrickensis* Tavener-Smith; *c*. Bivariate distribution of modal values from the same colonies, showing the location of the specimens listed in Table 2.

The central value, on the other hand, has much greater importance as it is from many points of view the most representative measurement for the colony concerned. This value is determined by the interaction of two sets of factors: genetic and ecological. A colony originates by sexual reproduction and therefore has its own particular genetic constitution that distinguishes it from all other colonies. Ecological considerations involve the relationship between a colony and its environment, and will vary with the situation. Within a colony disparities in the biochemical control of growth, and differences of micro-environment cause the dispersion of the data into a normal distribution, of which the central value reflects the interaction of the two basic factors.

Where a series of data shows an approximately normal distribution, either the mean, median or mode may, according to circumstance, be used to measure their central tendency. Although the mode is usually the obvious choice for this purpose, it has disadvantages in small samples, for in them it is very subject to random fluctuation. Difficulty may also arise becauses uch samples occasionally show more than one mode (e.g. three of the graphs in text-fig. 2*a*). The median and arithmetic mean are therefore often of greater practical value and, of these, the mean is the more useful statistic in comparative work. The mean of a series of readings made on a colony is, for these reasons, usually the single measurement best suited to represent it.



TEXT-FIG. 2. Graphs of measurements from colonies of *Ptilofenestella carrickensis* to illustrate the range of morphological variation. Each graph incorporates 15 readings, and the order of arrangements is the same in both diagrams.

If sets of readings from a number of conspecific colonies are plotted graphically, a series of overlapping distributions result (text-fig. 2). In such a series the ranges of individual colonies may differ appreciably from one another, and may even (as the diagram shows) be mutually exclusive. It is apparent from this that in a morphologically variable group such as the fenestrate cryptostomes the range of variation shown by a single colony may bear little relation to that of the species to which it belongs,

The lack of a direct relationship between intra- and inter-colonial variation can also be demonstrated by means of the technique of analysis of variance, to which the data are readily adapted. Four such analyses were made, one for each variate of the micrometric formula, the data being derived from specimens of *Ptilofenestella carrickensis* Tavener-Smith 1965. Between ten and fifteen measurements from each of 10 colonies were used, and in each case it was found that a significant difference ($P < 0{\cdot}05$) existed between the variance estimates. There is therefore a recognizable difference in pattern between intra-colonial and inter-colonial variation, and this being so, the range of a variate within a colony cannot justifiably be used as the basis for taxonomic comparisons between colonies.

When the central values of a number of colonies of the same species are assembled into a histogram it is seen that they also have an approximately normal distribution. In text-fig. 1*b* a group of modes is used to illustrate this point: the corresponding means would show a similar pattern. Samples of this kind are likely to be taxonomically useful because they are based on the most representative measurements of a group of colonies and (according to the number of specimens measured) will provide a more or less reliable indication of the range of variation in the species concerned. Distributions of this type are used as the basis for the comparative technique outlined later in this paper.

TABLE 1

	Fenestrule width.	Inter-ap. space.	Internodal space.	Branch width.	Apertural diameter.
Fenestrule length.	+0·6886	+0·4217	+0·3898	-0·4836	+0·5226
Fenestrule width.		+0·3899	+0·3274	-0·4471	+0·7169
Inter-ap. space.			+0·3014	-0·3214	+0·3605
Internodal space.				-0·2640	+0·1119
Branch width.					+0·3760

Ptilofenestella carrickensis: coefficients of correlation between pairs of structural features. The continuous variables used here include those that correspond most closely with the micrometric formula, namely: fenestrule width and length, inter-apertural space, and internodal space. In all cases $n=55$.

Another characteristic of fenestrate cryptostomes is the significant, though weak, correlation that exists between different structural elements in a colony (Table 1). This is evident from a consideration of micrometric formulae, in which a high count for the number of branches in 10 mm. is often accompanied by high numbers of fenestrules, apertures, and nodes (e.g. *Fenestella bicellulata* Etheridge: 24–27/27–28//27–29/29–31). The converse is generally true when the branch count is low (e.g. *F. oblongata* Koenig: 9–15/4–7//14–19/4–7). Although it is technically more correct to use a multivariate approach where sets of data are correlated, the correlations are here so weak that little is lost by using simpler univariate methods in comparing samples. Comparisons based on the micrometric formula are in this respect quite well adapted to the situation, for they function on this principle. Although each formula embodies the frequency or observed range of four variates, these are dealt with separately, and the comparisons are quite independent of one another.

Construction of the micrometric formula. There is no reason to doubt that the geometrical arrangement of structural elements in a fenestrate colony is of taxonomic value, and the spatial distribution of branches, dissepiments, zooecial apertures, and carinal nodes were considered by Nekhoroshev (1926) to be the most important variates involved. These features have come, by usage, to be the ones on which most reliance is placed in discriminating between species (Condra and Elias 1944, p. 54). They are therefore weighted for taxonomic purposes, as compared with others such as the width of branches or dissepiments, and the diameter of zooecial apertures, which are not included in the formula. Nevertheless, all these have been recognized at one time or another to have potential diagnostic value (e.g. Nekhoroshev 1932, p. 302; Miller 1962, p. 120). Their relative neglect is probably due to the tendency for secondary calcification to alter dimensions with increasing age, thus apparently nullifying the usefulness of these features in classification. It seems likely, however, that this objection is not insuperable. Certainly, the restriction of taxonomic consideration to the variates of the micrometric formula is in itself a disadvantage, for it is generally agreed that the best classification is that based on all relevant morphological data.

A standard method for measuring variates of the micrometric formula is described by Condra and Elias (1944, pp. 54–55). They recommend the use of the so-called space-unit count, which means that it is the space *between* selected structural features that is counted, and not the features themselves. Thus, the total per standard distance (5 or 10 mm.) is not the actual number in that distance, but one less than this. It is worth noticing that because the basis of each count is the linear distance between adjacent features, the variates are essentially continuous and not discontinuous, as first appearances suggest. It is therefore permissible and advantageous to use the mean rather than the mode as the central value of distributions relating to them.

The method of presenting structural data in the orthodox micrometric formula is extremely rudimentary. Only the observed range of the measurements is given for each feature, and sometimes this is abbreviated to a single figure, implying that there was no variation in the sample examined. No supporting data of any kind relating to the pattern of the distribution are given. Nor is it stated how many readings were made, or whether all were taken from a single specimen or from several. The work of Perry and his associates is, in this respect, an exception to the general rule. Utgaard and Perry (1960) give formulae supported by histograms showing the distribution of the variables, and Malone and Perry (1965) state a mean and standard deviation for each variate and the number of measurements made. They do not say, however, how many zoarial fragments were examined, or how many readings were taken from each. Both facts are relevant if comparisons are to be taxonomically valuable.

Effectiveness of the formula in taxonomic discrimination. To illustrate the use of the micrometric formula in structural comparisons an example is necessary, and a typical case occurs in recent work by Burckle (1960, p. 1083). This author measured some new material in order to ascertain whether it was conspecific with *Fenestella rectangularis* Ulrich, to which there was a superficial resemblance. Having derived a formula, he compared it with that of Ulrich's species in the usual way, namely by placing the two side by side and examining the ranges of each variable separately. The formulae were as follows:

F. rectangularis Ulrich: 20–26/17½–24//23–25/14–17
Burckle's material: 23–27/16–24//20–24/16–20.

He concluded that, while the ranges for the first three variables were close enough to be considered identical, those for carinal nodes indicated a clear difference between the samples. This he took to be of taxonomic as well as numerical significance, and accordingly founded a new species which he named *F. tooelensis*.

It is necessary to decide whether comparisons of this pattern are, in general, acceptable as a basis for taxonomic discrimination. The reasons given below suggest that they are not.

1. Micrometric formulae are usually stated in terms of the observed range of variates. This is generally acknowledged to be a poor basis for comparison, as the range of a sample is directly related to its size (Simpson 1941). Unless samples are uniform in this respect their ranges will be expected to differ, even if they are drawn from the same population, and such differences need have no taxonomic significance. If, in the example quoted above, each formula was based on only one specimen it would be quite unjustifiable to assume that the difference in node counts had taxonomic significance. But if, on the other hand, each was derived by measurement of twenty specimens, the case for a difference between them would be a strong one. As the number is not stated there is no way of deciding where the truth lies.

TABLE 2

	Branches in 10mm.	Fenestrules in 10mm.	Apertures in 5mm.	Nodes in 5mm.
A.	20 - 22	12 - 13	21 - 24	27 - 33
B.	13 - 17	8 - 12	17 - 19	21 - 27
C.	20 - 22	11 - 12	18 - 21	25 - 28
D.	14 - 18	9 - 10	17 - 21	30 - 38

Micrometric formulae measured on four selected specimens of *Ptilofenestella carrickensis*.

Formulae giving single figures for variates are even less useful than those that show the observed range. A single figure provides no idea of variation, and all that can reasonably be done is to treat it as the mean of the distribution it represents. Even then it is of no value for comparative purposes without information as to the number of specimens examined and measurements made. In view of the structural variability of fenestrate zoaria it seems likely that formulae giving this kind of information were measured on single small fragments.

2. Many micrometric formulae in the literature appear to have been measured on one specimen only, often a holotype (Condra and Elias 1944, p. 107; Elias and Condra 1957, p. 77; Koenig 1958, p. 135; Burckle 1960, p. 1087; Miller 1961, p. 231, and many others). Such formulae can only record intra-zoarial variation and this offers no foundation for inter-zoarial comparison because it is possible for the range of a variate to differ markedly in two specimens that are conspecific (text-fig. 2). A notable numerical discrepancy between observed ranges may have no taxonomic significance at all if the ranges were measured on single specimens. Table 2 shows the formulae of four specimens of *Ptilofenestella carrickensis* Tavener-Smith which occur at the extremes of a bivariate distribution of the number of branches and fenestrules per 10 mm. The graph is shown in text-fig. 1*c*. Because a weak positive correlation exists between the variables of the formula, extreme ranges for apertures and nodes occur in the same specimens. Discrepancies between the ranges of these formulae are enough to suggest separation

into 2, if not 4 species of the kind that Burckle recognized. Yet all 4 colonies are, in fact, conspecific. Comparisons involving formulae derived from single specimens are, it seems, unreliable for taxonomic purposes.

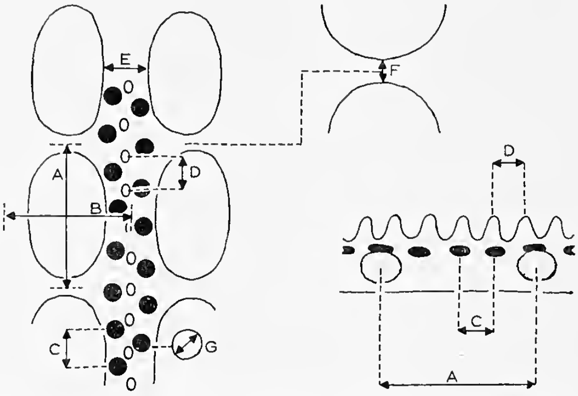
3. In comparisons of formulae such as that outlined earlier, the method is visual and subjective, each case being decided solely by the personal judgement of the author concerned. While such a procedure may be satisfactory if formulae happen to be identical or when they differ widely, in the great majority of intermediate cases there is much room for error. Results are most likely to be unreliable where the overlap between ranges is appreciable but not complete, and the dependability of the test will therefore be least exactly where it needs to be greatest. Because there is no objective way to decide whether an observed difference between the ranges of samples has taxonomic significance, uniformity of treatment can hardly be expected. A difference that is enough to justify the erection of a new species in the opinion of one author may seem insufficient for the purpose to another, and the classification suffers accordingly.

It is evident that there are serious deficiencies in the present method of comparing samples of structural data from fenestrate colonies. One result of this is an unreasonable increase in the number of recognized species. An improved procedure is needed, and two alternative courses are open: either the micrometric formula may be retained in a revised and expanded form, or it may be discarded in favour of a new approach. For reasons already stated, the formula can only provide a reasonable basis for comparison if the ranges given are those of groups of specimen means, and if the number in each group is known. Approximate statistics for the distribution can then be calculated, and a rough but objective comparison of samples made (Simpson 1941, pp. 788 and 793). However, the micrometric formula is founded on the observed range and even in its most acceptable form permits only a crude comparison of the kind mentioned above. It seems better, from all points of view, to discard the formula for comparative purposes, though it could be retained in descriptions as a means of indexing species. In effecting numerical comparisons it is the distribution of variables, not their ranges, that is important, and this is best defined in terms of orthodox statistics such as the mean and variance. If these are available samples can be compared by utilizing one of the significance tests common in modern biometric usage. Before outlining the kind of procedure that might be followed, it is advisable to consider the morphological features that could be compared, and the way in which they might be measured.

Dimensions to be compared. The fundamental purpose of the method outlined by Condra and Elias (1944, pp. 54–57) for measuring variable features on fenestrate bryozoans is to establish the average dimensions that characterize a particular fragment or series of fragments. Their procedure for doing this is clumsy and fails to provide an effective basis for comparison. Counting the number of branches, fenestrules and so on, per unit distance is merely an indirect and ineffective way of assessing the average distance between these structures. It is more satisfactory as well as simpler to make the necessary measurements directly, and to derive from them statistics that can be quickly and objectively compared by means of a significance test.

For comparisons to be valid it is essential that measurements should be made in a standardized manner, and text-fig. 3 suggests how this could be done. The variables of the micrometric formula are adequately represented by the basic measurements concerned, namely fenestrule width and length, together with inter-apertural and internodal distance. Fenestrule width is measured through the mid-point of a fenestrule, from the centre of the branch on one side to the centre of that on the other. Fenestrule length is the distance, along the mid-line of the fenestrule, between the centres of adjacent dissepiments. Inter-apertural distance and internodal distance are measured between the centres of pairs of the appropriate structures that are situated in the same row.

To these variates may be added others, such as branch width, dissepiment width, and apertural diameter. It is true that these are subject to secondary calcification, and their dimensions may be influenced by this factor. Nevertheless, if samples consist of groups of specimen means there is no reason why it should vitiate comparisons. Random samples of fenestrate colonies should contain sufficiently similar numbers of both young and old colonies to cause the influence of secondary accretion on measurements to balance out between samples. Its importance is therefore much less than would be the case in comparing single colonies.



TEXT-FIG. 3. Method of making measurements: *a*, fenestrule length; *b*, fenestrule width; *c*, inter-apertural space; *d*, internodal space; *e*, branch width; *f*, dissepiment width; *g*, apertural diameter.

Branch width is recorded at right angles to the branch axis and away from points of bifurcation and branch-dissepiment junctions. The width of dissepiments is measured midway along their length, where the structure is narrowest. In the case of zooecial apertures it is the internal diameter that is measured: for ovoid or pyriform apertures a longer and shorter dimension could be given.

Elias and Condra (1957, pp. 70–72) attached great taxonomic value to the number of zooecial apertures per fenestrule, and largely based their classification upon this. Many workers would not agree in according prime importance to this feature, but it is one that can sometimes be used with advantage in comparative work. An examination of the literature reveals, however, that there is a discrepancy in the method employed to make the necessary measurements. Some workers (e.g. Shulga-Nesterenko, 1951) count the actual number of apertures along one side of a fenestrule, while others use the space-count method of Condra and Elias and record one less than the actual number. As the numbers are always small such a discrepancy is likely to have unfortunate results, and it is important to standardize procedure. The second method of counting is recommended, as it accords with that used in measuring other variables, and in practice the number of apertures per fenestrule for a colony or fragment may be derived from the figures for mean fenestrule length and mean inter-apertural space.

Measurements of these features and any others that are desired can be made in the usual way with a microscope eyepiece micrometer. More accurate results are obtained by using a screw micrometer with travelling cross-wire, or better still, a traversing stage with a screw micrometer. Measurements should, wherever possible, be taken from mature parts of zoaria where structural variation is likely to be at a minimum (Miller 1961, pp. 222–3), rather than from the proximal region where growth is often irregular.

Method of comparison. In order to permit a realistic comparison to be made, samples must contain information from a number of specimens, not only one. This is because data from a single colony or fragment reflect intra-zoarial variation alone and this, for reasons already given, has little value in taxonomy. Also, only the central value of a series of measurements from a colony is taxonomically useful, and significance tests are not competent to discriminate between single values, but only between groups. The mean is the most convenient central value for most purposes, and a sample for comparison should therefore consist of a number of specimen means. The larger the number in the sample, the more accurately will it reflect the range of variation in the population from which it was drawn. Small samples of only a few specimens can also be used however.

The use of a recognized significance test ensures that an objective comparison of samples is made, and the one best suited to present requirements is the well-known t-test described in standard statistical texts (e.g. Fisher 1948, p. 122). When this method is used to compare samples, t is essentially the ratio of the difference between means to the standard error of the difference. It may be written:

$$t = \frac{\bar{x}_1 - \bar{x}_2}{s\sqrt{(1/n_1 + 1/n_2)}} \quad \text{for } n_1 + n_2 - 2 \text{ degrees of freedom,}$$

where $\bar{x}_1$ and $\bar{x}_2$ are the means of two samples, and n_1, n_2 are the numbers of specimens in those samples. Also:

$$s^2 = \frac{1}{n_1 + n_2 - 2}\{\sum (x_1 - \bar{x}_1)^2 + \sum (x_2 - \bar{x}_2)^2\}.$$

Having calculated t and knowing the number of degrees of freedom, the value of P (the probability that the difference between the means is due to the chances of sampling only) may be read from appropriate tables. If P is greater than 0·05 it is probable that the results are due to chance, and they are described as 'not significant'. If less than 0·01, then not once in 100 times could such a result have arisen by chance, and it may be considered significant. If the value of P lies between the 0·01 and 0·05 levels the result is probably significant. A suggested sequence for comparing samples of structural data by this method is outlined below. The procedure would have to be repeated for each variate.

(1) A series of readings should be made on each specimen for the variate under consideration. The number of measurements would depend on the size and state of preservation of the material: between 10 and 20 would be satisfactory. From these calculate the specimen mean.

(2) Repeat for each specimen, and then assemble the specimen means into a separate

distribution. It is this group, consisting only of specimen means, that constitutes the sample for comparison. Compute the sample mean and variance: these, together with the number of specimens in the sample, are the basic statistics used in comparison.

(3) Any two samples of this kind may then be objectively compared by using the t-test, as outlined above.

To illustrate the working of the method an actual example is quoted below. It concerns three superficially similar forms of *Fenestella* for each of which a number of specimens was available. It was desired to test these numerically in order to find whether the three groups could have been drawn from the same parent population. For this purpose each was represented by a sample of 25 specimens, referred to here as samples A, B, and C respectively. A number of variates were measured in each sample and comparisons made between them. The data for fenestrule width (corresponding to the number of branches per 10 mm. in the micrometric formula) were as follows:

	Sample A	*Sample B*	*Sample C*
$\bar{x}$:	0·573 mm.	0·598 mm.	0·432 mm.
$\sum (x-\bar{x})^2$:	0·069 mm.	0·155 mm.	0·104 mm.

On testing samples A and B it was found that:

$$\bar{x}_1-\bar{x}_2 = 0{\cdot}025 \text{ mm.}$$

$$s^2 = \frac{1}{48}(0{\cdot}069+0{\cdot}155) = 0{\cdot}0047.$$

So $$s = 0{\cdot}068.$$

Then $$t = \frac{0{\cdot}025}{0{\cdot}068}\sqrt{\left(\frac{25\times 25}{50}\right)} = 1{\cdot}299.$$

From the tables it is seen that for $n = 48$ this value of t indicates a probability of more than 0·1. The result is therefore not significant, and the samples could very well have been drawn from the same population. On comparing samples A and C, however, it is found that the value of t is much larger, being, in fact, 8·29. For the same number of degrees of freedom this represents a probability level of less than 0·001, and it is very unlikely that these two samples could belong to the same population. Comparison of forms B and C yields a similar result, the value of t this time being 7·41 (i.e. $P < 0{\cdot}001$). From these tests it appears that while samples A and B cannot be differentiated from one another, both are significantly different from sample C. Further tests on other variates gave confirmatory results and it was concluded that two distinct species were represented, A and B belonging to one, and C to the other. Additional confirmation of quite a different kind appeared later when it was found that specimens of groups A and B had triangular zooecial base shapes, while those of group C were hemi-hexagonal. It is worth mentioning that micrometric formulae based on the three samples showed much overlap in their ranges and gave no indication of the result that emerged quite clearly from the above tests. The formulae were as follows:

Group A: 7–12/3–6//11–15/2–6.
Group B: 8–13/3–8//12–16/3–7.
Group C: 10–14/5–9//13–17/4–9.

The recognition of significant differences between samples in all tests of a series leaves little doubt that the groups concerned belong to different species. Difficulty would arise, however, if it was found that the level of significance was exceeded in only, say, three out of six cases. Would it then be reasonable to differentiate the samples at specific level? In earlier work new species have sometimes been erected on the basis of a single quantitative difference between samples, as in the case of Burckle's species. More frequently two such differences are cited, and occasionally more. In discussing the application of biometrical methods to the classification of Caradocian brachiopods Williams (1962, p. 79) suggested that a significant difference in one feature, particularly if it could arise phenotypically, might serve to indicate the presence of separate sub-species, but that two or more such differences are needed to justify separation at the specific level. Such a scheme is, of course, arbitrary and the need to make exceptions to it might arise from time to time. Nevertheless, it seems to be in general accordance with established practice in the classification of fenestrate bryozoa, and its adoption would promote uniformity of treatment.

SUMMARY

The foregoing arguments and suggestions can be summarized as follows:

(*a*) The micrometric formula is of use as a descriptive aid because it conveys an immediate impression of the general characteristics of a fenestrate colony. It is also a convenient basis for indexing the numerous species of *Fenestella*, and as such will no doubt continue to be used.

(*b*) The formula presents information in the form of observed ranges of measurements unsupported by other data, and this precludes the use of conventional numerical techniques in comparing samples. Instead, simple visual methods are relied on to determine whether two formulae relate to the same species, and such tests are strongly subjective. In addition, it is probable that many formulae were measured on single specimens and are therefore unreliable as a basis for taxonomic comparisons. In view of these disabilities it is recommended that the micrometric formula should be discarded in comparative work: its continued use can only lead to further confusion.

(*c*) If adequate data are available, reliable and objective comparisons can be made between sets of measurements by utilizing one of the significance tests commonly used in biometrics. A method for doing this is outlined, based on the *t*-test. Techniques of this kind are only competent to discriminate between groups of data, and not between single measurements. Samples for comparison should therefore consist of a representative measurement from each of a number of colonies, and the arithmetic mean is best suited to this purpose. If provision is to be made for testing new material against established species, systematic descriptions must include certain essential statistics for each variate. These are the sample mean and variance, and the number of specimens in the samples. An indication of the number of measurements made on each specimen would also be of assistance, though not essential.

It may be objected that, although the comparative technique suggested here is in theory superior to the micrometric formula, it suffers from an important practical disadvantage, namely, that numbers of specimens are not usually available for comparison, but only one or two. To this criticism there is only one reply: unless adequate samples are available, attempts to make numerical comparisons of any kind are futile and the results misleading. If there is insufficient material on which to base such a comparison, there is no point in making one, and it is much better not to do so. Half a dozen specimens constitute a sample of about the minimum permissible size: less than that would yield results of doubtful value.

Although this paper is exclusively concerned with the numerical comparison of sets of structural data, it is not suggested that the classification of fenestrate cryptostomes should rest on these alone. Other factors, not so amenable to mathematical treatment, must also be considered, for example, the shape of the zooecial chamber. The prime purpose of the present paper is to draw attention to the shortcomings of the micrometric formula as a means of structural comparison, and to stress the need for a better comparative technique if taxonomic conclusions are to depend on the results of such comparisons. Finally, it seems possible that significance tests, used along the lines indicated above, might be a means of discriminating between other kinds of colonial organisms besides bryozoa, provided that samples of data are constituted as here suggested.

Acknowledgements. The author is indebted to Professor Alwyn Williams and to Messrs. C. D. Kemp and D. H. McNally for useful discussions on statistical aspects of the work. Professor Williams also kindly undertook to read through the manuscript prior to publication. Thanks are due to the Curator of the Sedgwick Museum for the loan of a specimen from which measurements were taken.

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A NEW PRODUCTID BRACHIOPOD FROM THE UPPER VISÉAN OF SCOTLAND

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ABSTRACT. *Promarginifera trearnensis* gen. et sp. nov. a productid brachiopod from the Upper Viséan of Ayrshire, Scotland is described. It occurs in the Dockra Limestone 65 ft. below the Viséan–Namurian junction. Morphologically the form has affinities with both the marginiferids and dictyoclostids but on the evidence of a marginiferid cardinal process and discontinuous marginal ridges it is classified as a marginiferid of the subfamily Costispiniferinae.

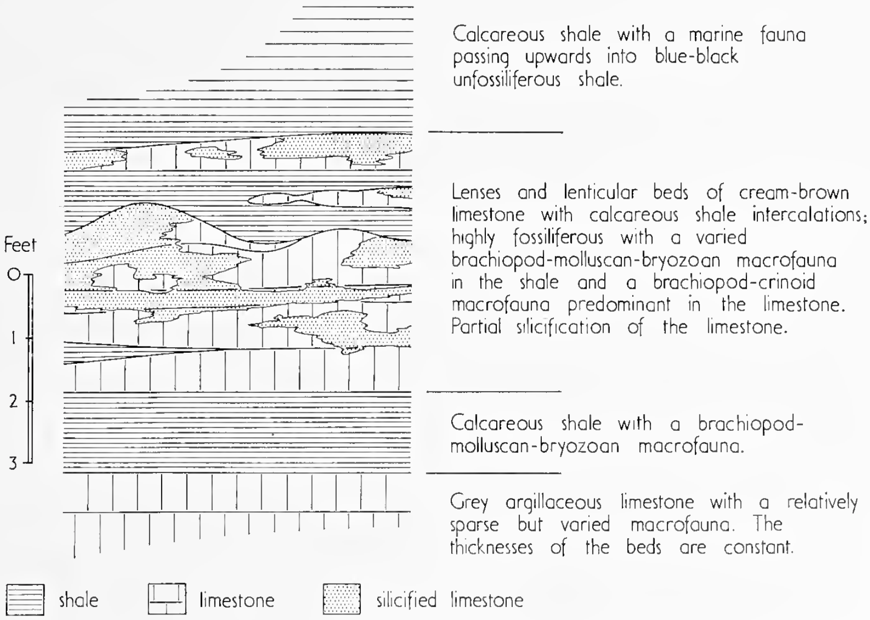
SPECIMENS of an unrecorded productid have been collected from the Upper Viséan of Ayrshire, Scotland. The form was first found at Trearne quarry (NS 37155340) 1·4 miles N. 108° E. of Beith, and has subsequently been obtained from the neighbouring Hessilhead quarry (NS 37755315) 0·4 miles N. 288° E. of Hessilhead Farm. Both of these quarries expose the Dockra Limestone, here 20–25 ft. thick, and up to 10 ft. of the overlying argillaceous succession. The base of the Dockra Limestone locally occurs 10 ft. above the base of the Lower Limestone Group of Scotland and is approximately 65 ft. below the shale underlying the Top Hosie Limestone which is considered on the evidence of *Cravenoceras scoticum* within the limestone and *Cravenoceras* sp. indet., within the shale to approximate to the Viséan–Namurian boundary (Currie 1954, pp. 534, 535). The Lower Limestone Group which is 80 ft. thick in the Beith district consists of a 95% calcareous-argillaceous succession; the massive section of the Dockra Limestone thins from 35 ft. near Dalry to 13 ft. near Lugton, being replaced in a west to east direction by shales and alternations of shales and limestone bands (Richey, Anderson, and MacGregor 1930, pp. 141–8, fig. 12).

The Dockra Limestone is in part lenticular with the development of a shell-bank facies of cream-coloured limestones within dark, thinly bedded, argillaceous limestones. Text-fig. 1 illustrates a measured section on the east end of the working north face of Trearne quarry which was accessible in May 1964. Cream-brown lenticular bedded calcarenites overlie a shale parting which in turn rests on grey argillaceous calcilutite forming the uniformly bedded upper portion of the main calcareous unit. The lenses of calcarenite are highly fossiliferous, the organic content of some is 90% composed of productids and crinoid remains, the brachiopod valves forming a shell-supported fabric with the interstices infilled with crinoid debris and matrix. These shell-bank accumulations were deposited in a moderately turbulent environment. The productids in the lenses include species of the genera *Productus*, *Krotovia*, *Buxtonia*, *Antiquatonia*, *Eomarginifera*, and *Promarginifera* gen. nov.; in some of the lenses *Promarginifera* forms 95% of the productid fauna.

The material for this study was collected from Trearne quarry. The specimens are preserved in three different ways: (i) calcareous shells in a calcareous matrix—the normal unreplaced condition, (ii) siliceous shells in a siliceous matrix—complete silicification of the rock either along layers parallel to the bedding or in irregularly shaped masses of

[Palaeontology, Vol. 9, Part 3, 1966, pp. 426–47, pl. 67.]

scattered distribution, (iii) siliceous shells in a decomposed ochreous matrix—the most useful, but relatively rare material. The visceral cavities of all the partially or completely silicified shells and 90% of the calcareous shells are infilled with a drusy growth of transparent quartz. Incomplete silicification and the growth of the quartz crystals within the visceral cavity have been responsible for the imperfection of internal detail observed in most specimens. Furthermore the infilling is stronger than the shell substance and its removal from the visceral cavity difficult. It is evident from the nature of the deposition of the *Promarginifera*-bearing lenses that the brachiopods are not found in their growth positions but have undergone varying degrees of reworking. This movement damaged the shells, especially stripping them of their spines and breaking the ears and trail. In a collection of approximately 500 specimens only 119 were sufficiently well preserved for statistical analysis. Of the latter, 62 specimens show the exterior surface of the pedicle valve, 7 of these also show the pedicle valve interior, and 37 others also show the brachial valve exterior. The remaining 57 specimens are fragmental brachial valves showing both interior and exterior surfaces. The collection on which the statistical analysis is based is deposited in the Hunterian Museum in the University of Glasgow. All linear measurements are given in millimetres, angular measurements in degrees.



TEXT-FIG. 1. Vertical section through the upper beds of the Dockra Limestone at Trearne Quarry, Ayrshire.

SYSTEMATIC DESCRIPTION

Suborder PRODUCTOIDEA Maillieux 1940
Superfamily PRODUCTACEA Waagen 1883
Family MARGINIFERIDAE Stehli 1954
Subfamily COSTISPINIFERINAE Muir-Wood and Cooper 1960
Genus PROMARGINIFERA gen. nov.

Plate 67, figs. 1–14

Derivation of name. Latin, *pro*—early; *marginifera*—margin bearer.

Type species. *Promarginifera trearnensis* sp. nov.

Diagnosis. Shell subquadrate, costate and rugate, with reticulate umbo. Spinose pedicle valve, spines arranged (i) in row along ear, (ii) in row down flank, (iii) scattered over valve on costae. Ears large and enrolled, demarcated from flank by sharp fold. No geniculation or thickening of trail of brachial valve. Non-crenulate marginal ridges extending laterally from cardinal process parallel to hinge-line. Dendritic, elevated adductor scars, variable cardinal process. Pedicle valve with flabellate diductor scars and adductor platform.

Description. Shell small, subquadrate, width exceeds straight length. Pedicle valve convex, flanks approximately normal to hinge-line at the posterior before curving anteriorly on to a broad venter; venter with or without sulcus, trail curved; flanks moderately steep and umbo incurved forming a uniformly convex visceral disc; ears large and enrolled, demarcated from flanks by sharp fold. Brachial valve with posterior of visceral disc plane or slightly concave, becoming rounded and concave anteriorly to form trail, no geniculation; trail is a single structure and is not thickened by additional laminae.

Both valves costate and rugate, umbonal region reticulate. Pedicle valve with erect or suberect spines, arranged, (i) in row near hinge margin, (ii) in curved row down flanks, and (iii) scattered over the visceral disc, venter, and flanks on supracostal positions. A few scattered spines may be present on the brachial valve.

Interior of pedicle valve with flabellate diductor scars which are longitudinally ridged and separated from each other by an elevated platform bearing two ovate adductor scars; the ears are demarcated from the visceral cavity by a sharp flexure.

Interior of the brachial valve with trilobate marginiferid cardinal process which may be highly variable in its attitude with respect to the posterior part of the valve and in the degree of separation of the lateral lobes; posteriorly the median septum is low and rounded or ill defined, anteriorly it extends into a blade-like structure; away from the median septum the marginal ridges follow close to the hinge-line and then swing anteriorly along the inner margin of the ears to finally die out on the flanks; brachial ridges are narrow, low, sometimes obscure, given off at anterior-lateral margin of adductor scars at a low angle to the hinge-line direction; each adductor has a double dendritic surface within the attachment area, the anterior scar being upraised along its anterior border; rows or scattered endospines occur anteriorly.

Remarks. *Promarginifera* combines both dictyoclostid and marginiferid characters. The reticulate umbo, flabellate diductor scars, adductor platform, and dendritic adductor scars are features usually associated with dictyoclostids. On the other hand the cardinal process is of a type strictly comparable to that found in the marginiferids and the possession of the marginal ridges is an essential character of that group. Furthermore, both the size and shape of the shell and the large, enrolled, well-demarcated ears are like those found in many marginiferids. The striking arrangement of spines on the pedicle valve of *Promarginifera* is not completely diagnostic since it is similar to that of several other genera including dictyoclostids such as *Antiquatonia* and *Costiferina*, marginiferids such as *Costispinifera* and *Liostella*, and the alleged buxtoniid *Protoniella*. An assessment of the taxonomic placing of *Promarginifera* suggests, therefore, that it is a marginiferid with dictyoclostid similarities. Since the marginiferids almost certainly evolved from the dictyoclostids in Lower Carboniferous times the balance or morphological attributes found in *Promarginifera* (a high Lower Carboniferous form) may indicate phylogenetic affinity with a dictyoclostid stock.

According to Muir-Wood and Cooper (1960, p. 205) two of the four subfamilies of the Marginiferidae, the Marginiferinae and the Costispiniferinae, are separated on internal features, especially in the degree of completeness of the marginal ridges. The condition in which the marginal ridges fuse anteriorly to form a continuous rim around the anterior of the visceral disc characterizes the Marginiferinae. If the marginal ridges are discontinuous and die out anteriomedianly the form belongs to the Costispiniferinae. The remaining two subfamilies of the Marginiferidae have special features such as the tubiform trail and row of endospines in the brachial valve of the Retariinae and the supplemented brachial trail of the Probolioniinae.

Promarginifera has certain external resemblances to the genera *Marginifera* and *Hystriculina*, both members of the subfamily Marginiferinae. The general shape and size of the shells, the dimensions of the costae, and to a lesser extent, the distribution of spines, are similar in all three genera. Another marginiferinid, *Eomarginifera*, is found associated with *Promarginifera* but can be easily distinguished externally by its six symmetrical spine bases. In internal detail, however, *Promarginifera* has discontinuous marginal ridges and is therefore distinct from the marginiferinids; it is clearly a member of the Costispiniferinae and is the first British genus to be ascribed to that group. *Promarginifera* shares some external features with other members of the Costispiniferinae, notably with *Costispinifera*, *Liostella*, and *Elliotella*. *Promarginifera* can be distinguished from *Costispinifera* by its less numerous spines, non-crenulate marginal ridges, non-geniculate but more costate brachial valve, and shorter endospines. Externally the pedicle valve of *Promarginifera* differs from that of *Liostella* in having a reticulate umbo and a row of spines on the ears close to the hinge-line. Internal distinctions include the more elevated and smooth marginal ridges of *Promarginifera* and differences in detail of the cardinal process, median septum, and adductor scars. *Elliotella* is more coarsely costate than *Promarginifera* and does not possess rugae on the pedicle valve. The orientation of the two spine rows near the hinge of *Elliotella* is different from that of *Promarginifera*. Internally, the marginal ridges of both *Elliotella* and *Costispinifera* diverge from the hinge immediately after leaving the cardinal process; they cannot, therefore, buttress the articulating surface as do those of Promarginifera (see description of *P. trearnensis*). The genus *Protoniella* simulates *Promarginifera* externally, particularly in the distribution of the spine bases; internally, however, they can be readily distinguished by the buxtoniid cardinal process and antron of the former.

Promarginifera trearnensis sp. nov.

Plate 67, figs. 1–14

Diagnosis. As for genus.

Type specimens. The type series consists of a holotype and 118 paratypes, the total collection on which the statistical analysis is based.

Specifications of the holotype: Hunterian Museum number L6202; Plate 67, figures 1, 2, 3:

Hinge width	19·5 mm.
Curved length of pedicle valve	29·0 mm.
Straight length	13·4 mm.
Thickness of visceral cavity (inclusive of shell)	6·0 mm.
Umbonal angle	90°
Extension of umbo posterior to hinge-line	0·7 mm.
Width of ears	8·5 mm.
Length of ears	3·6 mm.
Height of ears	0·7 mm.
Number of rugae	4
Number of costae	24
Nonsulcate; width of flat zone on venter	2·0 mm.
Number of spines on pedicle valve exterior	99

The figured paratypes (Pl. 67, figs. 4–14) are given Hunterian Museum numbers L6203–11, and the remaining paratypes are given Hunterian Museum numbers L6212/1–107.

Description. The shells are small (Muir-Wood and Cooper 1960, p. 18) with a sample mean hinge width (= maximum width) of 17·3±1·0 mm. The size of the species is more fully described by the statistics of Table 1 (all confidence limits are quoted at the 0·01 level of probability unless otherwise stated). The shell outline is subquadrate (Pl. 67, figs. 1, 3, 5); the outer surface of the pedicle valve is strongly convex and the outer surface of the brachial valve is strongly concave; neither valve is geniculated (text-fig. 2). The curvature of the posterior to anterior profile of the pedicle valve in the median plane of the shell (text-fig. 3, method after Prentice 1956) is a compound of three logarithmic spirals which from umbo to trail have spiral angles of 37°, 44°, and 81° respectively, the initial spiral being subject to secondary modification and is not precisely defined. In all

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EXPLANATION OF PLATE 67

Promarginifera trearnensis gen. et sp. nov.

Figs. 1–3. Holotype; Hunterian Museum L6202. 1, ventral view; 2, dorsal view; 3, lateral view. ×3.
Fig. 4. Paratype; H.M. L6209. Interior of brachial valve showing cardinal process of type 1. ×2·5.
Figs. 5–6. Paratype; H.M. L6204. 5, posterior view showing reticulate umbo; 6, ventral view showing costation of type 2. ×3.
Fig. 7. Paratype; H.M. L6211. Interior of brachial valve showing cardinal process of type 5. ×2·5.
Fig. 8. Paratype; H.M. L6207. Lateral view showing enrolment of ear. ×3.
Fig. 9. Paratype; H.M. L6208. Interior of pedicle valve showing diductor scars and adductor platform. ×4.
Fig. 10. Paratype; H.M. L6210. Interior of brachial valve showing cardinal process of type 6. ×2·5.
Fig. 11. Paratype; H.M. L6203. Posterior view. ×2·5.
Fig. 12. Paratype; H.M. L6206. Antero-ventral view showing costation of type 6. ×3.
Figs. 13–14. Paratype; H.M. L6205. 7, posterior view showing internal mould of diductor scars and adductor platform; 8, antero-ventral view showing costation of type 3. ×2·5.


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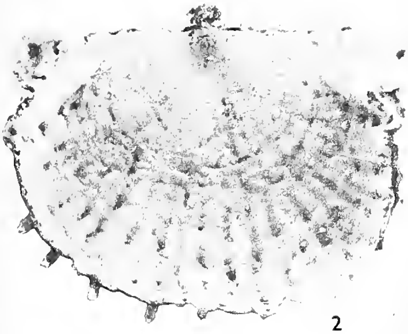
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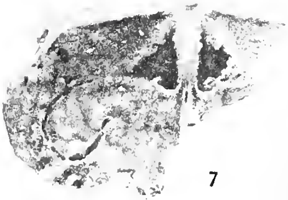
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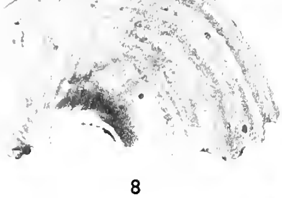
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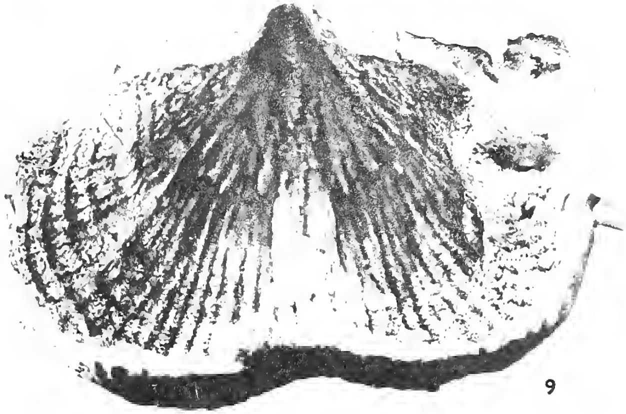
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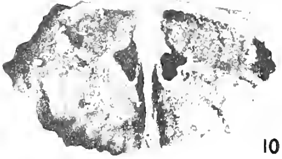
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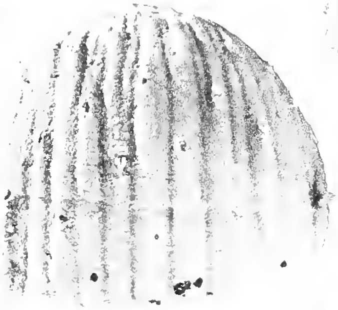
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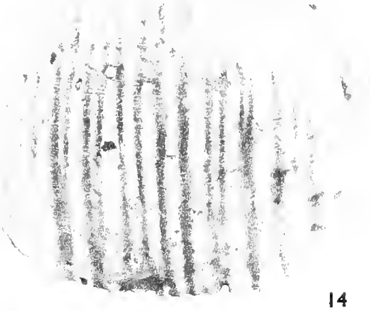
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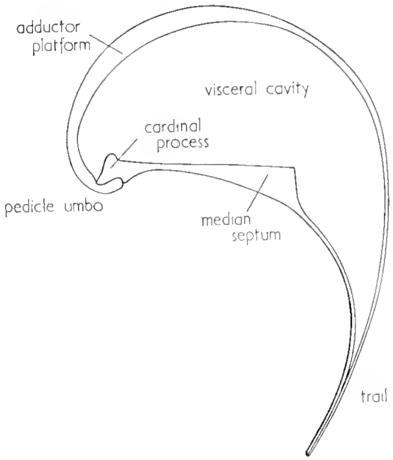
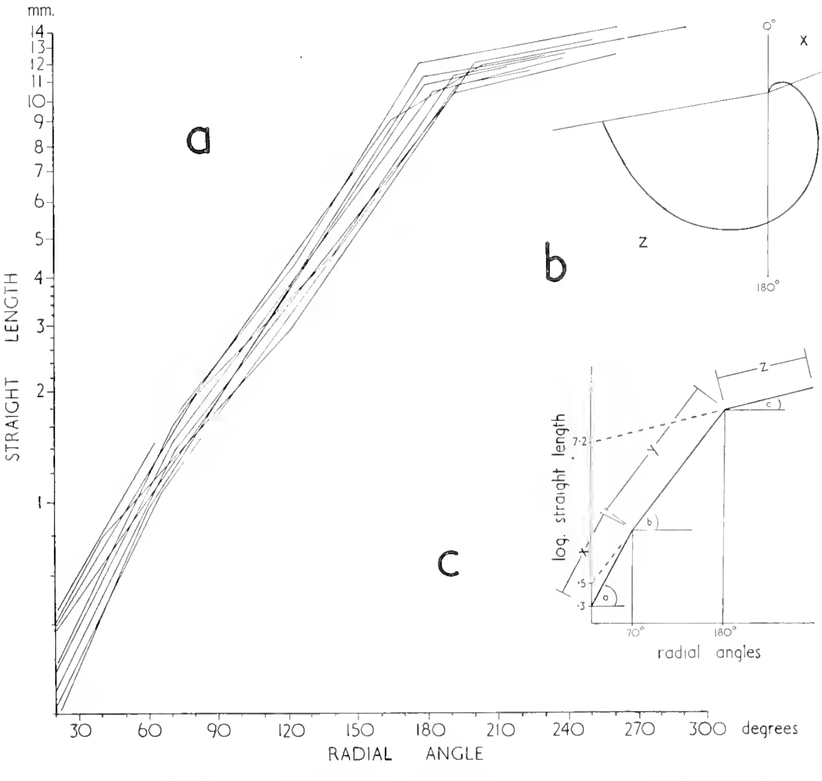
SHIELLS, Carboniferous *Promarginifera* gen. nov.



TEXT-FIG. 2. A median section of the shell of *P. trearnensis* showing the profile of the valves, the thickening of the pedicle valve in the region of the adductor platform, and a large cardinal process.

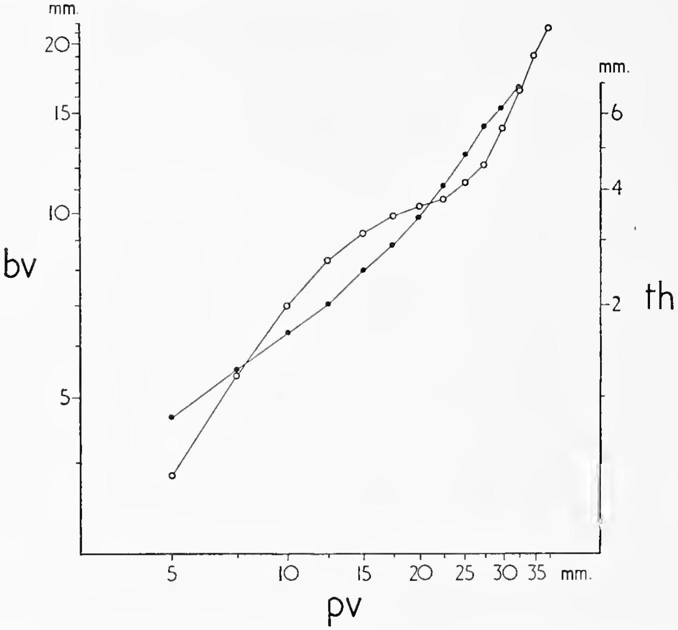


TEXT-FIG. 3. A plot of the straight length vectors which describe the growth spirals of the curved length of the pedicle valve. The principal changes in slope of the nine profiles plotted on (*a*) represent the change in spiral of the curves *x*, *y*, and *z* on (*b*). This is shown on the summation diagram (*c*) and the angles *a*, *b*, and *c* are the spiral angles.

specimens the hinge-line is straight and the hinge width is the maximum width of the shell; neither valve possesses an interarea.

GROWTH OF VALVES

The relative growth of the two valves and the increase in the thickness of the visceral cavity of *P. trearnensis* follow a pattern for strongly concavo-convex productids which is discussed elsewhere (Shiells 1965, pp. 878–80). Since the curvature of the valves is constant (within 5% angular variation), measurements of any individual of the sample population broadly characterize the species as a whole.



TEXT-FIG. 4. A plot on logarithmic coordinates of uniform growth increments to the curved length of the pedicle valve (*pv*) against (i) the corresponding increments to the curved length of the brachial valve (*bv*) shown as dots, and (ii) the corresponding increments to the thickness of the visceral cavity (*th*) shown as open circles.

It is observed that:

1. For unit increase in the growth of the curved length of the pedicle valve, the corresponding consecutive growth increments to the curved length of the brachial valve (*a*) systematically diminish until the pedicle valve has reached a length of approximately 22·5 mm., (*b*) progressively increase as the pedicle valve grows from approximately 22·5 to 32·5 mm., and (*c*) are equal in length for the remainder of growth (Table 2, text-fig. 4). From the first reliable measurements, i.e., when the curved length of the pedicle valve equals 5 mm., and the curved length of the brachial valve equals 3·8 mm., to the growth stage in which the curved length of the pedicle valve equals 11 mm., and the curved length of the brachial valve equals 7·5 mm., there is a simple allometric growth relationship between the valves. The allometric growth constant is 0·87 (text-fig. 5*a*). Subsequent growth of the two valves, however, deviates from simple allometry. As the two valves increase in curved length to approximately 22 mm. and 10·5 mm. for the pedicle and brachial respectively, there is a systematic decrease in the value of the allometric coefficient from 0·87 to 0·2. From this point until the growth stage in which

the curved length of the pedicle valve is 32·5 mm. and the curved length of the brachial valve is 16·5 mm., the values of the allometric coefficient rapidly increase to 1·98. Due to the parallelism of the valves further values for the allometric coefficient decrease until growth ceases.

2. For unit increase of the curved length of the pedicle valve as above, the corresponding increments to the thickness of the visceral cavity (*a*) are constant at first and then progressively increase until the pedicle valve has attained a length of approximately 27·5 mm., and (*b*) successively decrease as the pedicle valve increases from approximately 27·5 mm. to 32·5 mm. (Table 2, text-fig. 4). When the growth of the pedicle valve reaches approximately 32·5 mm., the brachial valve has become parallel to the pedicle valve. Since no specimen of *P. trearnensis* shows any thickening of the existing brachial valve or secretion of a new trail to the brachial valve, it follows that no further increase in the thickness of the visceral cavity can take place once this condition has been achieved. Allowing for a total maximum variation in the thickness of the shell substance of the valves, the sulcation, and costation, the estimate of the maximum thickness of the visceral cavity inclusive of the shell is 8±1·5 mm. As shown on text-figure 5*b* an isometric growth relationship (coefficient of allometry equal to unity) exists between the thickness of the visceral cavity and the curved length of the pedicle valve, until the latter reaches 17·5 mm. For further increase in the curved length of the pedicle valve, subsequent coefficients of allometry successively rise to a maximum value of 1·7, corresponding to a curved length of the pedicle valve of 27·5 mm. Finally, the values of the coefficient of allometry diminish in turn to 0·95 when the maximum thickness of the visceral cavity is attained.
3. For unit increase in the growth of the curved length of the brachial valve, the corresponding consecutive growth increments to the thickness of the visceral cavity (*a*) maintain a fairly constant size at first until the curved length of the brachial valve is 9–9·5 mm., (*b*) progressively increase as the curved length of the brachial valve is extended to 13–13·5 mm., and (*c*) successively diminish until the parallelism of the valves prevents further enlargement of the visceral cavity (Table 3, text-fig. 6). The relative growth of the thickness of the visceral cavity and the curved length of the brachial valve is shown on text-fig. 5*c*; the deviations from standard allometry are complex.
4. As shown on Table 4 the correlation of the hinge width with the curved length of the pedicle valve and the straight length is significant at a high level. However, such a correlation is subject to two interpretations. Firstly, in the light of the complex growth relationships between the curved lengths of the two valves it might be expected that an equally involved relationship would exist between the length of a valve and the hinge width, the correlation of the total data simply averaging the effect of the sample distribution about the true growth curve of the two characters. The growth of the two valves is controlled, however, by the common origin and common line of termination of any growth stage. In a comparison of the length with the width of the shell there is no similar direct functional dependence although an indirect cause is presumed. In the second place, therefore, it is possible that the growth of the hinge width matched that of either of the valves largely to substantiate the correlation. Unfortunately the growth laminae on the external surface of the shell proved insufficiently distinct to test these possibilities.

The slope of the flanks is inclined 65–80° depending on the completeness of the trail (Pl. 67, figs. 6, 11, 14). The shape of the venter is slightly convex, approximately flat, or sulcate (Table 1, Pl. 67, figs. 1, 5, 9, 12, 13). Of 44 specimens 18 (41%) possessed a sulcus and 26 (59%) were nonsulcate. A gradation exists between (i) nonsulcate forms, (ii) forms with a closed sulcate depression restricted to the anterior part of the visceral disc and the posterior end of the trail, and (iii) forms with an open sulcus beginning on the anterior part of the visceral disc and extending to the anterior extremity of the trail. The sulci of the open type are deepest on the anterior part of the visceral disc and the posterior end of the trail as demonstrated by the data of Table 5. Examination of the degree of correlation between the maximum width and maximum depth of the sulcus on 18 specimens just failed (by 0·001) to be significant at the 0·05 level of probability (Table 4). No significant correlation occurs between the height of the visceral cavity and the inward folding of the venter as possibly anticipated if the sulcation represented a simple structural modification of the test to strengthen an increasingly arched internal lumen (Table 4).

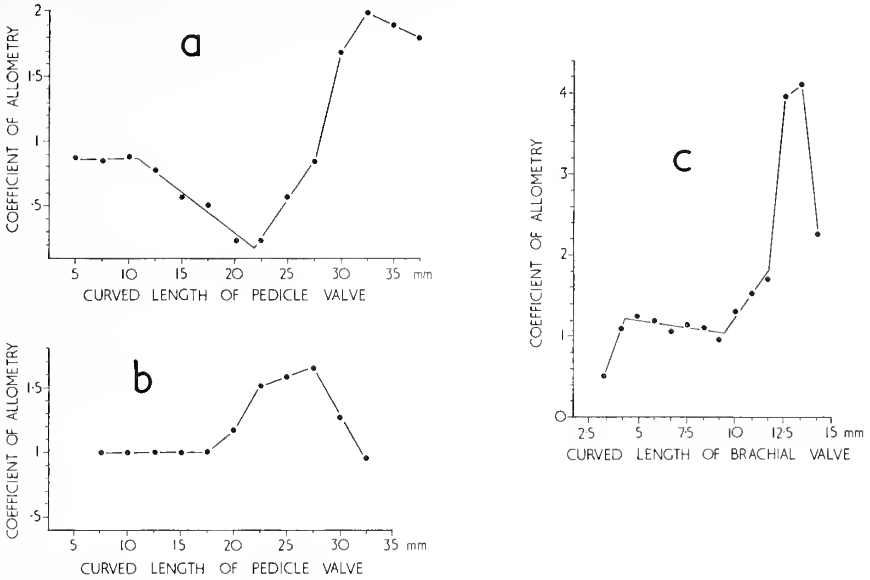
The umbo shows moderate expansion with a mean umbonal angle of 99·5±4·8° (Table 1). In all specimens the umbo projects posterior to the hinge (Table 1, Pl. 67, figs. 3, 6, 11, 14). Inflation of the umbonal cavity is expressed by corresponding increments (correlated at the 0·05 level of probability) to the umbonal angle and the distance to which the umbo extends posterior to the hinge (Table 4). Such inflation accompanies a general increase in gibbosity of the visceral cavity as shown by the significant correlation at the 0·05 level of probability between the height of the visceral cavity (plus the shell thickness of each valve) and the extension of the umbo posterior to the hinge. However, the very low (not significant) correlation between the hinge width and umbonal angle (indeed a low negative value was obtained—Table 4) suggests that an overall volumetric increase in the capacity of the shell interspace is not necessarily a function of gibbosity.

Prominent ears are an intrinsic feature of *P. trearnensis* (Pl. 67, figs. 1, 3, 8, 9). In shape they are triangular and enrolled, approximating either to a cylindrical sector or to a conical sector increasing in width and curvature towards the postero-lateral extremities. The mean dimensions of the structures are given on Table 1. Although the correlation between the width of the ear and the hinge width is significant at the 0·01 level and the correlation between the ear width and ear length is significant at the 0·05 level, the height of the ear, a measure of its curvature or degree of enrolment, varies independently (Table 4). The steeply inclined enrolled anterior slopes of the ears oppose the steeply inclined umbonal lateral surfaces to form a conspicuous groove, which either demarcates the slant side of the conical sectors or traces obliquely round the more cylindrical types of ear surface, increasing in depth towards the lateral margin of the shell.

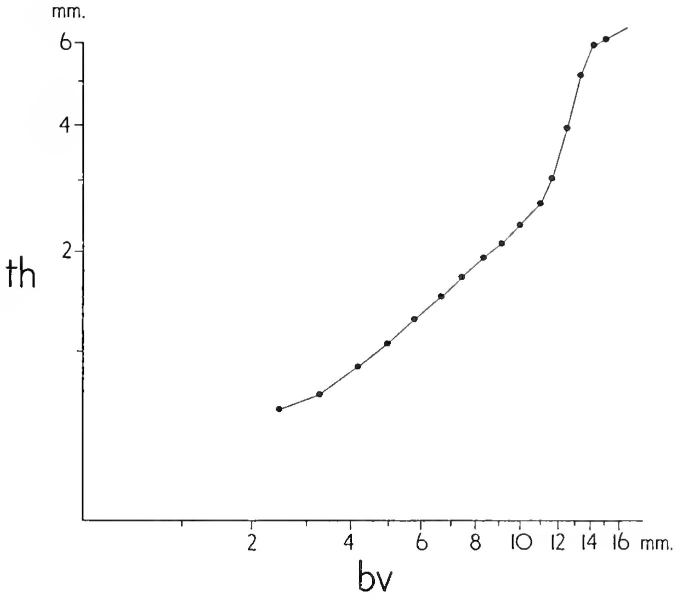
EXTERIOR OF PEDICLE VALVE

The exterior surface of the pedicle valve is conspicuously costate (Pl. 67, figs. 1, 5, 12, 13), the mean number of costae being 26±2 at the anterior margin (Table 1). Alternate costae and sulci diverge from an umbonal focus, each costa and sulcus proportionately increasing in width towards the anterior. The spread of the fan of costae is supplemented on the central, anterior, and antero-lateral regions of the visceral disc through additional costae being inserted or produced by bifurcation. On reaching the anterior of the visceral disc or the posterior part of the trail, expansion ceases and the costae and intercostal sulci continue as a set of parallel ridges and grooves down the length of the venter and antero-lateral surfaces of the trail to the valve extremity. Rarely, coalescence of costae takes place on the trail. Three properties of the costation (text-fig. 7), (i) the maximum widths of the costae attained on any specimen, (ii) the regularity of costation, and (iii) the shape or combinations of shape of the costae in transverse section, have been used to arbitrarily subdivide the continuously variable pattern for descriptive purposes. The six groups into which the costation may be subdivided are given in Table 6. The costation of 50 specimens has the following distribution; group 1—10 specimens (20%), group 2—9 specimens (18%), group 3—16 specimens (32%), group 4—8 specimens (16%), group 5—6 specimens (12%), and group 6—1 specimen (2%).

The exterior surface of the pedicle valve is rugate (Pl. 67, figs. 6, 11); the mean number of rugae is 7±1 (Table 1). The trace of the rugae and interrugal sulci approximates to a series of semi-ellipses about an umbonal origin. The majority of the rugae traverse the visceral disc but 0–2 of the inner rugae and 1–3 of the outermost rugae die out on the

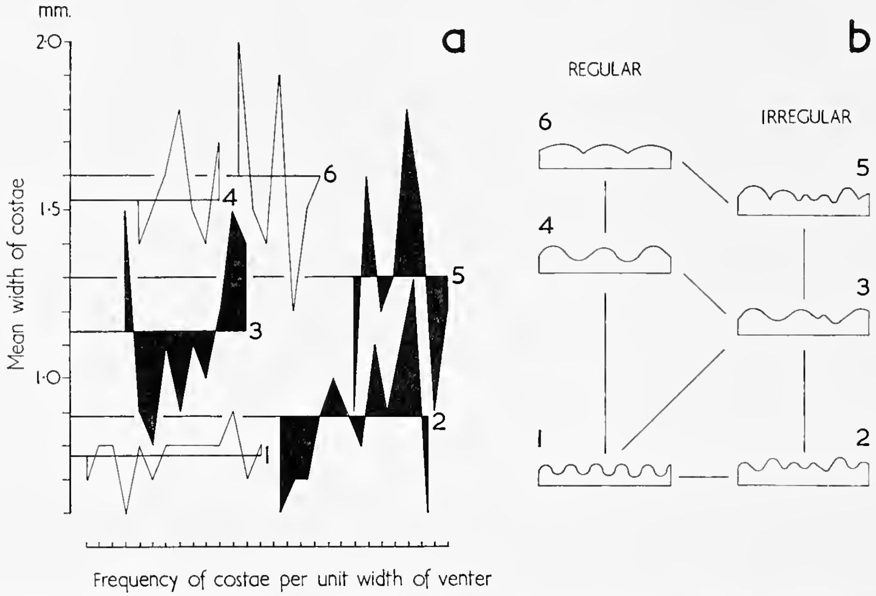


TEXT-FIG. 5. Deviations from simple allometry: (*a*) Coefficient of allometry for the relative growth of the length of the brachial valve and the length of the pedicle valve plotted against the length of the pedicle valve, (*b*) Coefficient of allometry for the relative growth of the thickness of the visceral cavity and the length of the pedicle valve plotted against the length of pedicle valve, and (*c*) Coefficient of allometry for the relative growth of the length of the brachial valve and the thickness of the visceral cavity plotted against the length of the brachial valve.



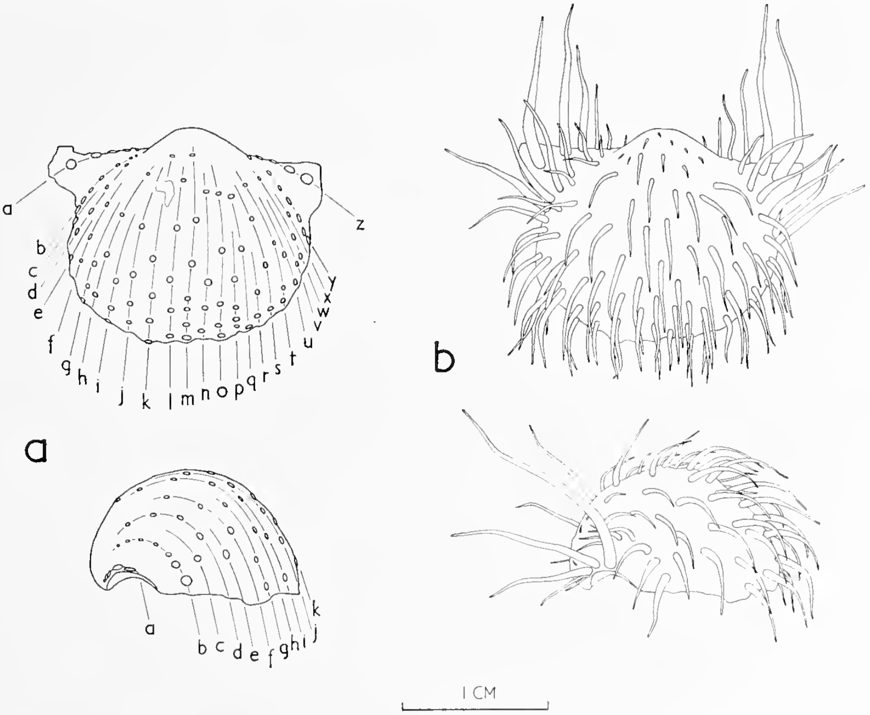
TEXT-FIG. 6. A plot on logarithmic coordinates of uniform growth increments to the curved length of the brachial valve (*bv*) against the corresponding increments to the thickness of the visceral cavity (*th*).

umbonal slopes. As the distance from the umbo increases there is a proportionate increase in the dimensions of the rugae. Furthermore, each of the outer rugae changes shape from an approximately equidimensional structure at the base of the umbonal slopes to one in which the posterior to anterior width of the ruga exceeds the height by a maximum factor of ten. Eight per cent. of the rugae bifurcate across the visceral disc. Measurements from a single specimen to demonstrate the progressive change in size of the rugae are given on Table 7. The rugae and costae lie normal to one another over the shell surface of the posterior region of the visceral disc, and the incidence of costae, intercostal sulci, rugae, and interrugal sulci produces a reticulated pattern. Close to the umbo the internodal intercepts on a costa are approximately twice the internodal intercepts on a ruga. However, as the rate of expansion of the rugation pattern exceeds that of the costation, the reticulation becomes progressively elongate in an anterior direction so that the internodal intercepts on a costa approaching the central part of the visceral disc are four times the internodal intercepts on a ruga in the same region. Measurements from a single specimen to show this relationship are given in Table 8. No significant association occurs between the type of costation and the number of rugae (χ^2 contingency only shows correlation at the 0·95 level of probability). The limitation of the rugae to the posterior surface of the visceral disc suggests that such corrugation may structurally reinforce the tightly convex umbonal slopes; however, no significant correlation ($r = -0{\cdot}244$) occurs between the frequency of the rugae and the size of the visceral cavity.



TEXT-FIG. 7. Variation of costation on the pedicle valve. The costation is arbitrarily grouped into six categories on the basis of regularity, size, and shape (*b*). Plots of examples of these groupings are shown on (*a*).

The pedicle valve is highly spinose with 50–100 erect, or suberect, halteroid spines projecting from its surface (text-fig. 8; Pl. 67, figs. 1, 2, 11, 13). The spines are situated on radii of umbonal origin and the spine bases progressively increase in diameter away from the umbo. The two spine rows on each side of the umbo which are closest to the hinge-line are especially distinct. They are characterized by a more regular spacing of the spine bases and, for an equivalent distance from the umbo, the spine bases are slightly greater in diameter than those on the remainder of the valve (Table 9). The posterior row is situated on the posterior enrolled slope of the ear and is subparallel to the hinge-line (maximum divergence from the hinge-line 15°). The anterior row is situated down the flank and initially diverges from the posterior row at an angle of 25–30°. All of the spines are supracostal except those on the ears and those on the posterior part of the row down the flanks.



TEXT-FIG. 8. Spinosity of the pedicle valve (ventral and lateral views). (*a*) Plot of spine bases on the holotype showing their distribution on 26 radii of umbonal origin (*a–z*); spine rows *b* to *y* are supracostal; spine rows *a* and *z* occur on the ventral and posterior ear slopes. (*b*) Reconstruction of spines; positions of the spine bases as for holotype, length and curvature of spines based on collective information.

The exterior surface of the pedicle valve shows concentric growth lamellae; the frequency of the lamellae is of the order of 7–9 per mm.

INTERIOR OF PEDICLE VALVE

The interior of the pedicle valve is strongly concave and is for the greater part an exact reflection of the convex exterior. The internal ridges and furrows which radiate from the umbo coincide with the intercostal sulci and costae of the exterior, simulating along the anterior margin of any growth stage a series of truly concentric folds through which the thickness of the shell remains constant. In the postero-central region, however, the interior of the pedicle valve is considerably modified by the attachment areas of the muscles (Pl. 67, figs. 9, 14). On either side of the mid-line of the valve two large (length 12–15 mm., maximum width 5–6 mm.), flabellate diductor scars diverge away from the umbo; each is longitudinally ridged. Posteriorly the diductor scars meet, but at a distance of approximately 5 mm. from the hinge-line they become separated by an upraised platform 1·5–2 mm. high, 5–6 mm. long, and 2–2·25 mm. wide. This is the adductor platform and it bears two ovate adductor scars near its posterior end, each 1 mm. wide and 3 mm. long. At a distance of approximately 1 mm. from the umbo the posterior margin of the pedicle valve becomes internally thickened; on occasion the internal thickening forms a distinct ridge up to 0·5 mm. high. Laterally this thickening or ridge bends towards the anterior and passes into the sharp flexure which abruptly demarcates the visceral cavity from the ears.

The interior surface of the pedicle valve is roughened by the anteriorly projecting calcicular rods of the taleolae. The density of thetaleolae (i.e. the number per unit length of the pedicle valve measured in thin section) ranges from 0–15 per mm. in various parts of the valve, with a mean density of 11 per mm. for the anterior region of the visceral disc and trail. Most of the taleolae are curved, forming a low angle with the plane of the shell surface at their termination within the shell substance, but projecting from the interior of the valve at an angle of approximately 50–70° to the valve surface.

EXTERNAL SURFACE OF BRACHIAL VALVE

The concave external surface of the brachial valve is costate and weakly rugate (Pl. 67, fig. 3). The costation is the exact reflection of that of the exterior surface of the pedicle valve, the costae of the latter being represented by the intercostal sulci of the brachial valve exterior. The postero-central portion of the valve is featureless except for a small protuberance situated on the hinge-line or the umbo (text-fig. 9). Up to six ill-defined rugae may occur, at least half the number being incomplete. The ears are demarcated from the rest of the shell by sharp folds which increase in amplitude towards the margin of the flanks and are complementary to the grooves demarcating the ears from the visceral disc of the pedicle valve. On two specimens several broken spines have been observed projecting at high angles to the anterior part of the visceral disc. The exterior surface of the brachial valve is otherwise smooth except for growth lamellae which are irregularly spaced but of the order of 7–9 per mm., as on the pedicle valve.

INTERNAL STRUCTURE OF BRACHIAL VALVE

Internally the bilateral symmetry of the brachial valve (Pl. 67, figs. 4, 7, 10) is reflected on either side of a slender median septum which extends 70–90% of the valve length from the posterior margin. The median septum has a mean length of 8·4±0·5 mm. (Table 1), and consists of two structural elements. The anterior 55% of the structure has a triangular blade-like form, 0·2–0·3 mm. wide, which arises from a position level with, or anterior to, the mid-point of the adductor scars. Towards the anterior the blade increases in height attaining a maximum elevation at, or within 0·5 mm. of, its anterior termination; the mean value for the maximum height of the median septum is 1·33±0·28 mm. (Table 1). The posterior section of the median septum is less well defined, comprising a low structure, semicircular in cross-section, with a maximum width of approximately

1 mm. and a maximum height of approximately 0·4 mm. Anteriorly it is contiguous with the blade-like portion of the septum; posteriorly it expands and fuses with the inflated ends of the marginal ridges to form a reinforced attachment with the cardinal process (Pl. 67, figs. 4, 10). In those specimens with a large cardinal process the posterior section of the median septum is weakly developed with an elevation of usually no more than 0·1 mm. The contour of the brachial valve is modified immediately anterior to the cardinal process by a dorsally concave and ventrally convex fold. The amplitude of this fold is slight with a maximum value of approximately 1·5 mm.; in shape it is elliptical with the long axis (3–6 mm.) orientated in a posterior to anterior direction. When the posterior section of the median septum is reduced in size the amplitude of the fold is generally large (1–1·5 mm.), the corrugation of the valve appearing, therefore, to compensate in part for the rigidity of a robust shaft. The value for the coefficient of correlation (r = 0·458) of the length and height of the median septum is not significant, and similarly there is no simple relationship between the size of the median septum and the size of the visceral cavity.

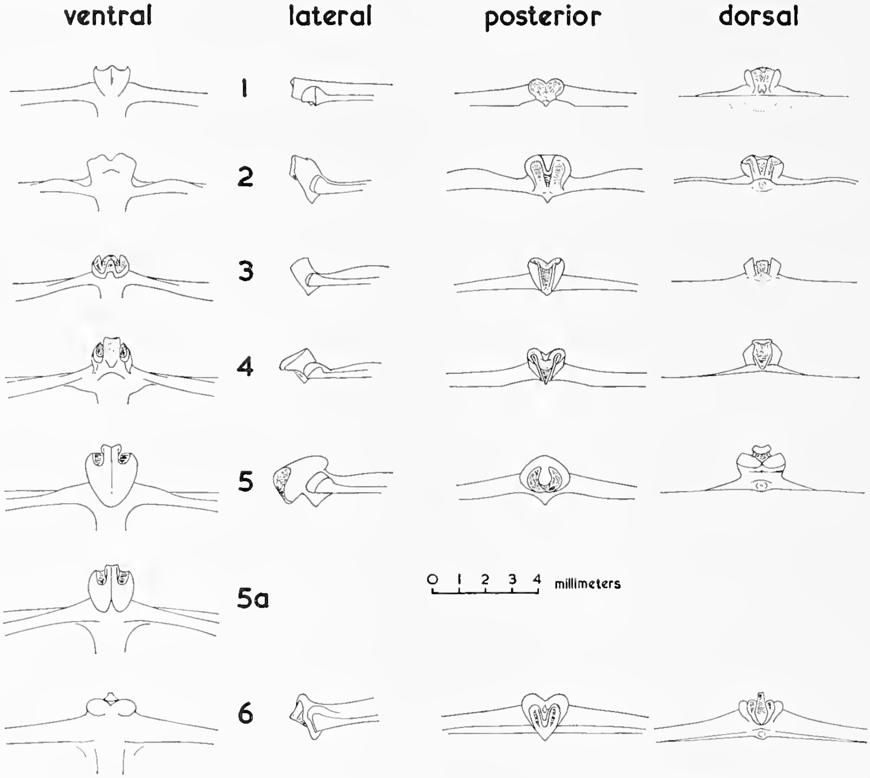
TYPES OF CARDINAL PROCESS AND MUSCLE SCARS

The cardinal process is a highly variable structure assuming a general costispiniferid form (Muir-Wood and Cooper 1960, pp. 28–29). It is trilobed, usually with a small median lobe, and is sessile; the overall dimensions are given in Table 1. Different types may be distinguished according to the degree of separation of the lateral lobes, and the inclination of the process with regard to the surface of the brachial valve (text-fig. 9; Pl. 67, figs. 4, 7, 10).

Type 1 (text-fig. 9–1; Pl. 67, fig. 4) is characterized by a horizontal posterior to anterior axis of the lateral lobes so that the process is in effect a lobed termination to the median septum. At the posterior extremity all three lobes are distinct, the small median lobe being little more than a V-shaped inflexion between the semiconical lateral lobes. The axis of the median lobe is disposed at 50° to the valve surface, and the anterior end continues into a distinct protuberance on the dorsal surface. The attachment area is directed postero-dorsally and the surface is roughened by the accentuation of growth lamellae. In ventral aspect the lateral lobes converge towards a mid-line before becoming fused anteriorly with the median septum. The cardinal process is buttressed by the swollen ends of the marginal ridges.

The cardinal process of type 2 (text-fig. 9–2) rises ventrally from the plane of the posterior part of the brachial valve at a steep angle (60°). When viewed from the posterior, two inflated lateral lobes are separated by a narrow median lobe which has a considerable extension in a postero-dorsal direction so that it makes an angle of only 30° with the brachial valve surface. The flexuous surface to which the diductor muscles were attached is roughened by irregular growth lamellae. Anterior to the median lobe the hinge-line bears a conspicuous protuberance which extends dorsally for approximately 0·3 mm. at right angles to the valve surface. In ventral aspect the lateral lobes converge and join the expanded end of the median septum.

The third type of cardinal process (text-fig. 9–3) has a similar upturned attitude in relation to the posterior part of the brachial valve to that of type 2. It differs from type 2, however, in the erect position of the median lobe and the anterior extension of the attachment surfaces of the lateral lobes, two features that enable the sinuous profile of the complete attachment surface to be clearly seen in the ventral aspect of the valve. The attachment surface is almost normal to the plane of the valve and is made asperous by uneven growth lamellae. Dorsally the cardinal process tapers into a distinct protuberance which has a relief of 0·2–0·3 mm., at right angles to the exterior surface of the valve. The process is supported by the marginal ridges which rise ventrally and fuse with the lateral lobes.



TEXT-FIG. 9. Variation in the form of the cardinal process of *P. trearnensis*.

The strong median lobe of type 4 (text-fig. 9–4) distinguishes it from the other types of cardinal process. The general attitude of the process is similar to that of types 2 and 3 but the median lobe extends further postero-dorsally and is much incurved, forming a lip which overhangs the attachment surface. The ventral surface of the median lobe is concave and bears a small pit. The axis of the median lobe curves slightly but is approximately at an angle of 50° to the plane of the posterior part of the brachial valve. Dorsally the tip of the median lobe forms a small protuberance. The attachment surfaces of the lateral lobes are almost closed by the enlargement of the median lobe; the whole of the attachment surface is roughened by uneven growth lamellae. In ventral aspect the cardinal process is supported by a swelling of the marginal ridge–median septum interangle.

The cardinal process of type 5 (text-fig. 9–5; Pl. 67, fig. 7) is distinguished both by its size and attitude in relation to the brachial valve. The process is bulbous and its axis has an antero-ventral to postero-dorsal incline, making an acute intersection with the brachial valve at 40°. The lateral lobes are much inflated and extended in an antero-ventral direction. In text-fig. 9–5 and Plate 67, fig. 7, the cardinal process has lateral lobes which are fused in a unified structure; the same type of cardinal process also occurs in which the lateral lobes are quite distinct anteriorly (text-fig. 9–5*a*). The median lobe is small and its dorsal extremity is posterior to the hinge-line and to a large protuberance 0·3–0·4 mm. in height which extends dorsally from the hinge-line at the mid-point of the valve. The involute attachment area is roughened in the usual way by growth lamellae. The cardinal process is supported by the thickened ends of the marginal ridges and the median septum.

The cardinal process of type 6 (text-fig. 9–6; Pl. 67, fig. 10) is similar to type 5 except that the incline of the process is increased so that the lateral lobes are directed dorsally, at right angles to the plane of the posterior part of the brachial valve. The median lobe has a conspicuous postero-dorsal extension, its axis being 40° to the surface of the valve. A protuberance extends dorsally, anterior to the median lobe. The attachment surface is roughened by growth lamellae and the process is supported by a swelling of the marginal ridges as they unite across the median septum.

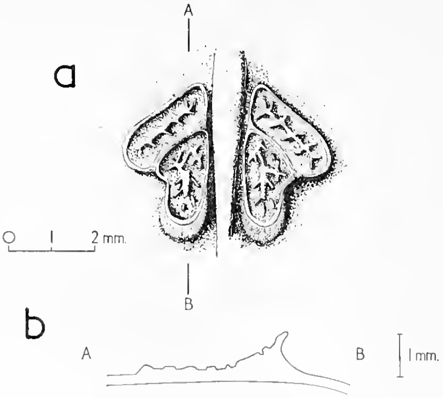
The distribution of the six types of cardinal process in a sample of 38 specimens is: type 1—7 specimens (18%), type 2—4 specimens (10·5%), type 3—6 specimens (16%), type 4—6 specimens (16%), type 5 and 5*a*—7 specimens (18%), type 7—8 specimens (21·5%).

The marginal ridges are asymmetrical elevations on the brachial valve which close the visceral cavity posteriorly and postero-laterally (Pl. 67, figs. 7, 10). From the cardinal process the ridges extend within 7° of the hinge-line a mean distance of $6{\cdot}1 \pm 0{\cdot}5$ mm. (Table 1), before swinging anteriorly through an angle of 110–145° and continuing a mean distance of 4·5–6·5 mm. to their termination on the flanks. At the mid-point of the valve they join the median septum and frequently swell to support the cardinal process (text-fig. 9). The section of the marginal ridges which extends from a quarter to a half of the distance along the hinge-line from the median septum to the lateral extremity of the ears, represents the main articulating surface of the two valves. It is only in these two short lengths on either side of the cardinal process that the marginal ridges are sufficiently close to the posterior edge of the brachial valve for them to combine with the shell substance of the main part of the valve in producing a reinforced pivot against the strain of a crude leverage of the valves imposed by the contraction of the diductor muscles.

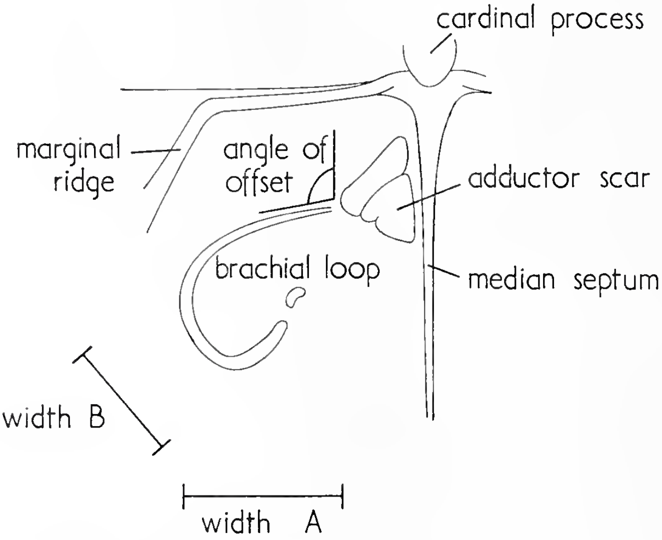
The adductor scars are two subtriangular elevated regions, the long sides of which are parallel to, and 0·1–0·3 mm. laterally separated from, the anterior blade of the median septum. The overall dimensions of the adductor scars and their location on the valve surface are given in Table 1. Each adductor scar has two main fields, each of which bears dendritic markings (text-fig. 10*a*). The anterior margin of the anterior field is steeply elevated above the valve surface (text-fig. 10*b*).

BRACHIAL RIDGES AND ENDOSPINES

The brachial ridges originate at the antero-lateral region of the adductor scars (Pl. 67, figs. 7, 10) and extend antero-laterally in a loop circumscribing a comparatively smooth, ovate area of the valve surface. The loop is incomplete at its anterior end (Pl. 67, fig. 7). The dimensions of the loop are given in Table 1; the positions of the measurements are shown in text-fig. 11.



TEXT-FIG. 10. (*a*) Reconstruction of adductor scars on either side of the median septum, each scar having two fields of attachment with dendritic relief. (*b*) Profile of adductor scar (section *AB* on (*a*)) showing steeply elevated anterior margin of the anterior field.



TEXT-FIG. 11. Diagram to show width *A*, width *B*, and angle of offset of the brachial loop (see Table 1).

It is estimated that 80–150 endospines extend anteriorly from the interior surface of the brachial valve. They are situated in a zone on the strongly convex anterior and antero-lateral slopes between the relatively flat postero-central disc and the trail. The majority are supracostal although others occur in sulci; they range in size up to 2 mm. and are inclined to the valve surface at approximately 45°. The taleolae of the brachial valve are variously distributed but attain a mean density of 11 per mm. at the anterior of the visceral disc and trail. As with the taleolae of the pedicle valve they are curved and anteriorly directed.

APPENDIX OF TAXONOMIC DATA

TABLE 1

Linear measurements in millimetres, angular measurements in degrees

Univariate Statistics of Selected Characters

Character	N	$\bar{x}$	s	OR	V	$\mu\,(P = 0{\cdot}05)$	$\mu\,(P = 0{\cdot}01)$
Hinge width of pedicle valve	45	17·3	2·49	13–22	14·38	16·6–18·0	16·3–18·3
Curved (or surface) length of pedicle valve	19	32·9	5·02	25–41	15·13	30·5–35·4	29·6–36·3
Straight length	19	13·6	1·42	11·4–17·2	10·43	12·9–14·3	12·7–14·5
Thickness (or height) of visceral cavity inclusive of shell	29	5·4	1·82	4·0–9·5	24·70	5·0–5·9	4·8–6·1
Width of sulcus	18	5·9	1·39	3–8	23·73	5·2–6·5	4·9–6·8
Depth of sulcus	18	0·87	0·356	0·5–1·5	40·69	0·70–1·05	0·63–1·12
Width of flat zone on venter of non-sulcate forms	26	4·5	1·98	1–8	45·47	3·5–5·1	3·3–5·4
Umbonal angle	32	99·5	9·81	85–135	9·86	95·9–103·0	94·7–104·1
Extension of umbo posterior to hinge	32	0·75	0·245	0·3–1·3	32·65	0·66–0·83	0·63–0·87
Ear width	27	7·32	1·12	5–10	15·20	6·47–8·17	6·17–8·47
Ear length	27	3·03	0·606	2–4	19·99	2·79–3·27	2·70–3·36
Ear height	27	0·85	0·351	0·2–1·7	41·32	0·71–0·99	0·66–1·04
Number of costae	34	26·0	4·42	18–39	16·99	25–27	24–28
Number of rugae	36	7·0	2·14	3–13	30·51	6–8	6–8
Length of median septum	22	8·4	0·91	7·0–10·5	9·91	8·02–8·83	7·87–8·97
Height of median septum at anterior end	16	1·33	0·38	0·7–1·9	28·74	1·13–1·53	1·05–1·61
Length of cardinal process	33	0·94	0·34	0·6–1·9	36·5	0·86–1·02	0·83–1·05
Width of cardinal process	33	1·17	0·26	0·6–1·7	22·4	1·08–1·27	1·05–1·30
Length of marginal ridge along posterior margin	11	6·1	0·54	5·3–7·0	8·89	5·74–6·46	5·56–6·62
Height of marginal ridge along posterior margin	28	0·25	0·064	0·2–0·4	25·53	0·22–0·27	0·21–0·28
Width of marginal ridge along posterior margin	28	0·32	0·121	0·2–0·6	37·12	0·28–0·37	0·26–0·39
Length of adductor scar	19	2·43	0·40	1·7–3·3	16·56	2·23–2·62	2·16–2·69
Width of adductor scar	20	1·61	0·29	1·3–2·5	17·91	1·48–1·75	1·43–1·80
Distance of posterior end of adductor scar from hinge-line	18	1·88	0·28	1·3–2·3	15·15	1·75–2·03	1·69–2·08
Distance of adductor scar from median septum	17	0·17	0·069	0·1–0·3	40·21	0·13–0·21	0·12–0·22
Width *A* of brachial loop	5	4·28	0·415	4·0–5·0	9·69	3·76–4·79	3·43–5·13
Width *B* of brachial loop	5	3·40	0·447	2·8–4·0	13·15	2·16–4·64	1·34–5·46
Angle of offset of brachial ridges	5	104	8	95–110	7·9	94–114	87–121
Width of brachial ridge	5	0·27	0·097	0·15–0·40	36·10	0·15–0·39	0·07–0·47
Distance of posterior end of brachial ridge from hinge-line	5	3·50	0·436	3·0–4·0	12·45	2·96–4·04	2·60–4·38

TABLE 2

Measurements to compare the relative increase in the length of the Brachial Valve and the thickness of the Visceral Cavity for unit increases in the length of the Pedicle Valve

Number of increments	*Curved length of p.v.*	*Increment to curved length of b.v.*	*Curved length of b.v.*	*Increment to thickness of visceral cavity*	*Thickness of visceral cavity*
1	2·5	2·08	2·08	—	—
2	5·0	1·75	3·83	—	0·83
3	7·5	1·58	5·41	0·42	1·25
4	10·0	1·54	6·95	0·42	1·67
5	12·5	1·33	8·28	0·42	2·09
6	15·0	0·92	9·20	0·42	2·51
7	17·5	0·75	9·95	0·42	2·93
8	20·0	0·34	10·29	0·59	3·43
9	22·5	0·29	10·58	0·66	4·09
10	25·0	0·67	11·25	0·75	4·84
11	27·5	0·91	12·16	0·83	5·67
12	30·0	1·92	14·08	0·66	6·33
13	32·5	2·42	16·50	0·50	6·83
14	35·0	2·50	19·00		
15	37·5	2·50	21·50		

TABLE 3

Measurements to compare the relative increase in the thickness of the Visceral Cavity for unit increase in the length of the Brachial Valve

Number of increments	*Curved length of b.v.*	*Increment to thickness of visceral cavity*	*Thickness of visceral cavity*
1	0·8		
2	1·7		
3	2·5		0·58
4	3·3	0·08	0·66
5	4·2	0·21	0·87
6	5·0	0·21	1·08
7	5·8	0·21	1·29
8	6·7	0·21	1·50
9	7·5	0·21	1·71
10	8·3	0·21	1·92
11	9·2	0·21	2·13
12	10·0	0·25	2·38
13	10·8	0·29	2·67
14	11·7	0·41	3·08
15	12·5	0·92	4·00
16	13·3	1·17	5·17
17	14·2	0·83	6·00
18	15·0	0·17	6·17

TABLE 4

Bivariate statistics of Selected pairs of Characters

Characters	*N*	*Coefficient of correlation*	*Coefficient of relative dispersion about reduced major axis*	*Level of significance*
Hinge width × curved length	19	0·681	11·58	0·01
Hinge width × straight length	19	0·536	10·83	0·05
Sulcation: width × depth	18	0·467	25·01	not significant
Thickness of visceral cavity × sulcation	10	−0·141	—	not significant
Umbonal angle × extension of umbo posterior to hinge	32	0·351	11·23	0·05
Extension of umbo posterior to hinge × thickness of visceral cavity	23	0·500	26·01	0·05
Umbonal angle × hinge width	29	−0·285	—	not significant
Hinge width × ear width	27	0·729	11·58	0·01
Ear width × ear length	27	0·428	17·97	0·05
Ear width × ear height	27	0·095	29·67	not significant
Ear length × ear height	27	0·181	51·46	not significant

TABLE 5

Measurements showing the changing proportions of the Ventral Sulcus

Position on valve surface	*Distance from umbo*	*Width of sulcus*	*Depth of sulcus*
Posterior of visceral disc	0–0·85	nonsulcate	nonsulcate
Mid-region of visceral disc	0·85–1·05	3·0	0·25
	1·05–1·25	4·0	0·50
	1·25–1·75	5·0	0·75
Anterior of visceral disc	1·75–2·25	5·0	1·00
Trail	2·25–2·60	5·0	0·75
	2·60–3·35	5·0	0·50

TABLE 6

Variation in Costation of the Pedicle Valve

<table>
<tr><td rowspan="4">A—REGULAR COSTATION
(costae approximately equal in width)</td><td colspan="2"><i>Width</i></td><td rowspan="2"><i>Nature of cross-section</i></td></tr>
<tr><td>Fine $<$ 1·2 mm.</td><td>Coarse $>$ 1·2 mm.</td></tr>
<tr><td>Group 1</td><td>Group 4</td><td>Rounded</td></tr>
<tr><td></td><td>Group 6</td><td>Scalloped</td></tr>
<tr><td rowspan="4">B—IRREGULAR COSTATION</td><td colspan="2"><i>Range of mean widths</i></td><td rowspan="2"><i>Nature of cross-section</i></td></tr>
<tr><td>No. of Fine $>$ Coarse Mean width $<$ 1·0 mm.</td><td>No. of Coarse $>$ Fine Mean width $>$ 1·0 mm.</td></tr>
<tr><td>Group 2</td><td>Group 3</td><td>Rounded</td></tr>
<tr><td></td><td>Group 5</td><td>Rounded & scalloped</td></tr>
</table>

TABLE 7

Measurements showing the progressive change in size of successive Rugae on the Pedicle Valve of a single specimen

No. of ruga	*Total length of ruga*	*Trace of visceral disc in plane of ruga*	*Max. distance from ruga immediately posterior*	*Max. posterior to anterior width of ruga*	*Height of ruga at position of maximum width*
1	2×4	11	—	—	—
2	12	12	0·8	0·4	0·05
3	14	14	0·8	0·5	0·05
4	16	16	0·7	0·4	0·075
5	18	18	0·9	0·3	0·1
6	22	22	1·2	0·6	0·1
7	25	25	1·5	0·8	0·2
8	30	30	2·0	0·8	0·3
9	32	32	2·0	1·0	0·1
10	2×10	33	—	—	—

TABLE 8

Measurements showing the progressive Elongation of the Reticulation on the Pedicle Valve of a single specimen

Distance from umbo	*Intercept on ruga*	*Intercept on costa*	*Ratio of intercept on ruga to intercept on costa*
5	0·4	0·8	1 : 2
9	0·45	1·6	1 : 3·5
12	0·5	2·0	1 : 4

TABLE 9

Distribution of Spines on the Pedicle Valve of the holotype of *Promarginifera trearnensis* gen. et sp. nov.

Spine		*Distance of largest spine from umbo*	*Spine bases numbered from anterior to posterior Distance between adjacent spines in each row—d.*												
			1	*d*	2	*d*	3	*d*	4	*d*	5	*d*	6	*d*	7
Ear row		9·5	0·7	2·0	0·4	1·4	0·35	1·0	0·2	1·0	0·1		—		—
Flank row		14	0·6	0·9	0·55	1·2	0·4	0·8	0·3	0·8	0·3	1·1	0·2	0·7	0·15
Other rows	1	24	0·4	4·5	0·3	4·5	0·25	2·3	0·2		—		—		—
	2	22	0·3	2·5	0·3	4·2	0·2	2·0	0·2		—		—		—
	3	24	0·4	2·2	0·2	1·9	0·3	1·5	0·25		—		—		—
	4	25	0·4	2·3	0·35	2·3	0·2	1·8	0·2	4·0	0·1		—		—

Acknowledgements. I thank Professor T. Neville George, Dr. J. D. Lawson, and Dr. W. D. I. Rolfe for reading the manuscript; to them and to Dr. J. K. Ingham I am indebted for many helpful discussions and advice. The work was carried out in the Department of Geology in the University of Glasgow and I gratefully acknowledge the assistance of the technical staff during various stages of the work.

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DESCRIPTION OF DIMORPHISM IN *STRIATOPORA FLEXUOSA* HALL

by WILLIAM A. OLIVER, JR.

ABSTRACT. *Striatopora* Hall comprises branching favositoid tabulate corals with thick, dilated walls near the outer surface of the colonies. Study of serial sections of the type species, *S. flexuosa* Hall, shows that individuals within colonies commonly originated in one of two positions, either near the axis of the colony or near the boundary between inner thin-walled and outer thick-walled zones. Corallites originating in the two positions are morphologically distinct and were produced alternately by corallites of the first type. Corallites of the second type did not reproduce asexually. Previous descriptions of *S. flexuosa* have been based on exteriors of colonies or on material other than the type specimens. Redescription of the type specimens based on thin section studies provides a better basis for understanding the genus.

Other named genera of morphologically comparable corals can be differentiated on the basis of wall microstructure or other features, or are possible subjective synonyms of *Striatopora*.

THE tabulate coral genus *Striatopora* Hall has been widely accepted since its first description in 1851, and specimens ranging in age from Silurian to Permian, from most continents, have been referred to it. Most workers have loosely conceived of the genus as a branching favositoid with a certain amount of wall dilation in individual corallites, especially near the surface of the colony. This concept was based on Hall's description and illustrations of the exterior of the Silurian type species, *S. flexuosa*. In recent years the accepted concept has been narrowed, good redescriptions of the type species have been published, and additional genera have been erected to include forms once referred to *Striatopora* sensu lato. Although the type species is now comparatively well known, much of the available descriptive information is based on specimens other than the syntypes, which have not previously been sectioned. The purpose of this paper is to describe the developmental pattern within colonies, to redescribe the type specimens so that there will be a satisfactory basis for understanding the genus, and to outline the problems connected with this and other morphologically similar genera.

Acknowledgements. The redescription was undertaken at the suggestion of Professor Dorothy Hill, Brisbane, Australia, who pointed out the need for a fuller understanding of *Striatopora flexuosa*. I am indebted to Professor Hill for her comments on an early draft of the description and generic discussion, many of which have been incorporated in the text. The manuscript also profited from review by Dr. Richard S. Boardman, U.S. National Museum, who suggested that the included analysis of colony growth be undertaken. The syntype collection is housed in the American Museum of Natural History (AMNH) and was loaned to me by Dr. Roger L. Batten. Topotype collections in the U.S. National Museum (USNM) were made available by Dr. Boardman. Photographs are by Robert H. McKinney (exteriors) and David H. Massie (thin sections). Publication is authorized by the Director, U.S. Geological Survey.

PATTERN OF GROWTH

After initial study of Hall's original specimens (see below), two topotype fragments of *S. flexuosa* were prepared by making two series of 8 and 10 thin sections, transverse to the branch axis at 1 mm. intervals. In these and other specimens, offsets (new corallites;

[Palaeontology, Vol. 9, Part 3, 1966, pp. 448–54, pls. 68–71.]

'buds') were formed only in two positions, at the branch axis and near the boundary between the inner (thin-walled) and outer (thick-walled) zones.

Offsets originating at the branch axis (**a**-offsets in the following discussion) appear on the axial side of the thin-walled part of the protocorallite (**a** on Pl. 69, fig. 1, and Pl. 70, fig. 3). A polygonal bulge in the parental wall precedes the development of a new wall separating parent and **a**-offset (several examples can be seen in Pl. 71, figs. 1–6). Initially, **a**-offsets have thin walls with minimal light-coloured lamellar deposits.

Offsets appearing at the boundary between the inner and outer zones (**b**-offsets) also appear on the axial side of the protocorallite but seemingly form on the thick lamellar part of the parental wall (**b** on Pl. 69, fig. 1, and Pl. 70, fig. 3).

a- and **b**-corallites are morphologically distinct. Measured to the nearest millimetre, 14 **a**-corallites range in length from 5 to more than 9 mm., 6 mm. being the most common observed length; 15 **b**-corallites range from 2 to 4 mm. in length with 10 individuals being 3 mm. long. In addition, wall dilation is limited to the distal one-third to one-half of each **a**-corallite, whereas **b**-corallite walls are dilated along their entire length.

Within the studied material the pattern of colony development seems to be consistent. Each **a**-corallite gives rise to two offsets ('buds'). An **a**-offset is formed as the parent separates from the axis; a **b**-offset is formed as the parent becomes thick-walled. Both types are labelled in longitudinal sections illustrated on Plates 69 and 70. **b**-corallites do not produce offsets. The result of obtaining two offsets from each **a**-corallite and none from **b**-corallites is the **a**–**b** alternation which is so clearly shown in the illustrations. The lack of alternation at the top of the figured longitudinal sections is only apparent. Presumably each of the adjacent **a**-corallites produced **b**-corallites above the limits of the thin section.

If the described pattern of development were invariable, **a**- and **b**-offsets should appear in equal numbers. Counts were made in the two serial series with these results: in specimen USNM 146505 (Pl. 71, figs. 1–6), I identified 10 **a**-offsets and 10 **b**-offsets in the 5-mm. length illustrated; two other offsets are of uncertain origin. In the second specimen I found 8 **a**-, and 10 **b**-offsets in 5 mm. Although based on a small sample, these data do support the suggested alternation of **a**- and **b**-types. There are exceptions, however. On Plate 71, corallite 7 gives rise to **a**-offset 23 in fig. 4; 2 mm. higher in the branch (fig. 6), the same corallite gives rise to two more offsets which are completely separated from corallite 7 in a thin section taken 1 mm. higher. The upper offsets are probably **b**-types, although this is not certain from the section; neither is included in the previous offset count because no new wall was formed within the 5-mm. portion on which the count was based. Perhaps the 'extra' corallite was needed to fill space in the colony.

The dimorphism represented by **a**- and **b**-corallites was probably significant in the development of the living colony. **a**-polyps went through a longer development period. This may have been required for the attainment of full maturity, and **a**-polyps may have reproduced sexually as well as asexually. **b**-polyps apparently skipped early growth stages. They may have attained normal maturity for some functions, such as feeding or defence, but not for others, such as reproduction. Alternate production of **a**- and **b**-polyps permitted faster colony growth, which may have given the species certain advantages in food and/or oxygen intake or in some other way. Presumably both types of polyps competed for space with surrounding individuals but in somewhat different micro-environments.

The formation of **a**- and **b**-offsets is in some ways similar to lateral and peripheral offsetting, respectively, in rugose corals.

SYSTEMATIC DESCRIPTION

Genus STRIATOPORA Hall

Striatopora Hall 1851, p. 400; 1852, p. 156; Wells 1944, pp. 259–60 [part]; Hill and Stumm 1956, pp. 464 [part]; Lafuste 1959, pp. 85–87.

Type species. By monotypy, *S. flexuosa* Hall 1852, p. 156, pl. 40B, figs. 1*a–e*. Middle Silurian, Rochester Shale, Lockport, New York.

Diagnosis. Ramose favositoid coralla with cylindrical or slightly compressed branches. Corallites gently curve away from axial region, opening obliquely to surface on small branches, perpendicularly on large branches. Corallite walls thin axially, strongly dilated distally, distinctly lamellar. Corallites polygonal in cross-section, but lumen round because of dilation. Mural pores common. Septal spines project into lumen, expressed as septal ridges in calice. Tabulae complete.

Discussion. Several genera of ramose cerioid tabulates with greater or lesser dilation of distal corallite walls have been described, and it is not at all clear how they interrelate. Wells (1944) discussed the morphologic series *Favosites*→*Thamnopora*→*Striatopora*→*Trachypora* as one of increasing wall dilation with complete gradation in this character, but subsequent work indicates that the phylogenetic relationships are more complex than this would suggest. The genera were originally described without adequate analysis of similarities and differences and without knowledge of the morphology of even the type species of earlier genera. Some of these genera are briefly discussed below with emphasis on apparent differences from *Striatopora*.

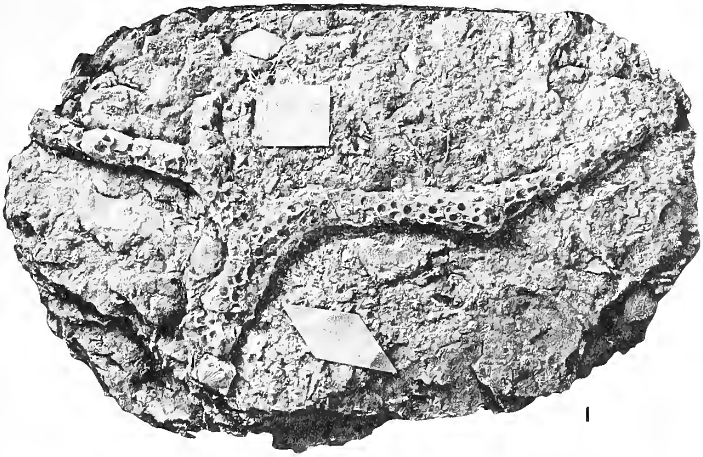
Thamnopora Steininger (1833; see Lecompte 1939, pp. 102–4) has cylindrical or compressed branches; corallite walls are moderately dilated, the dilation increasing distally; septal spines are weak or lacking. Lecompte (1936, pp. 14–16), working with the Middle Devonian type material, and Lafuste (1958) have described the wall structure as fibrous, the fibres arranged more or less normal to the wall surface (radial-fibrous). Similar wall

EXPLANATION OF PLATE 68

Figs. 1–7, *Striatopora flexuosa* Hall. 1–4, Lectotype corallum, AMNH 1685:1, the original of Hall 1852, pl. 40B, fig. 1*a*. 1, Exterior of complete specimen (× 1), thin sections were taken from the distal end of the right-hand branch. 2, Enlargement of central portion of corallum (× 2). 3–4, Longitudinal and transverse thin sections (× 20), note the relatively thin walls in this 'young' portion of the colony. 5, Paralectotype, AMNH 1685:2; exterior (× 2); the original of Hall 1852, pl. 40B, fig. 1*b*. 6, Paralectotype, AMNH 1685:6; exterior (× 2); not illustrated by Hall; see also pl. 70, fig. 6. 7, Paralectotype, AMNH 1685:3; exterior (× 2); note that septal ridges are especially well preserved on this specimen; original of Hall 1852, pl. 40B, fig. 1*c*.

EXPLANATION OF PLATE 69

Figs. 1–5, *Striatopora flexuosa* Hall. Paralectotype, AMNH 1685:4; not illustrated by Hall; see also Pl. 70. 1–2, Longitudinal thin section (× 10) and detail of same (× 50), note mural pores, septal spines and lamellar wall-structure; **a**- and **b**- corallites are so labelled. 3–4, Transverse thin section (× 10) and detail of same (× 50), note septal spines and lamellar wall-structure. 5, Another transverse thin section (× 10), showing mural pores and excessive wall dilation.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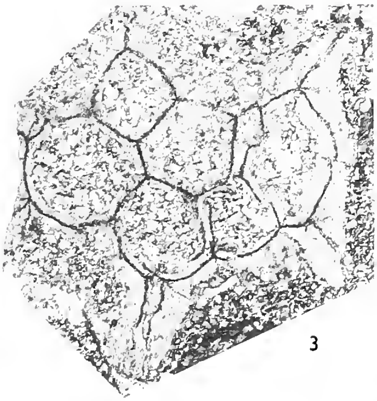
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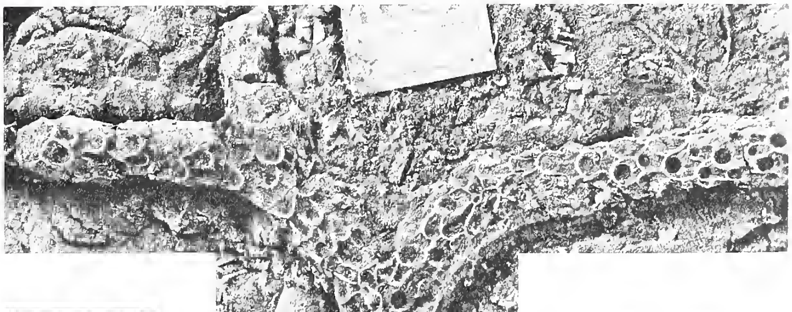
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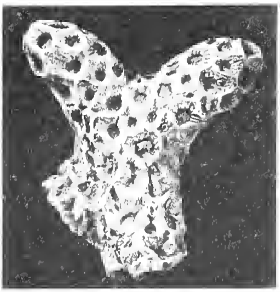
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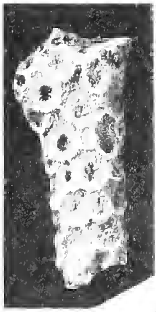
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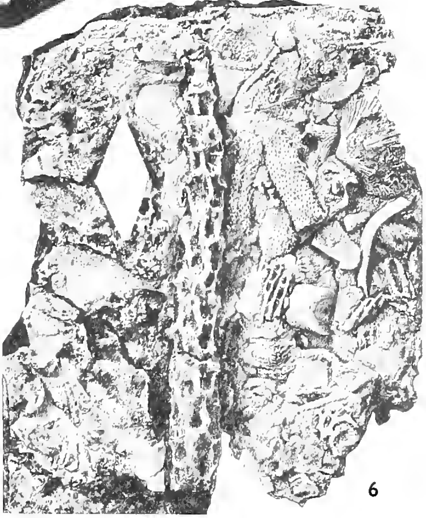
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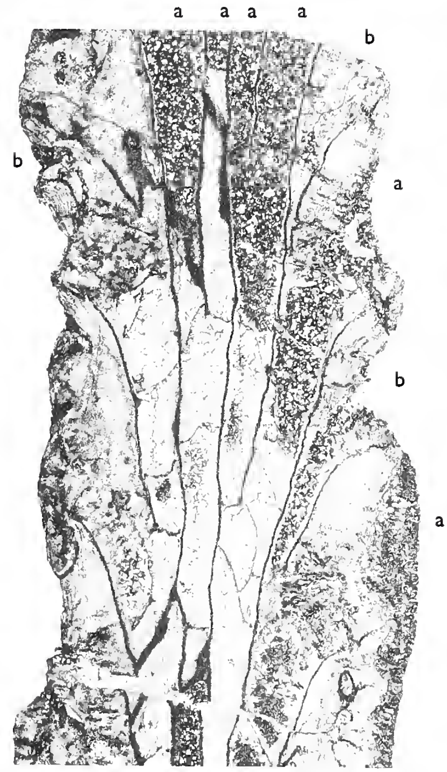
OLIVER, *Striatopora flexuosa* Hall



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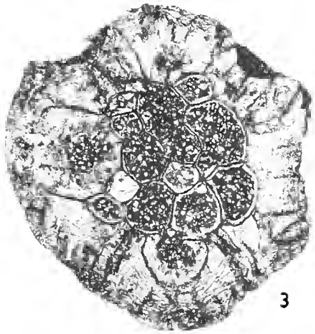

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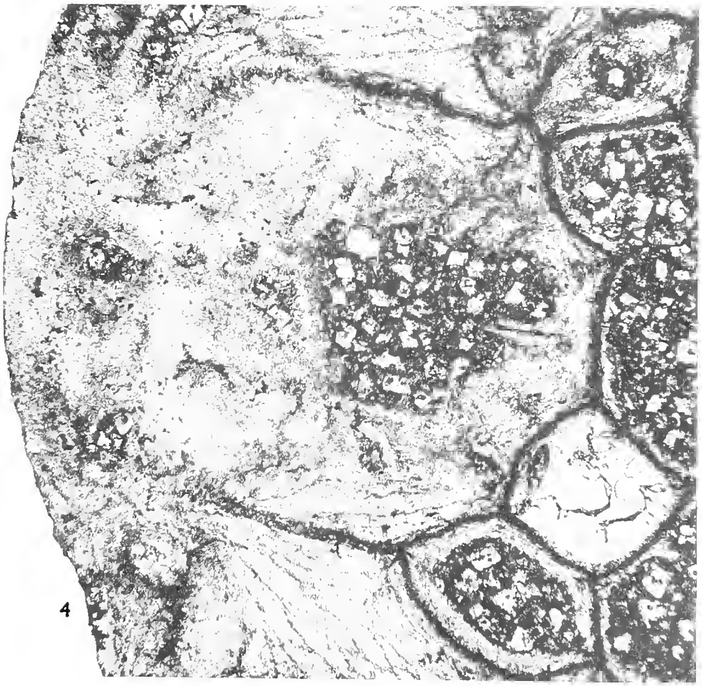

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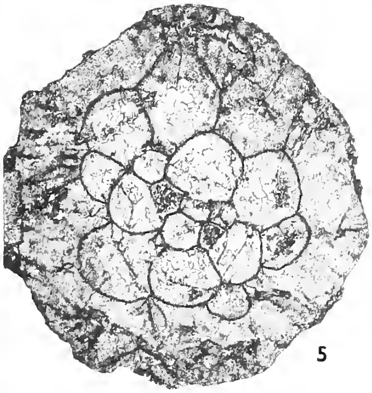

5

OLIVER, *Striatopora flexuosa* Hall

structure is known in many Devonian species of '*Favosites*' (Swann 1947, Lafuste 1962) and *Thamnopora* is considered by many workers to be closely allied to that genus. Lafuste, however, has restudied the wall structure of *Favosites gotlandica* Lamarck, the Silurian type species, and describes it as lamellar (concentric) and 'apparently identical to that which has been observed in *Striatopora flexuosa* Hall . . . ' (Lafuste 1962, p. 106). Lafuste suggests that *Favosites* s.s. should include only forms with lamellar wall structure.

The type species of *Trachypora* Milne-Edwards and Haime (1851, pp. 158, 305, *T. davidsoni*, pp. 305–6, pl. 17, figs. 7, 7*a*, Upper Devonian) has widely spaced calice pits separated by a great deal of stereoplasm (possibly a symbiotic stromatoporoid, according to Lecompte, 1939, pp. 147–8), the outer surface of which is covered by vermiform marks. As far as I know, the type species has never been sectioned. Subsequent workers have based the genus on the excessive amounts of stereoplasm and the general external appearance. Hollard and Lafuste (1961, pp. 71–76) described the microstructure of *Trachypora* based on the American Middle Devonian *T. limbata* (Eaton). According to them, the heavily dilated walls of this species are lamellar and similar in structure to those of *Favosites gotlandica* and *Striatopora*.

The type species of *Cladopora* Hall (1851, p. 400; 1852, p. 137; *C. seriata* Hall, 1852, pp. 137–8, pl. 38, fig. 1 *a–m*) has recently been redescribed on the basis of thin sections (Stumm 1960; Oliver 1963). The species is of small diameter; corallites intersect the surface at a low angle, walls are only slightly thickened, mural pores are rare, and tabulae are lacking; no septa have been observed; the microstructure is lamellar.

Parastriatopora Sokolov (1949; 1955*b*, p. 32, based on *P. rhizoides*, p. 32, pl. 50, figs. 2–4) is diagnosed as follows: 'Fasciculate and finger-like coralla, formed by prismatic corallites, radially diverging from the axis of the corallum and opening normal to its surface. The stereoplasm zone is sharply demarcated at the periphery' (Sokolov 1955*b*, p. 32, translated by George Rabchevsky). The species description and subsequent usage of the genus by Russian workers emphasize the sharp separation of an inner thin-walled zone from an outer zone of heavily dilated walls. Illustrations make clear that dilation is strong, and that the two zones are sharply and smoothly separated. Sokolov also noted that septal spines are weakly developed (p. 32). Microstructure of *Parastriatopora rhizoides* was described and diagramed by Chudinova (1958) and Sokolov (1962).

Chudinova (1958, following in part Sokolov, 1955*a*) and Sokolov (1962) described three types of microstructure within their family Thamnoporidae or Pachyporidae (Chudinova 1958, pp. 30–31, figs. 8–10; pp. 36–37, 45, 53, 67–68; Sokolov 1962, p. 206, fig. 7 *a–c*; pp. 228–9):

1. 'Fibrous microstructure' has 'fibres' arranged parallel to the corallite walls (i.e. concentrically) without layering. This characterizes the Parastriatoporinae.
2. 'Concentric microstructure' has short 'fibres' arranged perpendicularly to the wall (i.e. radially); the fibres are thin, short, hard to discern, and in distinct concentric layers. This characterizes the Striatoporinae.
3. 'Radially-fibrous microstructure' has 'fibres' arranged perpendicularly to the wall (i.e. radially); the fibres are coarse, long and tend to fuse and obliterate the boundaries of the concentric layers. This characterizes the Thamnoporinae.

As indicated in previous paragraphs, the separation of a radial structure (3) from a concentric one (1 and 2) has been observed by several workers. The recognition of two types of concentric structure seems doubtful, as this will be very much a matter of preservation. This opinion is strengthened by present observations which indicate that the structure of typical *Striatopora* is closer to the Chudinova-Sokolov type 1 (their Parastriatoporinae) than to their type 2 (their Striatoporinae).

Chudinova separates the Parastriatoporinae from the Striatoporinae on the following characters in addition to microstructure: the Parastriatoporinae have a sharp break between an inner zone of little wall dilation and the outer dilated zone, they have more widely distributed mural pores, and their corallites open at right angles to the outer surface of the branch; the Striatoporinae show gradual increase in wall dilation with growth, fewer rows of mural pores, and corallites opening at an angle to the surface. These features are a questionable basis for even generic separation and seem quite inadequate for subfamily definition.

If wall structure can be shown to be primary, the following grouping of the discussed genera would be suggested by the available data: 1. radial-fibrous group, *Thamnopora* and many '*Favosites*'; 2. concentric group, *Favosites* s.s., *Striatopora* (and *Parastriatopora*), *Cladopora*, and *Trachypora*.

The problem of phylogenetic relationships is beyond the scope of the present paper which primarily is to redescribe the species and type specimens on which the genus *Striatopora* is based. It is clear that much remains to be done with all genera. The difficulties that result from long-distance interpretation of genera and type species are not to be easily overcome.

Striatopora flexuosa Hall

Plates 68–71

Striatopora flexuosa Hall 1851, p. 400 (nomen nudum); 1852, p. 156, pl. 40B, figs. 1 *a–e*; Wells 1944, p. 260, pl. 40, figs. 1–2; Hill and Stumm 1956, figs. 352, 5*a–b*; Lafuste 1959, pp. 85–87, text-figs. 1, 2, pl. 1, figs. 1–3.

External features. Coralla are ramose with cylindrical or compressed branches varying in diameter from 3 to 5 mm. The lectotype corallum bifurcates at intervals of from 11 to 22 mm.; bifurcation is common in other specimens, but none is complete from one

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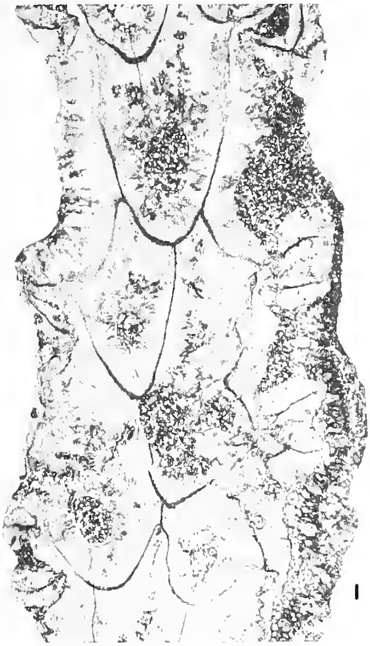
EXPLANATION OF PLATE 70

Figs. 1–6, *Striatopora flexuosa* Hall. 1–2, Paralectotype, AMNH 1685:4, not illustrated by Hall; see also Pl. 69; thin section tangential to colony branch showing transverse sections of corallites in mature region (×10); detail (×50). 3–4, Paralectotype, AMNH 1685:5, not illustrated by Hall; longitudinal and transverse thin sections (×10). 5, Topotype, USNM 146506; detail of longitudinal thin section (×50) showing tunnel-like mural pores. 6, Paralectotype, AMNH 1685:6; longitudinal thin section (×10) of specimen illustrated on Pl. 68, fig. 6 (section was taken from the portion of the branch below the crack).

EXPLANATION OF PLATE 71

Figs. 1–6, *Striatopora flexuosa* Hall. Topotype, USNM 146505; serial transverse thin sections (×15) taken at right angles to the branch axis at 1 mm. intervals; figure 1 is the lowest section, 6 is the highest. Corallites are numbered for recognition in successive sections but numbers are omitted where their inclusion would cover important detail. Corallite origin is as follows: **a**-corallites, 13, 14, 15, 16, 17, 23, 24, 27, 28, 29; **b**-corallites, 8, 9, 10, 12, 18, 20, 21, 22, 25, 26; corallites of uncertain origin, 11(**b**?), 19(**a**?).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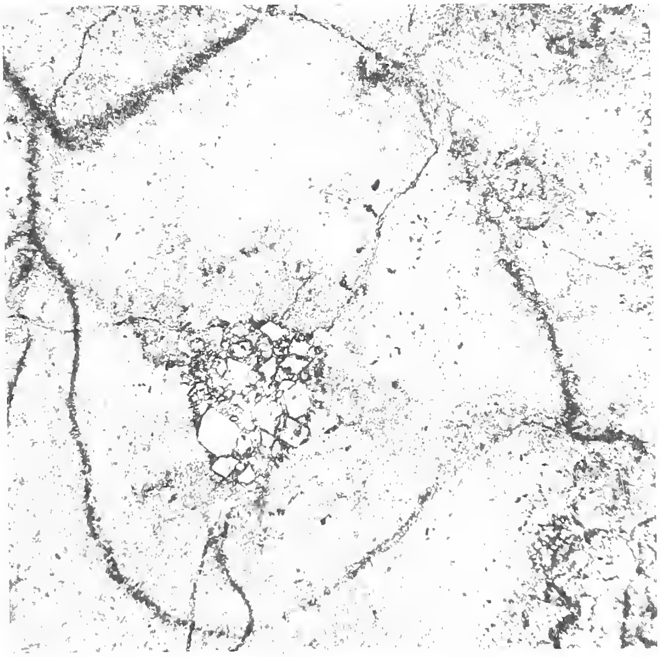
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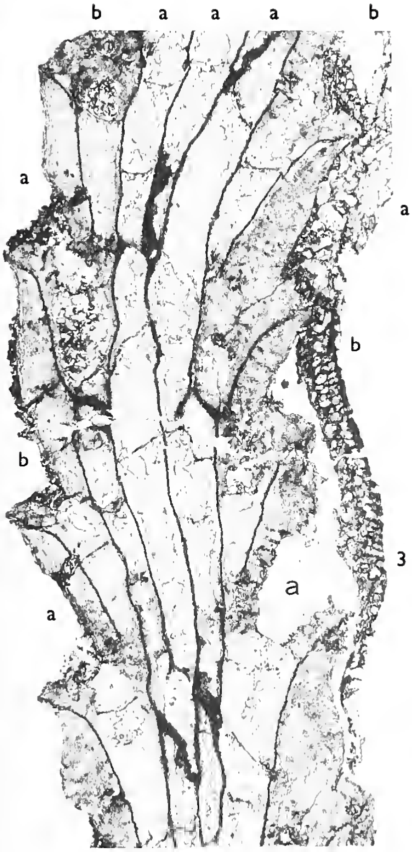

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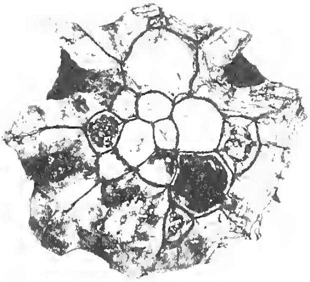
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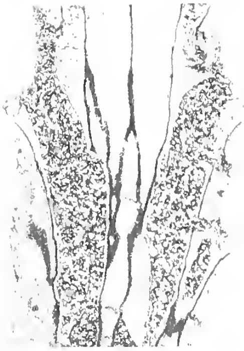
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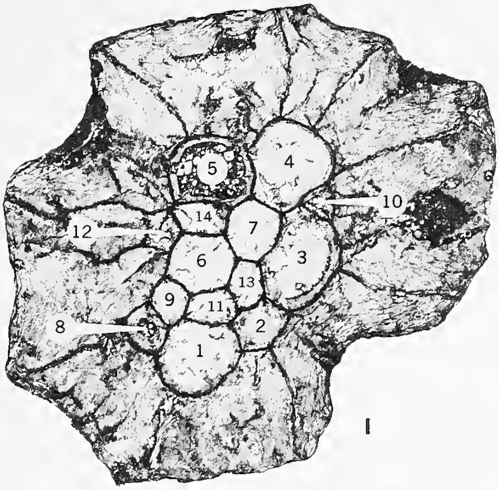
OLIVER, *Striatopora flexuosa* Hall



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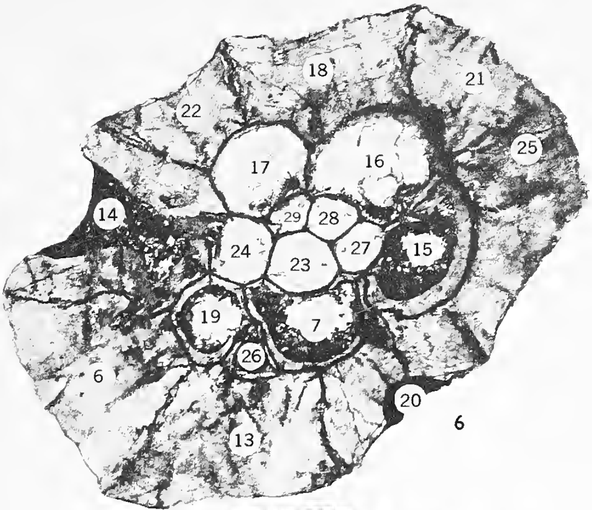

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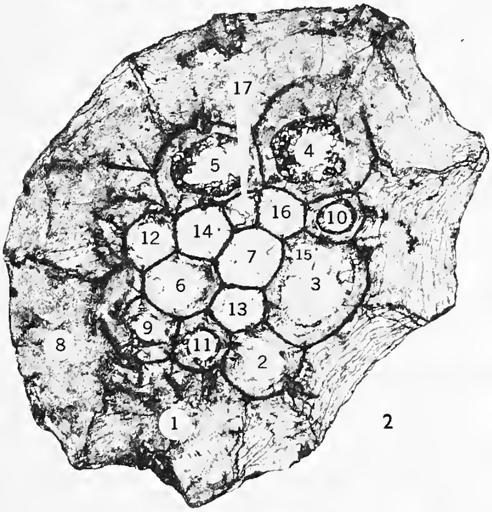

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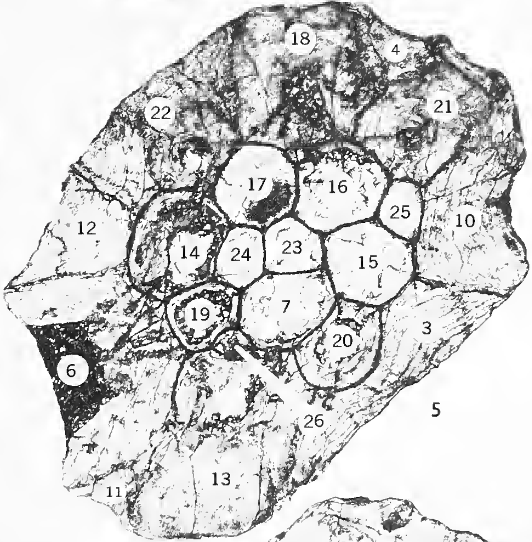

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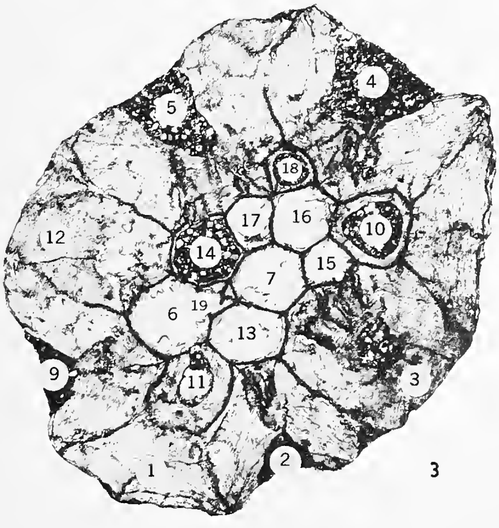

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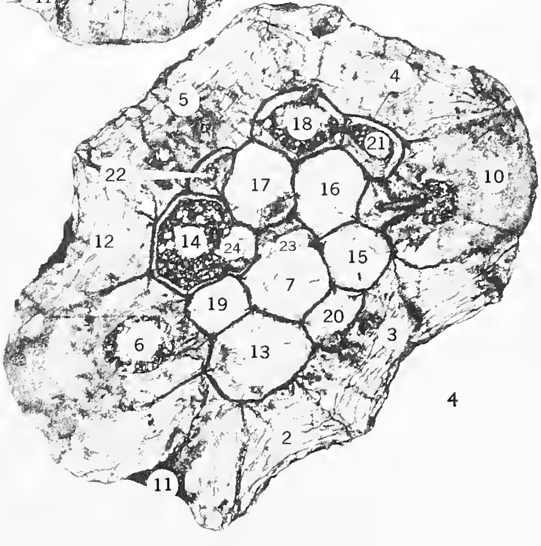

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OLIVER, *Striatopora flexuosa* Hall

bifurcation to the next. Above bifurcations, branch diameters are commonly sub-equal, although unequal in some cases. The largest known specimen is the lectotype (Pl. 68, fig. 1) with a spread of 85 mm. between the ends of the two main branches.

Corallite boundaries are clearly defined. Calices are broad and shallow, normally deepest near the proximal margin. Calice walls slope gently from margin to pit; in slender corallum fragments, walls tend to be concave, rising to sharp ridges which separate corallites; in more robust fragments of coralla, outer parts of calice walls are gently convex so that the marginal ridges are subdued.

Where well preserved, calices are marked by low, broad septal ridges radiating from the axial pit; these are best developed on more robust fragments of coralla. In the few calices where septa can be counted with any degree of certainty, they are 12 in number.

The number of corallites was counted on the outer surface of five branch fragments with counts ranging from 2·9 to 4·5 corallites per mm. of branch length. This agrees with counts of 4·4 and 3·6 new buds per mm. in two serially sectioned branches. The variation between specimens indicates differences in rates of budding relative to rates of skeletal accretion and probably represents varying environmental conditions.

Internal features. Corallites originating near the axis of the corallum (**a**-corallites) extend upward and outward, initially at very small angles to the axis; distally, these corallites turn away from the axis and intersect the surface at angles of 60 to 80 degrees. **b**-corallites originate in the zone where the outward bending of earlier corallites takes place; these expand more rapidly and are initially at a high angle to the branch axis. Corallite walls consist of a very thin dark granular layer (epitheca of some workers) which separates corallites, and a light lamellar layer which is very thin near coralla axes, but which thickens with growth and is very thick peripherally. Mural pores are common at all stages of corallite growth; in thickened walls they appear as tunnels with lengths several times their diameters. In places, a low ridge surrounds the pore on one side of the wall (e.g. Pl. 70, fig. 5).

Tabulae are thin, complete, and irregularly spaced, composed of a dark, basal tissue overlain by varying thicknesses of light-coloured stereoplasm in lamellae continuous with those of the wall. They are commonly not at right angles to the axis or walls of the corallite but are inclined away from the branch axis.

Septa are irregular in their appearance and occurrence. They are rare in thin-walled parts of corallites, common in thick-walled parts. They appear to be low, broad ridges or spines projecting into the lumen, formed by the inward bending of the wall laminae, which are continuous around and through the septa.

Microstructure of the dark wall layer is obscure. The light tissue is distinctly lamellar parallel to the inner surface of the corallite wall.

Remarks. As the description indicates, two more or less distinct zones can be recognized in sections through or at right angles to the corallum axes. An inner zone is characterized by corallites having small total diameters, thin walls, occurring at low angles to branch axes, and being polygonal in internal cross-section. The outer zone has corallites having large total diameters, and thick walls; these corallites occur at high angles to branch axes and are circular in internal cross-section. Transverse sections of mature parts of corallites are seen in sections tangential to the branches (Pl. 70, figs. 1, 2).

Slender corallum fragments (diameters 3–4 mm.) apparently represent portions of colonies with minimal development of outer zone characters. The portion of the lectotype that was removed for thin sectioning was from a slender part of the right-hand branch (Pl. 68, fig. 1) near a growing tip and shows the characters of corallites in an early stage of 'maturity' (Pl. 68, figs. 3, 4). Although not sectioned, the oldest part of the holotype specimen is more robust, with larger corallites and thicker walls. The paralectotype illustrated on Plate 69 and Plate 70, figs. 1 and 2, is robust and shows full development of 'mature' characters. Note that the lectotype thin sections are illustrated at ×20 whereas the others are at ×10. Presumably corallite growth was continuous, and branch robustness and 'maturity' are a function of corallite age and environmental conditions.

Material. Lectotype, AMNH 1685:1; paralectotypes illustrated by Hall, 1685:2, :3; other paralectotypes, 1685:4–:8; 12 topotype fragments, USNM 114214; illustrated topotypes from the same collection have been renumbered USNM 146505 and 146506.

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A PHYLLOCERATID AMMONITE FROM THE SPEETON CLAY (LOWER CRETACEOUS) OF YORKSHIRE

by P. F. RAWSON

ABSTRACT. *Hypophylloceras* cf. *perlobatum* (Sayn) is described and illustrated. It is the first phylloceratid ammonite to be recorded from the Neocomian of Britain.

IN Europe during the Lower Cretaceous period, the phylloceratid ammonites were essentially restricted to the Tethyan faunal province, and few specimens have been recorded from more northerly areas. In Britain, Spath (1923, pp. 15–20) described a few specimens of *Phylloceras subalpinum* (d'Orb.) and *Hypophylloceras seresitense* (Pervinquière) from the Gault but no phylloceratids have been recorded from the Lower Greensand (Casey 1960, p. xxxv) or from earlier Cretaceous beds. Outside Britain few phylloceratids have been described from the Neocomian Boreal province. Von Koenen (1902, p. 39) recorded one specimen of *Phyllopachyceras* aff. *winkleri* (Kilian) from the Lower Hauterivian Radiatus Zone of North Germany, and Donovan (1953, p. 100) described a single specimen of *Phylloceras* sp. from the Middle Valanginian of Traill Island, East Greenland.

Recent collecting at the type locality of the Speeton Clay in Filey Bay, Yorkshire, has yielded a specimen of *Hypophylloceras* cf. *perlobatum* (Sayn) from bed C8 of the Lower Hauterivian. Its occurrence in this bed is of particular interest as several other genera of Tethyan affinity found at Speeton are first recorded at this horizon, including *Lytoceras* (C. W. Wright collection), *Eodesmoceras*, *Spitidiscus*, and rare crioceratids. The crioceratids become much more common in the overlying bed C7.

The specimen is deposited in the author's collection in the Department of Geology, the University of Hull, catalogue number HU.C/Rn.460.

SYSTEMATIC DESCRIPTION

Family PHYLLOCERATIDAE Zittel 1884
Subfamily PHYLLOCERATINAE Zittel 1884
Genus HYPOPHYLLOCERAS Salfeld 1924
Hypophylloceras cf. *perlobatum* (Sayn)

Plate 72, figs. 1–3; text-fig. 1*a*

Cf. 1901 *Phylloceras serum* Oppel var. *perlobata* Sayn (p. 7, fig. 3, pl. 1, figs. 6–8).

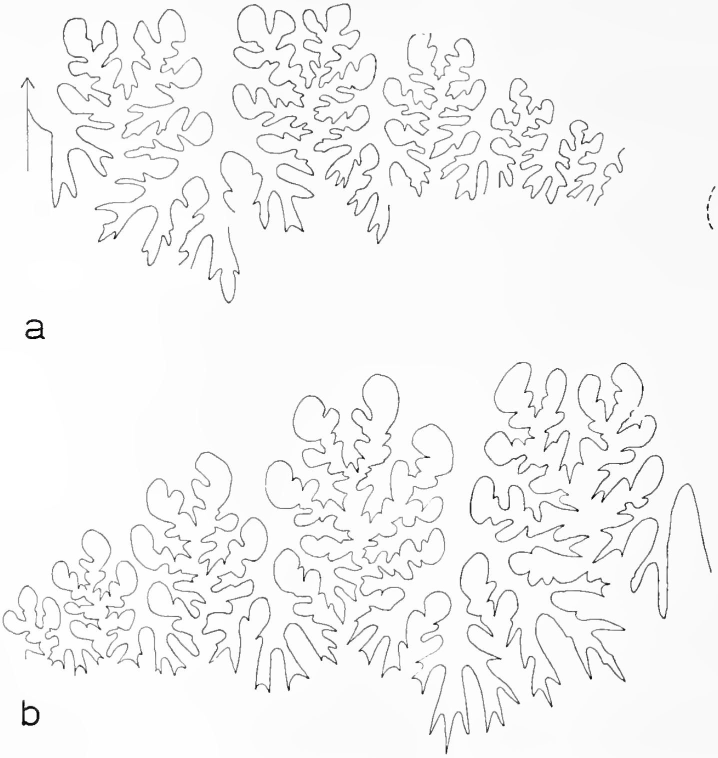
Description. The specimen is a wholly septate pyritized nucleus, with fragments of the original shell preserved. The test is compressed and involute, with a steep umbilical wall. The whorl flanks are flat, even near the umbilical edge, and the venter rounded. The shell is covered with fine, dense, and slightly sinuous striae, which cannot be seen on the internal mould. The suture (fig. 1*a*) is complex; the first lateral lobe is asymmetrical and

[Palaeontology, Vol. 9, Part 3, 1966, pp. 455–7, pl. 72.]

much larger than the ventral and second lateral lobes, and the saddle endings are tetraphyllic.

Dimensions: Maximum diameter: 31·5 mm.; at diameter of 28·2 mm., whorl height 16·9 mm. (59·9%), thickness 9·5 mm. (33·7%), width of umbilicus 2·0 mm. (7·1%).

Remarks and Affinities. The classification of the Phylloceratid ammonities at generic and subgeneric level fluctuates considerably from author to author, but most recent authorities (for example Arkell 1957, and Wiedmann 1963) place the compressed, finely ribbed species with tetraphyllic saddle endings and asymmetrical lobes in *Hypophylloceras.* It is this more complex suture-line which distinguishes *H.* cf. *perlobatum* from *Phylloceras serum* and allied species which resemble *H.* cf. *perlobatum* in general form and sculpture.



TEXT-FIG. 1. *a*, Suture-line of *Hypophylloceras* cf. *perlobatum*, HU.C/Rn.460. *b*, Suture-line of *Hypophylloceras perlobatum*, reproduced from Sayn (1901, p. 8, fig. 3). Both figures × 6.

Few species of *Hypophylloceras* have been described from the Valanginian and Hauterivian of the Tethyan province, so that it is very difficult to make a close comparison with other forms.

EXPLANATION OF PLATE 72 (continued on p. 460)

Figs. 1–3. *Hypophylloceras* cf. *perlobatum* (Sayn). Lateral and ventral views. HU.C/Rn.460, × 2.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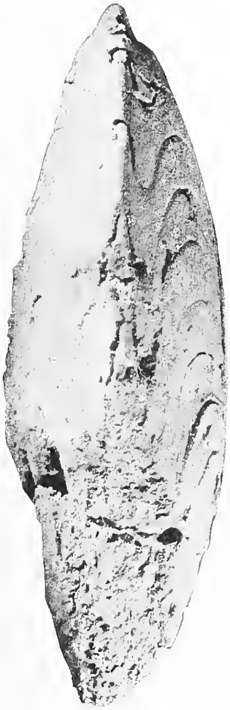
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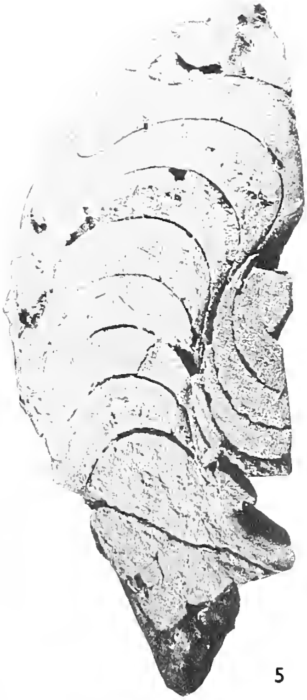
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RAWSON, *Hypophylloceras* from the Speeton Clay
JENKINS, *Cheiloceras* from New South Wales

The Valanginian specimens of *H. perlobatum* figured by Sayn are closely similar to the Speeton form. Sayn's drawing of the suture is reproduced in text-fig. 1*b*. It can be seen that the terminal folioles of the second lateral saddle are only slightly subdivided, while those of the present specimen are more strongly tetraphyllic. The minor differences between the two suture-lines could be accounted for by specific variation.

Phylloceras spathi Collignon (1949, p. 63) from the Hauterivian of Madagascar, compares closely in the degree of flattening of the whorl flanks, but the suture line is insufficiently known for closer comparison to be made.

From the Barremian of Algeria, Busnardo (in Busnardo and David 1957, p. 86) has described *Hypophylloceras barremense*, which is slightly more inflated than *H.* cf. *perlobatum.* The sutures of the two forms are very similar, but the terminal folioles of *H. barramense* are more elongate. *H. betieri* (Busnardo) (op. cit., p. 84) is a form with marked flattening of the flanks, but the terminal folioles are even more elongate: this is a feature typical also of the more numerous Aptian, Albian, and Upper Cretaceous species of *Hypophylloceras*, such as *H. seresitense* (Pervinquière), with which *H.* cf. *perlobatum* could otherwise be compared.

Stratigraphical horizon: Lower Hauterivian, Radiatus Zone, Sulcosa Subzone. Bed C8, 2 ft. below the top and approximately 6 ft. above the base, in Middle Cliff, Speeton.

Acknowledgements. This paper forms part of a larger study of British Valanginian and Hauterivian ammonites being carried out during the tenure of an S.R.C. Research Studentship. I thank Professor D. T. Donovan and Mr. C. W. Wright for helpful discussion and advice, Dr. J. W. Neale and Mr. C. W. Wright for reading the manuscript, and Mr. B. Nettleton for assistance with photography.

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THE UPPER DEVONIAN INDEX AMMONOID *CHEILOCERAS* FROM NEW SOUTH WALES

by T. B. H. JENKINS

ABSTRACT. *Cheiloceras acutum* (Münster) from a presumed equivalent of the Baldwin Formation (Upper Devonian) near Tamworth, N.S.W. is described as the first occurrence of this index genus in eastern Australia.

AMMONOID cephalopods of Devonian age are very rare in eastern Australia. Teichert's (1948) description of goniatites from the Buchan district of Victoria was the first authentic report of Devonian ammonoids from eastern Australia, previous records being probably erroneous (Teichert 1943). Subsequently, Pickett (1960) has described a new species of clymenid and a doubtful *?Platyclymenia* from different horizons in the Upper Devonian of northern New South Wales. Taxonomic work by Erben (1960) has indirectly contributed to a revised view of the correlation of Teichert's Buchan goniatites (Philip and Pedder 1964), but there have been no further records of Devonian ammonoid discoveries in eastern Australia. The present note is thus only the third such published record. A fourth occurrence is mentioned herein and will shortly be documented.

The goniatites here recorded were found near Keepit Dam (see text-fig. 1), a recently completed structure on the Manilla (or Namoi) River between the towns of Manilla, Tamworth, and Gunnedah. A reasonably complete statement of the regional geology of the surrounding country has been achieved by the work of several authors summarized by Voisey and Williams (1964) and White (1964, 1965). The present writer has mapped formations in detail through a north–south belt which includes Keepit Dam.

The dam lies on the western limb of the long submeridionally trending syncline which, by reversals of plunge, forms the closed Werrie and Belvue Basins. Dips are consistently 40° to 50° at N. 30° to 55° E. within the area of text-fig. 1, and only minor faulting occurs. The succession is broken by a disconformity at the base of the Carboniferous strata, with the lowest Carboniferous formation overstepping northwards on to lower beds within the Upper Devonian. Evidence from fossil ammonoids points to the absence hereabouts of the upper half of the Upper Devonian.

There is also a possibility of an erosional break lower in the Upper Devonian, at the base of what has been called the Keepit Conglomerate, but there is no local evidence for an angular unconformity at this horizon such as has been claimed for adjacent areas (White 1964, 1965).

Below the Keepit Conglomerate the Upper Devonian succession near the dam consists chiefly of volcanic detritus. It contains a thick unit, over 2,000 ft., of alternating shales and tuffs which yield marine fossils (including *Cheiloceras*) at the level indicated in text-fig. 2.

Described specimens are in the fossil collection of The University of Sydney Geological Department and are referred to by USGD catalogue numbers.

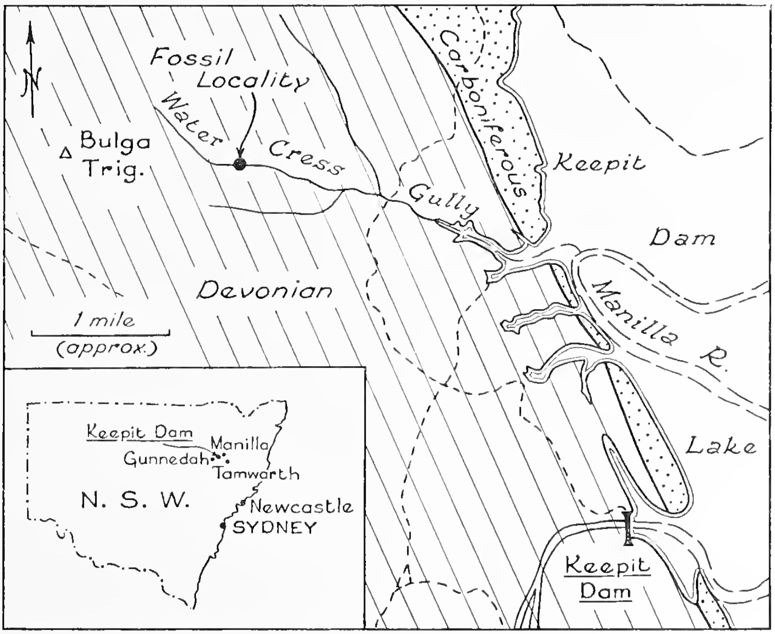
[Palaeontology, Vol. 9, Part 3, 1966, pp. 458–63, pl. 72.]

SYSTEMATIC DESCRIPTION

Superfamily CHEILOCERATACEAE Frech 1897
Family CHEILOCERATIDAE Frech 1897
Genus CHEILOCERAS Frech 1897

Type species (by subsequent designation of Wedekind 1918, p. 144): *Goniatites subpartitus* Münster 1839, p. 18 (loc. cit. fide Frech 1902, p. 69).

Remarks. The mode of division of the dorsal lobe of the suture has been mainly used to separate from *Cheiloceras* Frech 1897 the subgenera *Torleyoceras* Wedekind 1918 (?= *Staffites* Wedekind 1918) and *Dyscheiloceras* Schmidt 1921 and the genus *Paratorleyoceras* Bogoslovsky 1957, thus leaving *Cheiloceras* (*Cheiloceras*) to receive the species having an undivided, flat, or gently bowed dorsal lobe of the suture.



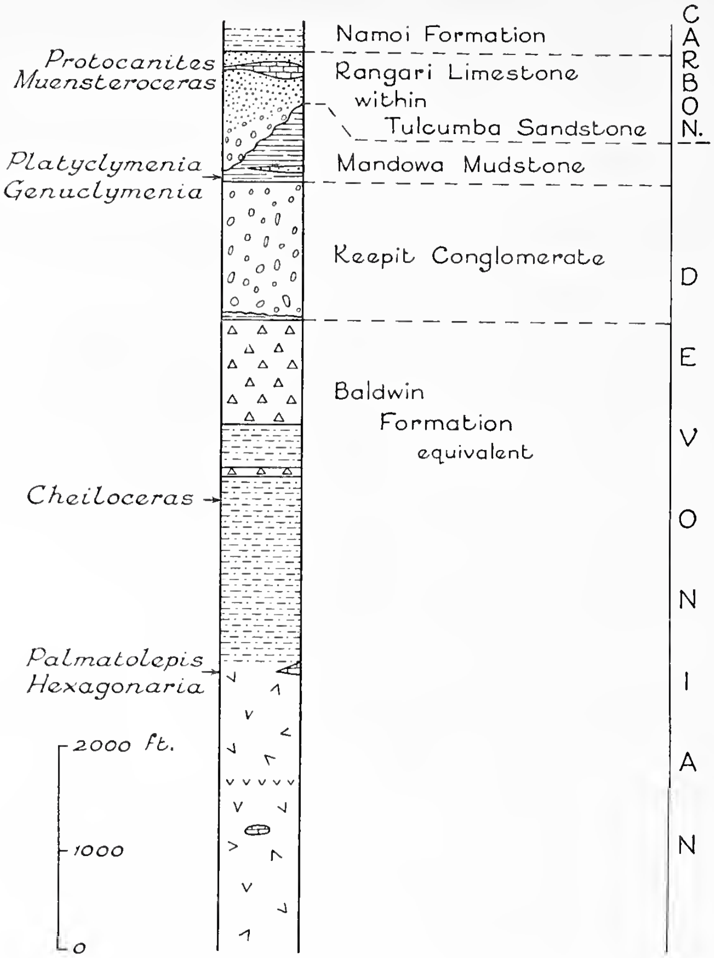
TEXT-FIG. 1. Map of Water Cress Gully locality, showing tracks.

In the southern hemisphere *Cheiloceras* is known only from Western Australia (Fitzroy Basin) but is now known from all the northern continents having been recently reported from North America (House 1962, House and Pedder 1963).

Cheiloceras (*Cheiloceras*) *acutum* (Münster)

Plate 72, figs. 4–6; text-fig. 3 *a–e*

1839 *Goniatites acutus* Münster, p. 110, pl. 16, fig. 11 (fide Frech 1902, p. 71).
1852 *Goniatites retrorsus* var. *acutus* G. and F. Sandberger, p. 108, pl. 10, fig. 10; pl. 10*a*, figs. 1, 2.
1902 *Cheiloceras acutum* Minister emend. Sandberger; Frech, p. 71, pl. (3)4, fig. 6.
1918 *Cheiloceras acutum* Sandberger; Wedekind, p. 146, fig. 46, i.
1918 *Cheiloceras acutum* Frech; Wedekind, pl. 18, fig. 7.



TEXT-FIG. 2. Stratigraphic column for the area near Keepit Dam, showing ammonoid horizons.

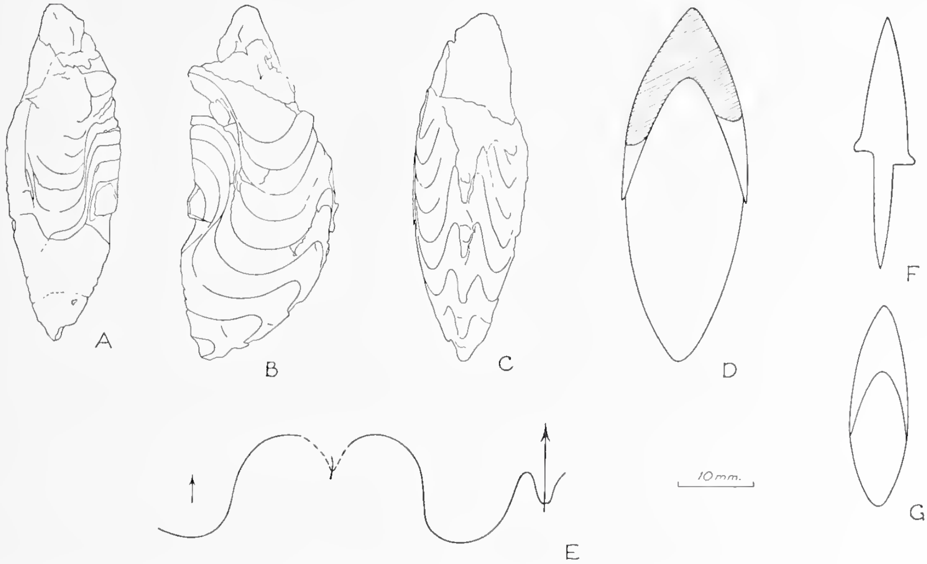
Material. One specimen, an uncrushed internal mould of a segment of the outer whorl, lacking the umbilicus but preserving the greater part of several sutures (external and internal) and a part of the body chamber.

Description. Shell form thickly lenticular with whorls deeply overlapping. Whorl sides are flatly curved and meet at an acute angle along the venter. No trace of an umbilical shoulder is to be seen. The dorsum is more broadly rounded, the flanks of the impressed area converging to a wider but still noticeable angulation. Whorl sides and the adjacent flanks of the impressed area converge very gradually towards the axis of coiling; extrapolation of the partial cross-section (text-fig. 3*d*) suggests a closed umbilicus.

EXPLANATION OF PLATE 72 (see also p. 456)

Figs. 4–6. *Cheiloceras* (*Cheiloceras*) *acutum* (Münster) from an equivalent of the Baldwin Formation in Water Cress Gully, 1·9 miles north-west of Keepit Dam, near Tamworth, N.S.W. Ventral, lateral, and dorsal views respectively of USGD6870, ×2.

Maximum dimension of the specimen is 46 mm., measured as an incomplete chord of the venter's spiral curve and ending adorally within the body chamber. Diameter of the entire shell therefore exceeded 46 mm. by an amount depending mainly on the unknown length of the body chamber. Maximum whorl width of the preserved segment is 15·1 mm.; the reconstruction (text-fig. 3*d*) shows whorl width as 16·5 mm. at a diameter of 47 mm.



TEXT-FIG. 3. *a–e*, *Cheiloceras* (*Cheiloceras*) *acutum* (Münster), based on specimen USGD6870. *a–c*, dorsal, lateral, and ventral views; *d*, cross-section, reconstructed from preserved portion shown by oblique ruling; *e*, suture. *f*, *g*, based on specimens USGD 6871 and 6872 respectively, cross-sections of two indeterminable external moulds. All × 1. All specimens from the same bed in an equivalent of the Baldwin Formation.

Sutures have six lobes, of which the pair on the umbilicus is partly inferred, the umbilicus being missing (text-fig. 3*e*). The ventral lobe and flanking saddles are narrow elements, in contrast to the broad, rounded character of other preserved sutural elements. External sutures are spirally confluent where the broad, slightly asymmetrical U-shaped lateral lobe passes into a wide, evenly rounded dorso-lateral saddle. Internal sutures are similarly confluent where the flatly rounded dorsal lobe passes into the adjacent saddle.

Remarks. In shell form and external suture *Cheiloceras acutum* (Münster) closely resembles the coeval *Tornoceras acutum* Frech so that complete internal moulds of the two species are homoeomorphic. Distinctions have been recognized on form of growth-lines and on internal sutures (e.g. Wedekind 1908, p. 585; 1918, p. 101). The internal suture of *Tornoceras acutum* Frech shows a deep, narrow dorsal lobe flanked by broader saddles (Wedekind 1908, pl. 39, fig. 4; Schindewolf 1923, p. 508). The broad, flatly rounded dorsal lobe of the present specimen is typical of *Cheiloceras* sensu stricto and resembles that of the internal suture of *C. circumflexum* Sandberger which was cited by Wedekind (1908, p. 585) as similar to that of *C. acutum*.

Petter (1959, p. 195) has pointed out that *Tornoceras iowaense* Miller 1938 may belong to *Cheiloceras acutum* since neither its internal suture nor its growth-lines have been recorded.

The specimen here described is the largest heretofore figured as, or authentically assigned to, *Cheiloceras acutum*. Lange (1929, p. 36) records a specimen 90 mm. in diameter but indicates doubt on generic allocation. The venter of the described specimen is somewhat more acute than that of other figured specimens of *C. acutum* but since whorl shape changes with growth to a more acute form of venter, this constitutes no objection to the specific allocation (cf. Sandberger 1852, pl. 10*a*, fig. 2).

Cheiloceras acutum seems to be previously recorded only from Germany. Wedekind noted *acutum* as a rare species of the lower portion of the *Cheiloceras* Stufe (= IIα). Lange (1929) named '*?Cheiloceras acutum*' as a zonal fossil for the lowest of three subdivisions of the *Cheiloceras* Stufe.

Other material. Two indeterminable external moulds of coiled cephalopods were found in the bed of tuff which yielded *C.* (*C.*) *acutum*. The cross-section of one of these external moulds (text-fig. 3*a*) may be compatible with an immature stage of *C.* (*C.*) *acutum*. The other mould is a slightly asymmetrical oxycone (text-fig. 3*f*) with an umbilical structure somewhat similar to that figured by Clarke (1899, p. 112) for *Tornoceras uniangulare* (Conrad), i.e. the umbilical lip is produced laterally giving a small spiral prominence on the axis of coiling.

Horizon and locality. The specimens were found in Water Cress Gully, 1·9 miles north-west of Keepit Dam, which is on the Manilla (= Namoi) River, between Tamworth and Gunnedah in northern New South Wales. The fossil locality is in shaly volcanic tuff, a presumed equivalent of the Baldwin Formation. According to local inhabitants it is close to the spot whence Mitchell (1921, 1924) described *Merista plebeia* Sowerby and other brachiopods. The horizon is some 3,000 ft. below another ammonoid bed with *Platyclymenia* and *Gonioclymenia*, indicating *Platyclymenia* Stufe and strongly suggesting an expanded stratigraphic succession. The bed with *Cheiloceras acutum* is some 1,700 ft. above the highest known local occurrence of the conodont *Palmatolepis*.

Acknowledgements. The writer thanks Dr. B. F. Glenister, State University, Iowa, U.S.A. for helpful correspondence and acknowledges financial assistance from the University of Sydney Research Grant.

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SCHIZOCHROAL EYES AND VISION IN SOME PHACOPID TRILOBITES

by E. N. K. CLARKSON

ABSTRACT. Some aspects of vision in nine species of phacopid trilobites are described. Methods of study, which primarily consist of the investigation of the morphology of the visual surface and the extent and nature of the visual field, are identical with those of previous work.

Divergent interpretations of intraspecific variation in the lens number of *Phacops sp.* are discussed and sexual dimorphism is advanced as a tenable hypothesis. Phacopids generally have a fixed pattern of lens distribution, though the individual lens formation and arrangement varies in different species.

Individuals within a species have visual fields of similar extent and type, regardless of dimorphism. In different species, however, there is wide variation in visual type, largely as a result of distinct modes of curvature of the visual surface, affecting the angular bearings of the lens-axes.

Three principal visual types are distinguished, presumably reflecting adaptations to distinct ecological conditions. In the first, the visual field has a relatively wide vertical range and the eye is slightly astigmatic; in the second there is much greater astigmatism and a narrower visual field; the third type combines features of the other two.

INDIVIDUAL phacopid trilobites are sometimes found in an excellent state of preservation, showing no distortion and retaining their original convexity. Such specimens are of great value for functional as well as for morphological studies, since it is often possible to interpret exoskeletal structures or organs in terms of adaptive morphology. The methodology of such functional interpretation of fossil structure is fully discussed by Rudwick (1964).

Recently the author studied the eyes and some aspects of vision in a small group of well-preserved Silurian trilobites (Acastinae) (Clarkson 1966*a*). Some other phacopids, of ages ranging from Ordovician to Devonian, have also been studied and the results of these investigations are presented here. The chief limitation to this work has been the difficulty in obtaining enough perfectly preserved material; only a few adult specimens of each species were available. The methods of approach were the same as in my previous work because the material consisted of museum specimens which could not be sectioned. These methods include detailed descriptions of the external visual surface, the size and distribution of the lenses, the angular extent of the visual field, and the nature of vision as deduced from the manner in which the axes of the individual lenses are distributed within the visual field.

This information gives some conception of trilobite visual processes but needs to be supplemented by further work, and in particular by the study of the internal structure of the eyes of well-preserved specimens. The only significant research on this subject hitherto was undertaken by Lindström (1901), who obtained little information about the sublensar structure of schizochroal eyes.

Techniques of study are identical with those described in my former work. The same terminology has been retained throughout, apart from the use of the term 'genal field' proposed by Shaw and Ormiston (1964) which is substituted for 'eye platform' as used by Harrington *et al.* in the 'Treatise'.

[Palaeontology, Vol. 9, Part 3, 1966, pp. 464–87, pls. 73–75.]

The material examined includes the following species:

1. Superfamily Phacopacea. *Phacops rana* (Green), Devonian of New York State; *Phacops fecundus* Barrande, Silurian, Bohemia; *Phacops breviceps* Barrande, Devonian, Bohemia; *Phacops latifrons* (Bronn), Devonian, Germany (briefly referred to); *Phacops batracheus* Whidborne, Devonian, S.W. England; *Phacops boecki* Hawle and Corda, Devonian, Bohemia.
2. Superfamily Dalmanitacea. *Dalmanites vulgaris* (Salter) and *Dalmanites caudatus* (Brünnich), Silurian, Dudley, England; *Chasmops odini* (Eichwald), Ordovician, Estonia.

The eyes of some of these species are quite well known and have been described by systematic palaeontologists. The existing accounts of their morphology are referred to throughout but since a clear understanding of the function of any organ depends so greatly upon detailed knowledge of its structure, it has been necessary to supplement these short accounts by fuller descriptions.

The eye and its position upon the cheek are of great importance in phacopid taxonomy, and certain matters of taxonomic interest came to light in the course of this study. An example of this is the variation in lens number between adults of an apparently single species, which at least in the case of the genus *Phacops* led to divergent interpretations of systematic relationships. But although much phacopid taxonomy is rather confused, any attempt at systematic revision of the species in question would be beyond the scope of the present work. Hence existing systematic categories are used, even though some of these are known to be unsatisfactory. Such taxonomic problems as were encountered are, however, noted and described in full.

Owing to the relative scarcity of perfect specimens it has been possible to analyse only one or two adults of each species, and comparatively few other individuals were normally available for comparison. It has been already established that the number of lenses per eye and their distribution may vary considerably within a species. These factors are related to the size of the specimen and in some cases to sexual dimorphism (Clarkson 1966*a*). The problem thus arises as to how far the specimens examined are representative of the species as a whole.

This problem, as shown below, is rather complex, and in the absence of full growth stages cannot fully be eliminated. I have endeavoured to minimize it as far as possible by the following procedures: (*a*) by selecting only large sized specimens showing the most obviously adult features, (*b*) by comparison with other material and previously published descriptions, particularly in the case of the Bohemian material exhaustively described by Barrande, and (*c*) by distinguishing dimorphs where the supply of specimens was adequate.

It is worth noting that in spite of the variation in lens number, etc. within a species, the angular range of vision described for single specimens appears to be fairly constant for the species as a whole, whatever the stage of development. Increase in lens number with age does not lead to an increase in the angular range of vision. In *Acaste downingiae* (Murchison) and in *Phacops fecundus* Barrande, enough specimens were available to demonstrate that the surface curvature of the eye is established at an early stage in post-larval development, and remains much the same though the visual surface grows while new lenses are added. This leads to a larger number of lens axes covering the same area.

A short discussion of the variation in the eyes of *Phacops* is given in the next section.

FUNCTIONAL DESCRIPTIONS OF EYES

Superfamily PHACOPACEA

Variation in the eyes of Phacops *s.s.* The eyes of various species of *Phacops* s.s. have been studied in somewhat greater detail by previous authors than have those of other Phacopina. Among the best known of all are those of *Phacops rana* (Green) where the variation present has led to divergent taxonomic and developmental interpretations. This confusion is illustrated by the following history of research upon the eyes of *P. rana*.

1. A very detailed account of the morphology and development of the eyes of *P. rana* was given by Clarke (1889). From observations of the number, and manner of development of the lenses in specimens of various sizes, he concluded that lens number increased from youth to maturity following a constant pattern of development, and then declined again from maturity to senescence. This decline, as he stated, could have taken place only by the sclerosis of the lenses, or by their absorption by the palpebral lobe.

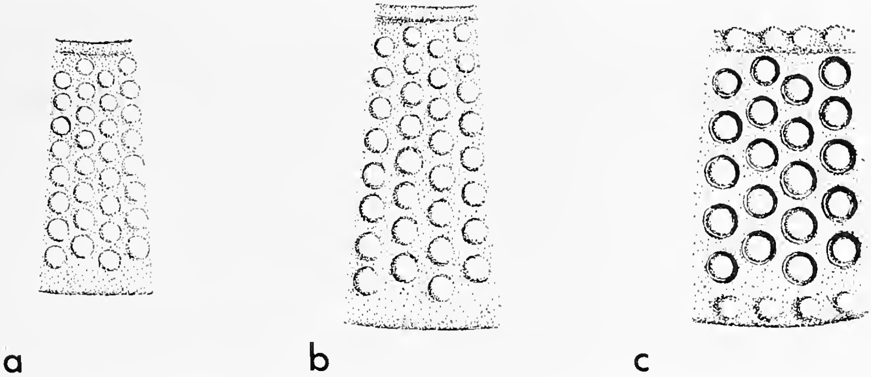
2. Beckmann (1951) worked principally upon the development of the eyes of *P.* cf. *breviceps* and *P. schlotheimi* from Germany, but referred also to *P. rana*. In the German species he found an increase in lens number from youth to maturity but no gerontological decline. He gave strong evidence that two forms of *P. rana* had been confused by Clarke, one with a larger adult number of smaller lenses than the other. The author's studies of acastid eyes (Clarkson 1966*a*) gave a general agreement with Beckmann's conclusions; two variant eye forms were distinguished and tentatively attributed to sexual dimorphism.

3. Systematic revision of the species *P. rana* by Stewart (1927) and Stumm (1953) led to the erection of several subspecies. The principal diagnostic features on which these subspecies were distinguished included the overall structure of the eye and the number and arrangement of the lenses, though neither author referred to Clarke's work. Typical eyes of all these subspecies were figured by Stumm.

A similar variation occurs in several species of *Phacops* related to *P. rana*. Barrande's (1852) observations on Bohemian phacopids were not mentioned by Clarke, but in many respects they are quite comparable. Barrande's fullest descriptions (1852, p. 514) were of the eyes of the common Bohemian species *P. fecundus*. With his anatomical studies he included a table showing the number and distribution in files of the lenses in the eyes of twelve specimens in various stages of development. In these the maximum number of lenses per eye ranged from 64 to 136. Barrande noted that the number of lenses depended upon the size of the specimens, but was also partially controlled by the particular conformation of the eyes of each individual. None of the largest specimens possessed the maximum number of lenses, but they did exhibit a higher degree of scleral inflation and a relatively wider degree of spacing of the lenses. He also figured the eyes of three specimens of *P. fecundus major*, reproduced here (text-fig. 1), which if considered as growth stages would indicate an exactly comparable situation to that described by Clarke, i.e. an apparent decrease of the lens number with senescence. Very large specimens of *P. breviceps* and *P. latifrons* again have larger, fewer, and more widely spaced lenses than smaller specimens.

The nature of eye-variation in *P. rana* and in all these other species is therefore a matter of some uncertainty, and has been variously interpreted by these different authors firstly as the result of a peculiar developmental pattern; secondly as ecological or sexual dimorphism; and thirdly as merely natural subspeciation.

At present the state of taxonomic confusion of the genus *Phacops* renders it difficult to distinguish the most probable of these alternatives. It is quite likely that more than one factor is involved. Abandonment of Clarke's hypothesis is, however, strongly advocated by Beckmann's work, and this conclusion is substantiated by the extreme variability of *P. rana* as shown by its number of possible subspecies. The similarity between the different eye-variants of *P. rana* and those of related species would indicate, nevertheless, that natural subspeciation could be complicated by sexual dimorphism occurring in all these related species. The possibility of such dimorphism has not always been taken account of by systematists.



TEXT-FIG. 1. *Phacops fecundus major* Barrande. Parts of the visual surface of the eyes of three specimens increasing in size from *a* to *c*. The last may possibly be interpreted as a different eye-variant from *a* and *b*, hence this series may reflect a sexually dimorphic condition. (Redrawn from Barrande 1852.) (*a* ×8, *b* ×8, *c* ×6.)

It has been necessary to defer complete studies of eye development and variation within these species until such taxonomic revisions have been made which would provide a sounder basis for such studies. The purpose of the present study is to show something of the range of visual types within phacopid trilobites. Thus the course adopted here has been to describe and analyse functionally, as individual visual organs, one or two of the representative eye forms of each species or subspecies in question.

Phacops rana (Green 1832)

1832 *Calymene bufo* var. *rana* Green, p. 42.
1888 *Phacops rana* (Green); Hall and Clarke, pp. 19–26, pl. 7, figs. 1–11; pl. 8, figs. 1–8; pl. 8*a*, figs. 21–33.
1889 *Phacops rana* (Green); Clarke, pp. 253–70, pl. 21.
1940 *Phacops rana* (Green); Delo, p. 22, pl. 1, figs. 1, 2.

All available material was referred to the two subspecies *P. rana milleri* Stewart and *P. rana crassituberculata* Stumm. Stumm remarks that the only characters whereby the subspecies may be distinguished are the structure of the eyes and their number of lenses. It is therefore of particular interest to compare the functional characteristics of their eyes.

Phacops rana milleri Stewart 1927

Plate 73, figs. 10–11; text-fig. 2 *d–f*

1927 *Phacops rana* var. *milleri* Stewart, pp. 58–60, pl. 5, figs. 14–17.
1940 *Phacops rana* var. *milleri* Stewart; Delo, p. 23, pl. 1, fig. 3.
1953 *Phacops rana milleri* Stewart; Stumm, pp. 137–8, pl. 9, figs. 1–4, pl. 10, figs. 1–10.

A single adult specimen, SM H 6033, from the Hamilton Group, Devonian, Western New York State, was analysed. Both eyes are preserved, the left is slightly warped, the right is in perfect condition apart from the very bottom of the central region, which is slightly dislodged from its true position. The external morphology of the specimen accords with *P. rana milleri* but there are slightly fewer lenses than in *P. rana rana* which has 104–124. Nevertheless the comparative diameters and the degree of spacing of the lenses is identical with Stewart's type specimens.

Eye morphology (left eye SM H 6033). Dimensions of eye: L. (max.) 7·5 mm. (min.) 5·8 mm.; W. (max.) 4·8 mm. (min.) 4·0 mm.; H. 4·8 mm., where cephalic length (sag.) is 14 mm. and breadth 26 mm.

Eye large and prominent, occupying much of the upper part of the librigena, about half the length and two-thirds the total height of the cephalon but not rising quite as high as the crown of the glabella. The anterior and posterior edges lie approximately in the same exsagittal plane. The eye, which is in the form of a lunate segment of a cone, stands out laterally from the librigena, its base being bounded by a deep groove. In plan the visual surface is rather flattened anteriorly, but very sharply reflexed behind; in profile, the lower part of visual surface again is flattened but the curvature increases upwards, becoming very strong just below the facial suture. Palpebral lobe broad (*tr*), coarsely tubercular, slightly inflated, rising gently from the narrow rim above the facial suture, and declining to the distinct palpebral furrow. Palpebral area lying below the level of lobe, open posteriorly and continuous with surface of librigena.

Lenses disposed in 17 files, which diverge ventrally at a moderate angle, as follows:

466 767 676 655 442* 2* 2; Max. 7; Total 84. (* denotes irregularity.)

(The lower ascending diagonal row is complete apart from the bottom lenses of rows 15 and 16. If this row were unbroken, as would probably be the case in a more normal eye, there would be 86 lenses.) Lenses rather widely spaced between files, but within each file the lowermost lenses are almost contiguous, the spacing increasing upwards so that the top lenses are quite far apart. Lens diameters: Maximum 0·5 mm. (in the upper lenses of

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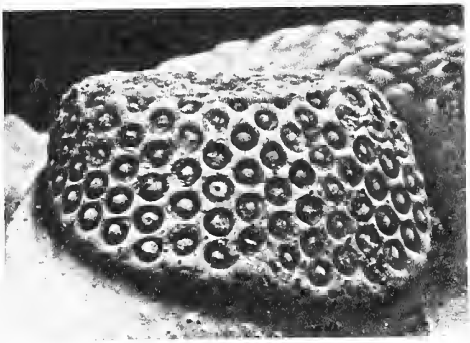
EXPLANATION OF PLATE 73

Figs. 1–4. *Phacops rana crassituberculata* Stumm. SM H 7259. Silica Formation, Devonian, Lucas Co., Ohio. Right and left eyes in lateral and dorsal aspects. × 5.

Figs. 5, 6. *Phacops latifrons* (Bronn). SM H 4840. Devonian, Rhineland. Right eye in dorsal and lateral aspects. × 5.

Figs. 7–9. *Phacops fecundus* Barrande. SM A 49374. Stage E_2, Silurian, Dlauha Hora, Bohemia. 7, Central region of the left eye, showing irregular distribution of the lenses. × 25. 8, 9, Left eye in lateral and dorsal aspects. × 5.

Figs. 10, 11. *Phacops rana milleri* Stewart. SM H 6033. Hamilton Group, Devonian, New York State. Right eye in lateral and dorsal aspects. × 5.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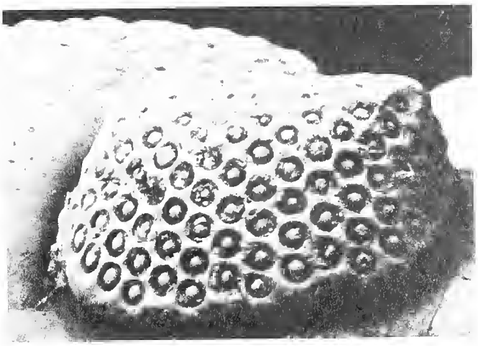
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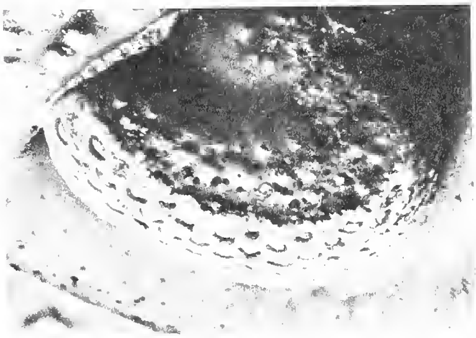
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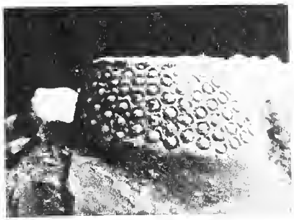
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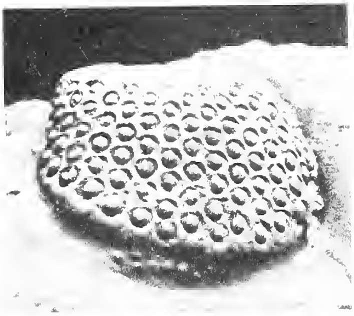
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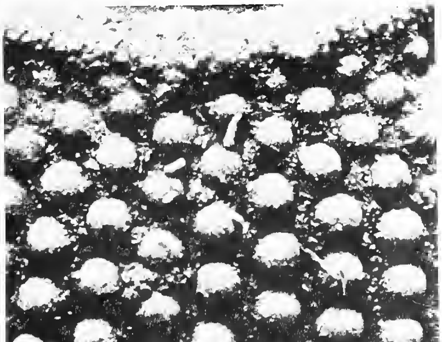
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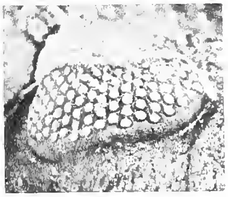
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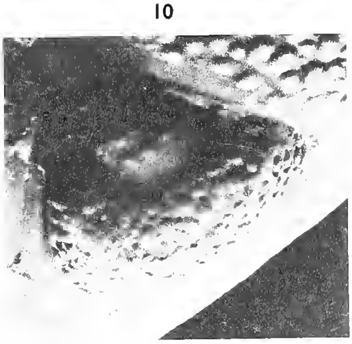
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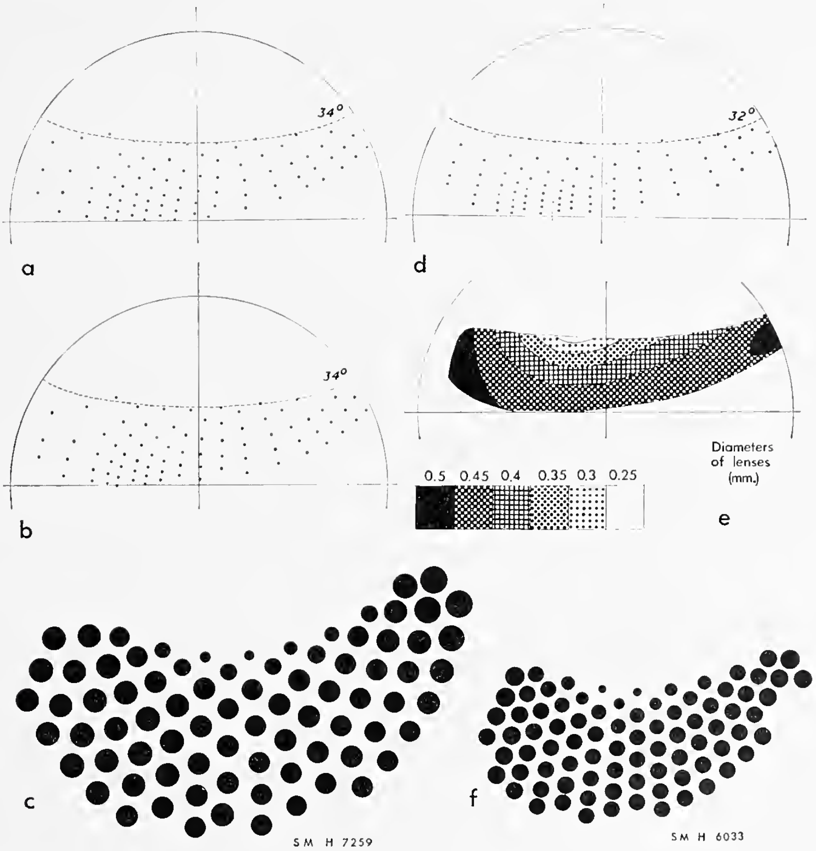
CLARKSON, Schizochroal eyes in phacopid trilobites

the first and last few files), average 0·4 mm. (in the central files), minimum 0·2 mm. (in the centre of the upper horizontal row). Apart from in the latter region and in the first and last files, the lens diameters are fairly constant.

Interlensar sclera only slightly inflated, generally giving the appearance of indistinct intersecting hexagons but flattened above the upper horizontal row, so that the upper rim of the inflated part of the sclera appears undulose, with each lens of the upper row lying in a trough. Each lens is situated in a shallow crater-like depression, above which the crown of the lens just projects, but in the posterior few files these depressions become shallower so that the bases of the lenses are almost flush with the surface of the sclera. All the lenses of the upper horizontal row are set at an angle to the surface of the sclera so that their axes have a lower latitudinal bearing than would be expected from the declination of the surface of the eye.



TEXT-FIG. 2. *a–c. Phacops rana crassituberculata* Stumm. SM H 7259. *a*, *b*, Stereograms showing visual fields of left and right eyes respectively. *c*, Projected visual surface of left eye (× 5). This eye has one more lens (file 9) than the right eye and the bottom lens of file 8 is slightly displaced. *d–f. Phacops rana milleri* Stewart. SM H 6033. *d*, Stereogram of right eye. *e*, Contoured stereogram showing coverage of different regions of the visual field by lenses of various sizes. *f*, Visual surface of right eye (× 5).

Character of visual field. The maximum range of vision is 16–184° longitudinally and 0–32° latitudinally. The upper visual limit is latitudinal, but the elevation of the lens-axes of the lower ascending diagonal row increases posteriorly, hence there is a postero-ventral lacuna in the potential visual field. The coverage of different regions of the visual field by lenses of various sizes is shown in text-fig. 2*e*.

The strong differentiation in the curvature of certain regions of the visual surface in plan and profile results in a high concentration of lens-axes in the lower region of the visual field between 45° and 80° long., which is covered by files 3–10. Here the longitudinal axial angles average 6°, but increase anteriorly to 14°, and posteriorly where the curvature is extreme, to 20°. Latitudinal axial angles about 3° in the region of maximum concentration, increasing upwards to 14°; in other parts of the visual field averaging 10°. The axes of the lenses of the upper horizontal row are latitudinal, those of the lower rows are sublatitudinal.

Whereas in each of the anterior and central files, the lens-axes all have about the same longitudinal bearing, in the posterior files there is a marked change in axial direction from top to bottom, and this arrangement of lens-axes enables a considerable angular range to be covered with a maximum economy of lenses.

Phacops rana crassituberculata Stumm 1953

Plate 73, figs. 1–4; text-fig. 2 *a–c*

1953 *Phacops rana crassituberculata* Stumm, pp. 136–7, pl. 9, figs. 5–13, pl. 10, figs. 19–21.

The available material was an enrolled and complete topotype, SM H 7259, of very large size with both eyes perfectly preserved.

Eye morphology (SM H 7259). Dimensions of eyes: L. (max.) 11 mm. (min.) 8 mm.; W. (max.) 5·5 mm. (min.) 4·5 mm.; H. 6 mm., where cephalic length (sag.) is 22 mm., and breadth 38 mm.

The chief morphological differences between the eyes of this subspecies and *P. rana milleri* consist only of the relative size of the eye, the number and arrangement of lenses, and the degree of inflation of the sclera. The lenses in SM H 7259 are disposed as follows in 18 files:

Right eye: 345 565 655 555 544 323; Max. 6; Total 80
Left eye: 345 565 656 555 544 323; Max. 6; Total 81

The files diverge ventrally as in *P. rana milleri*, but the lenses are much more widely and evenly spaced, and none are contiguous. Variation in lens-size in different parts of the visual surface resembles that in *P. rana milleri*. Lens diameters: Max. (posterior two files) 0·7 mm., average (central and anterior files) 0·6 mm., Min. (centre of upper horizontal row) 0·25 mm.

Interlensar sclera more highly inflated than that of *P. rana milleri*, hence all the lenses are more deeply sunken, and the depressions in which the posterior lenses lie are more profound, though less deep than those in the central region.

Character of visual field. In both eyes, the visual range is almost identical in extent with that of *P. rana milleri* in spite of the difference in arrangement of lenses (15–180°, long., 0–34° lat.), and there is a similar concentration of lens-axes anterior to the polar meridian. There is less extreme variation in latitudinal axial angles owing to the shorter dorso-ventral files; here they range from 4 to 12°. The difference in longitudinal bearing between the upper and lower lenses of the posterior files is rather higher than in H 6033, hence the rows of points indicating the axes of the lenses of these files on the stereogram appear more slanted.

Phacops fecundus Barrande 1846

Plate 73, figs. 7–9, Plate 74, figs. 3, 6; text-fig. 3 *a–d*

1846 *Phacops fecundus* Barrande, p. 46.
1852 *Phacops fecundus* Barrande; Barrande, pp. 514–18, pl. 21, figs. 1–27, pl. 22, figs. 32, 33.
1872 *Phacops fecundus* Barrande, and vars. *communis* and *degener* Barrande, pp. 24–25, pl. 13, figs. 1–14.

Variation in the eye of *P. fecundus* as described by Barrande, has already been noted (p. 466). In subsequent accounts of recorded occurrences of *P. fecundus* and varieties (Erben 1952, p. 328–30, with synonomies), no further details as to the morphology of the eyes have been given. Only one adult eye-variant has been examined. Several specimens, SM A 49374, 49375, from Stage E_2 (Barrande 1852), Silurian, Dlauha Hora, Bohemia, and others were examined. The former is the best preserved, and shows an interesting irregularity in the disposition of the lenses.

Eye morphology (left eye SM A 49374). Dimensions of eye: L. (max.) 4·3 mm. (min.) 4·0 mm.; W. (max.) 2·8 mm. (min.) 2·0 mm.; H. 2·0 mm., where cephalic length (sag.) is 12 mm., and breadth 20 mm.

Eye of moderate size, not very prominent, situated near the anterior angle of the librigena, and occupying the central third of the total cephalic length. The anterior edge almost touches the axial furrow; the posterior edge lies further from the sagittal line and is separated from the axial furrow by a broad inflated palpebral area. In this specimen the latter edge falls far short of the posterior marginal furrow, but Barrande regarded this character as variable. In profile the base of the eye lies about half way between the plane of the genal angle and the glabellar crown; the palpebral lobe lies well below the latter.

Curvature of visual surface moderate and fairly uniform, in plan slightly increasing posteriorly. Lenses set on a thickened inflated pad, which is bounded ventrally by a deep groove, and which projects laterally outwards from the librigena, but does not reach as far as the plane of the cephalic border. Outer tuberculate rim of palpebral lobe greatly thickened, projecting outwards above facial suture, and separated adaxially from the slightly inflated centre of the palpebral lobe by a smooth deep groove. Palpebral area strongly inflated, slightly higher than lobe, opening posteriorly to the outwardly declined librigena.

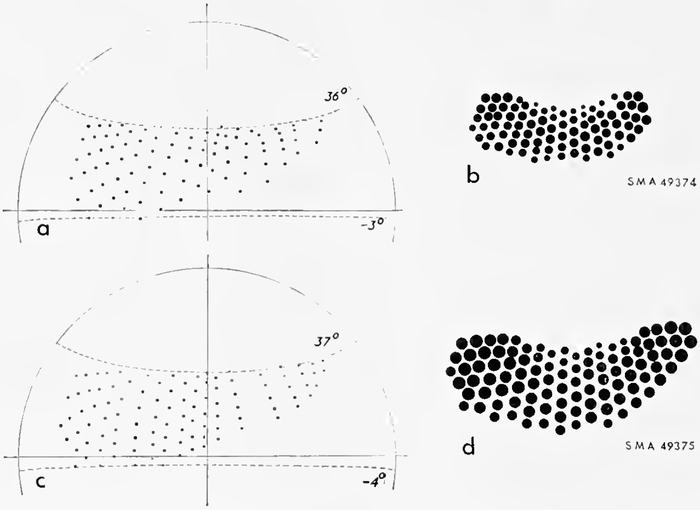
Lenses disposed in 17 files, regularly arranged apart from in the hiatus which lies between the 12th and 16th dorso-ventral files.

456 666 666 664* 655 43; Max. 6; Total 90. (* denotes irregularity.)

The first three files converge ventrally, the rest diverge at a moderate angle. Spacing of lens centres within files is almost uniform. The lens pattern is complicated by the great variation in lens size, which decreases ventrally in the outer files. Lenses of central files separated by more than a lensar radius; elsewhere they may be almost contiguous.

Largest lenses 0·25 mm., average 0·2 mm., smallest 0·1 mm. Very small lenses occur at the bottom of the diagonal rows as well as in the centre of the upper horizontal row. The former are immature. Accessory upper horizontal row present, arising in file 11, but disrupted by hiatus in files 12–16, where the upper lenses are displaced anteriorly from their true position.

Interlensar sclera hardly inflated, finely granular, with larger tubercles in places, forming irregular zigzag rows between the dorso-ventral files.



TEXT-FIG. 3. *Phacops fecundus* Barrande. *a*, *b*. SM A 49374. Visual surface of left eye (× 5) and stereogram. The hiatus breaking up of the regularity of the lenses, and the effects of this hiatus upon the dispersal of lens-axes are visible. *c*, *d*. SM A 49375. Visual surface of right eye (× 5) and stereogram.

Text-fig. 3*d* represents for comparison the visual surface of a slightly larger specimen SM A 49375, in which the lenses (maximum diameter 0·35 mm.) are disposed regularly in 19 files as follows:

346 676 767 667 665 543 2; Max. 7; Total 102.

Character of visual field. In SM A 49374 the maximum visual range is 27–150° longitudinally, and —3 to 36° latitudinally. A large postero-ventral lacuna is present. The lens-axes are dispersed more uniformly than in *P. rana*, except for the region of the described hiatus. Axial separations in both directions range between 4 and 7°, increasing slightly posteriorly and ventrally. The visual field of SM A 49375 is very similar in extent, 25–153° long., and —4 to 39° lat. Owing to the larger number of lens-axes covering a visual field of similar extent to SM A 49374, latitudinal separations are slightly less and are more uniform.

Phacops breviceps Barrande 1846

Plate 74, figs. 1, 2, 4, 7; text-fig. 4 *a–e*

1846 *Phacops breviceps* Barrande, p. 71.
1852 *Phacops breviceps* Barrande; Barrande, pp. 518–19, pl. 22, figs. 24–31.
1951 *Phacops* cf. *breviceps* Barrande; Beckmann, pp. 126–41, pl. 10, 16 figs.

Barrande (1852) recorded 18–22 files per eye, each file containing 5–8 lenses (normally 7), the overall number of lenses ranging from 83–128 according to the age of the specimen. He noted that in the larger specimens the lenses were much more widely spaced and the degree of scleral inflation was greater.

Beckmann (1951) did not distinguish any notable variation in the number and arrangement of the lenses in *P.* cf. *breviceps*, but in the species defined by Barrande variation similar to that of *P. fecundus major* (text-fig. 1) occurs in different specimens found in the same beds. The two principal adult eye-variants found here are for convenience designated eye-variant A and B. Nine cephala, all from Koňeprusy Limestone, Stage F_2 (Barrande 1852), Devonian, Koňeprus, Bohemia, were examined. A specimen of average size, H 8442 (eye-variant A), and the largest specimen, SM H 8440 (eye-variant B) are described here.

Eye-Variant A (right eye SM H 8442). Dimensions of eye: L. (max.) 6·5 mm. (min.) 5·0 mm.; W. (max.) 3·5 mm. (min.) 2·0 mm.; H. 3·0 mm., where cephalic length is 10 mm. and breadth 22 mm.

Eye medium-sized, quite prominent, visual surface extending from the axial furrow just anterior to the median transverse line, almost to the posterior marginal furrow. Both edges lie approximately in the same exsagittal plane, but owing to the strong rearward convergence of the axial furrows, the posterior edge is separated from the glabella. In profile, the eye occupies the central third of the height of the cephalon, hence the palpebral lobe falls short of the glabellar crown. Plan curvature of visual surface moderate, increasing behind transverse line; in profile the lower part of the eye is seen to be flattened; the degree of flexure increases upwards, becoming extreme just below the facial suture. Eye surface projects outwards above the shallow groove at its base, reaching laterally almost to the plane of the antero-lateral cephalic border. Palpebral lobe sparsely tubercular, rising gently from thickened rim above the facial suture to the curved palpebral furrow, beyond which the smooth palpebral area shelves adaxially to the axial furrow. Lenses disposed as follows in 18 dorso-ventral files:

456 566 666 565 544 332; Max. 6; Total 87.

All files diverge ventrally at a high angle, which is less in the first three files. Lenses quite closely packed, showing little variation in spacing within each file, almost contiguous in outer files. Size distribution as in *P. rana*, largest lenses 0·45 mm., average 0·35–0·4 mm., smallest 0·15 mm. In the ascending diagonal rows there is a rearward increase in diameter, and in the descending diagonals a forward increase.

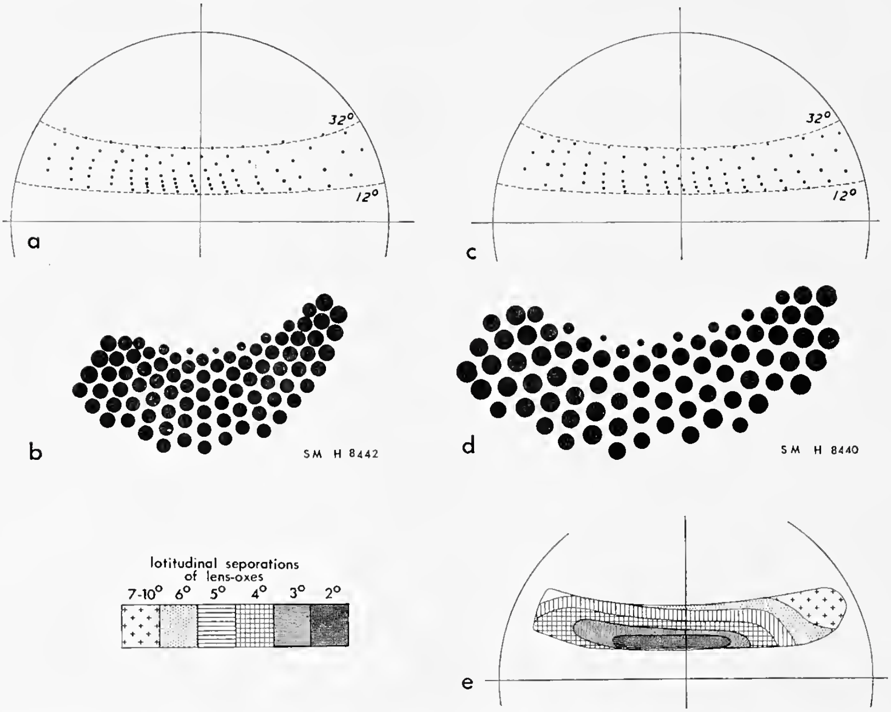
Interlensar sclera somewhat inflated and smooth.

Eye-Variant B (left eye, SM H 8440). Dimensions of eye: L. (max.) 10 mm. (min.) 7·0 mm., W. (max.) 6·0 mm. (min.) 4·5 mm., H. 4·5 mm., where cephalic length (sag.) is 18 mm. and breadth 38 mm.

The position and overall appearance of the eye is not dissimilar to that of SM H 8442 (eye-variant A), but the palpebral lobe shows a higher degree of inflation and is more coarsely tuberculate, and its outer edge where it contacts the facial suture is thickened. As seen directly in lateral aspect this ridge is slightly downwarped. The chief morphological differences between the two eye-variants are exhibited by the visual surface. In this specimen the last two files have been broken off. Impressions of the inner surfaces of the lenses have, however, been left on the underlying matrix, and have been used for spatial and angular measurements. Lenses disposed as follows in 19 files which diverge ventrally as in eye-variant A:

345 455 555 454 544 443 1; Max. 5; Total 79.

Lenses quite widely spaced, the periphery of each generally lies at a distance of more than a lensar radius from that of its neighbours, but in the first and last few files, where their diameter is particularly large, they are almost contiguous.



TEXT-FIG. 4. *Phacops breviceps* Barrande. *a*, *b*, SM H 8442 (eye-variant A). Stereogram and visual surface of right eye (× 5). *c–e*, SM H 8440 (eye-variant B). *c–d*, Stereogram and visual surface of left eye (× 5). *e*, Contoured stereogram showing latitudinal separations of lens-axes. Longitudinal separations average 7–10°.

Largest lenses (files 17, 18, 19), 0·55 mm. diam., average 0·4 mm., smallest 0·15 mm., those of the first file (1) increasing ventrally from 0·45 mm. to 0·525 mm.

Interlensar sclera inflated so that each lens lies in a shallow cup, but the top of each lens projects above the level of this sclera.

Characters of visual field. The species *Phacops rana*, *P. fecundus*, *P. latifrons* (Pl. 73, figs. 5–6), and *P. breviceps* all exhibit a fairly similar pattern of lens number and distribution. The visual fields of the first three are likewise similar, having a wide latitudinal range, (*c*. 35°), and a strong postero-ventral lacuna. The visual field of *P. breviceps* however, differs radically from these, having a comparatively narrow latitudinal range and no lacuna. In both eye-variants the total range is about 15–175° longitudinally, and 12–32° latitudinally.

The pattern of lens-axis dispersal is peculiar. The profile surface curvature of the eye in the lower part of the visual field is slight, and axial separations are only 2° or so, but owing to increasing upward curvature, they may reach 10°. The plan curvature is much higher and axial separations vary between 7 and 10°. There are thus partial visual strips, strongly evident in the lower and central parts of the visual field, but which become less distinct towards the top. In eye-variant B there are fewer lenses per file, and the strips are not quite so apparent. Anteriorly the strips are longitudinal, but in the central and posterior regions they run diagonally across the visual field.

Phacops batracheus Whidborne 1889

Plate 74, figs. 5, 8; text-fig. 5 *a*, *b*

1889 *Phacops batracheus* Whidborne, pp. 2–4, pl. 1, figs. 2–7.

Whidborne (1889, p. 2) commented in his full description of this species that the lenses of the eyes were 'very large and convex, in 18 perpendicular rows of from four to six lenses each, between 80 and 90 in all'. He figured the cephalon and left eye of SM H 4072 (1889, pl. 1, fig. 5), which is described here.

All Whidborne's syntypes from the Middle Devonian, at Lummaton, Devon (SM H 4067–74), and many other specimens were available. There is apparently only one eye-variant present, typified by Whidborne's figured specimen, which is perfectly preserved and undistorted, though the surfaces of a few lenses are slightly damaged.

Eye morphology (right eye SM H 4072). Dimensions of eye: L. (max.) 4·5 mm. (min.) 3·5 mm.; W. (max.) 2 mm. (min.) 1·5 mm.; H. 1·75 mm., where the length (sag.) of the cephalon is 9·5 mm., and breadth 20 mm.

Eye large, prominent, lunate, lying in the posterior half of the cephalon, occupying half its total length (sag.), extending from just anterior to the median transverse line to within 0·5 mm. of the posterior marginal furrow. The posterior edge is further from the sagittal line. In profile the eye occupies less than a third of the total height of the cephalon. The base of the visual surface is situated midway between the plane of the genal angle and the glabellar crown. Since the vertical extension of the eye is small as compared with its longitudinal span, the palpebral lobe lies well below the level of the glabella. The visual surface projects laterally almost to the antero-lateral cephalic border.

Plan curvature moderate, increasing posteriorly; profile curvature similar increasing ventrally. Palpebral lobe sparsely tuberculate, rising adaxially above narrow outer rim, becoming horizontal near axial furrow. Palpebral area continuous with lobe; there is no palpebral furrow.

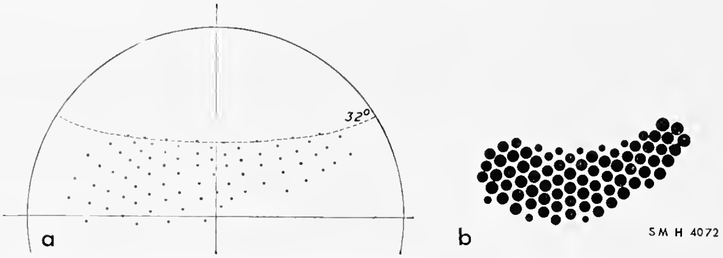
Lenses strongly convex, disposed in 18 files:

355 565 656 554 444 332; Max. 6; Total 80.

The first three files are parallel, the others diverge ventrally at a rather high angle. Individual lenses quite closely packed, almost contiguous in outer files, elsewhere there is about half a lensar radius between them. Within the files each lens centre is situated at a uniform distance from its neighbours. Lens diameters: largest (files 17 and 18) 0·4 mm.

diam.; average 0·375 mm., minimum 0·15 mm., in the centre of the upper horizontal row, and at the lower ends of the longest diagonals. There is no accessory upper horizontal row.

Interlensar sclera only slightly inflated, each lens projects conspicuously from the visual surface. The lenses of the upper horizontal row lie in shallow crater-like depressions, each of which has a prominent scleral rim. The lower edges of the rims are more strongly pronounced, and the lenses set obliquely to the surface of the sclera, and are thus directed at a lower angle to the horizontal than if they had been normal to the surface (cf. *P. rana*).



TEXT-FIG. 5. *Phacops batracheus* Whidborne. SM H 4072. *a*, *b*. Visual surface of right eye (×5) and stereogram.

Characters of visual field. The maximum range of vision is 20–156° longitudinally, 3–32° latitudinally. The upper visual limit is latitudinal and there is a deep postero-ventral lacuna present. The lens-axes are dispersed regularly and uniformly without any tendency to cluster or form visual strips. Both the latitudinal and longitudinal separations are about the same, averaging 7°. The separations in the lower part of the visual field are slightly greater.

Phacops boecki Hawle and Corda 1847

Plate 74, figs. 9, 10; text-fig. 6 *a*, *b*

1847 *Phacops boeki* Hawle and Corda, p. 107.
1852 *Phacops boecki* Corda; Barrande, p. 513, pl. 20, figs. 30–32.

The fullest previous description is that of Barrande (1852) who recorded 18–21 files per eye, with 5–8 lenses as a maximum depending on the size of the specimen. The total number of lenses ranged from 66–134.

EXPLANATION OF PLATE 74

Figs. 1, 2, 4, 7. *Phacops breviceps* Barrande. Koňeprusy Limestone, Stage F_2, Devonian, Koňeprus, Bohemia. 1, 2, SM H 8440 (eye-variant B). Left eye in lateral and dorsal aspects. ×5. 4, 7, SM H 8442 (eye-variant A). Right eye in lateral and dorsal aspects. ×5.

Figs. 3, 6. *Phacops fecundus* Barrande. SM H 49375. Stage E_2, Silurian, Dlauha Hora, Bohemia. Right eye in lateral and dorsal aspects. ×5.

Figs. 5, 8. *Phacops batracheus* Whidborne. SM H 4072. M. Devonian, Lummaton, Devon. Right eye in lateral and dorsal aspects. ×5.

Figs. 9, 10. *Phacops boecki* Hawle and Corda. SM H 8439. Dvorce Limestone Stage G_1 (lower part), Devonian, Dvorce, Bohemia. Left eye in lateral and dorsal aspects. ×5.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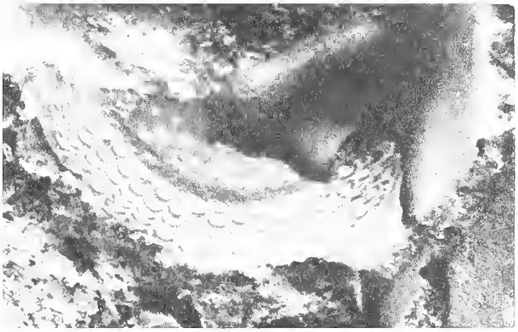
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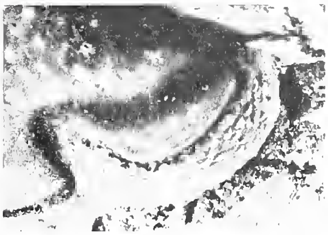
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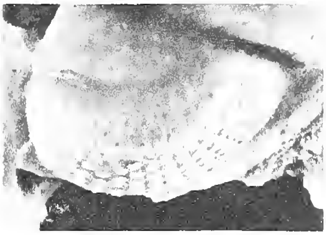
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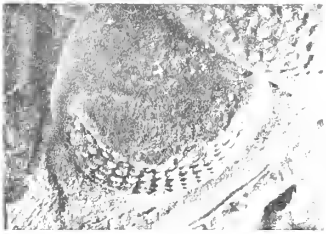
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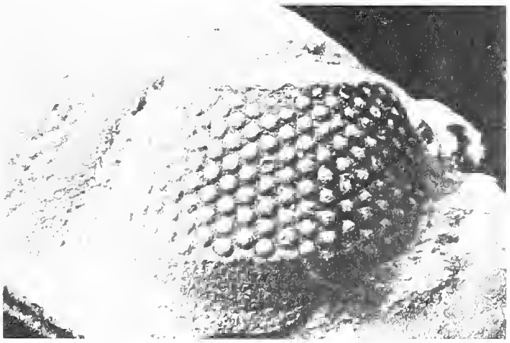
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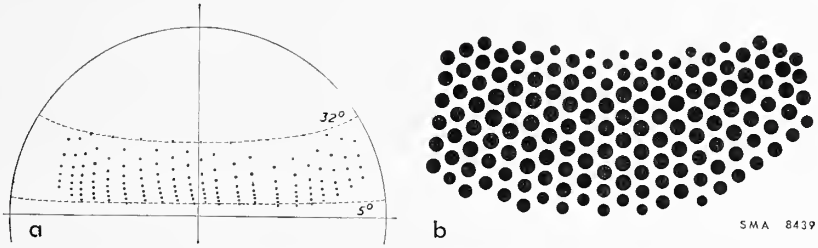
CLARKSON, Schizochroal eyes in phacopid trilobites

Only one well-preserved specimen was available, so only the one eye-variant has been noted. SM H 8439 is a very large adult from Dvorce Limestone, Stage G_1 (lower part) (Barrande 1852), Devonian, Dvorce, Bohemia. Both eyes are well preserved, though the surfaces of some of the lenses are slightly roughened by weathering.

Eye morphology (left eye SM H 8439). Dimensions of eye: L. (max.) 7 mm. (min.) 5 mm.; W. (max.) 4 mm. (min.) 3 mm.; H. 4 mm., where cephalic length is 13 mm., and breadth 23 mm.

Eye very large, prominent, occupying almost half length (sag.) of cephalon, visual surface extending from just anterior to median transverse plane of cephalon almost to the posterior marginal furrow. Both edges lie in approximately the same exsagittal plane. In profile, the eye base is set low on the cephalon, the palpebral lobe standing not quite as high as the glabellar crown. The visual surface forms a conic segment, with parallel upper and lower borders, whose height/base ratio, if projected to form a cone would be 5:1. Eye surface bounded ventrally by an inwardly shelving flat strip, projecting laterally so as to overhang cephalic border. Plan curvature uniform, moderate; profile curvature very low ventrally, increasing dorsally. Palpebral lobe smooth, bounded laterally by thickened rim, somewhat inflated, shelving adaxially to indistinct palpebral furrow. Palpebral area flat, open posteriorly.



TEXT-FIG. 6. *Phacops boecki* Hawle and Corda. SM H 8439. *a*, *b*. Visual surface of left eye (× 5) and stereogram.

Lenses, as far as can be ascertained, strongly convex, disposed in 21 files:

678 788 888 888 878 776 654; Max. 8; Total 150.

All files diverge ventrally at a very low angle.

Lenses rather widely spaced, generally separated by distance of a lensar radius and remarkably constant in size throughout the visual surface, peripheral lenses generally slightly smaller. Largest lenses 0·35 mm., diam. smallest 0·2 mm.

Interlensar sclera only slightly inflated between lenses of central files.

Character of visual field. The maximum range of vision is 25–172° longitudinally, 5–32° latitudinally. Both the upper and lower limits are almost entirely latitudinal. In spite of the proximity of the posterior edge of the eye to the rear border of the cephalon, there is only a slight upward deflection of the lower limit in the hindermost part of the visual field, posterior to 140° long. and covered by files 18–21.

Owing to the extremely low profile curvature of the visual surface near the base of the eye, the axes of the lower lenses of the dorso-ventral files are concentrated in visual strips, in which axial separations are as low as 1°; but the upward increase in curvature results in separations of up to 12° near the top of the visual field and the strips fade out dorsally. The visual strips are quite regularly spaced, and the angles separating them vary between about 7 and 10° of longitude.

Superfamily DALMANITACEA

Dalmanites vulgaris (Salter 1849)

Plate 75, figs. 1–4; text-fig. 7 *a–e*

1822 *Asaphus caudatus* Brongniart, p. 22, pl. 2, figs. 4 *a–d*.
1845 *Dalmannia caudatus* (Brünnich); Emmerich, p. 38.
1849 *Phacops caudatus* (Brünnich) var. *vulgaris* Salter, pp. 1–6, pl. 1, figs. 1–12, 15.
1864 *Phacops* (*Odontochile*) *caudatus* (Brünnich) var. *vulgaris* Salter; Salter, pp. 49–53, pl. 3, figs. 4–17. (= *Dalmanites caudatus* (Brünnich) of later writers.)
1935 *Dalmanites vulgaris* (Salter); Delo, pp. 424–6, pl. 48, figs. 8, 9.

Salter's descriptions of 1849 and 1864 include good illustrations of the eye. He recorded about 240 lenses per eye, and 8–10 per file. He also noted that in some specimens the eyes were larger than in others and referred this difference to sex, concluding that the male had larger eyes.

Many specimens from the Wenlock Limestone have been examined, but although some variation is apparent within the species there is as yet no conclusive evidence of sexual dimorphism.

In the best-preserved specimen examined, SM A 28635, both eyes are well preserved, though part of the left eye is chipped and two patches of polyzoa have encrusted the upper rim of the right eye, obscuring a few lenses. The lenses retain their full convexity.

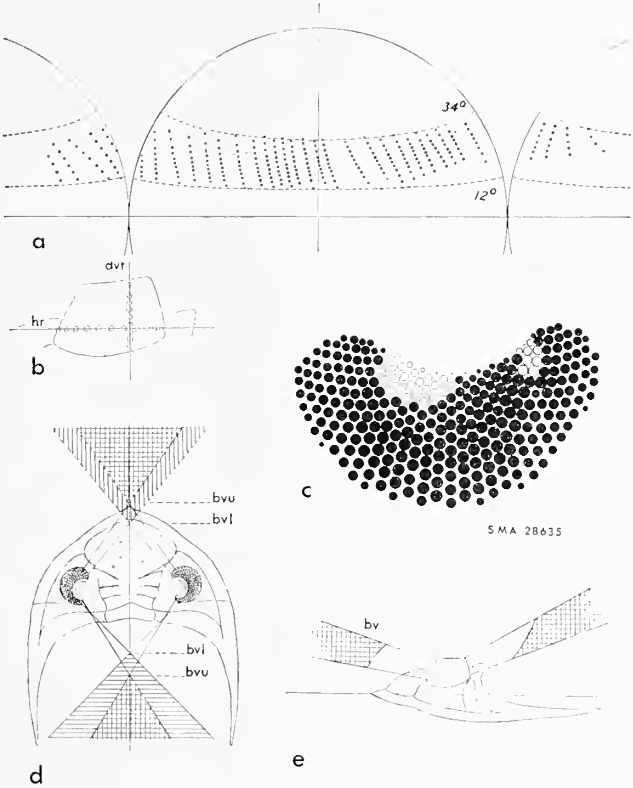
Eye morphology (right eye SM A 28635). Dimensions of eye: L. (max.) 5 mm. (min.) 3 mm.; W. (max.) 4 mm. (min.) 2·5 mm.; H. 3 mm., where cephalic length (sag.) is 17 mm., and breadth 30 mm.

Eye large, situated posteriorly on the cephalon, standing high above the glabella, and forming a truncated cone whose height/base ratio, if projected to form a cone would be 4:1. The anterior edge is separated from the axial furrow, and the posterior edge lies further from the sagittal line. The eye base occupies the summit of the librigena, and is surrounded by a moat-like depression, with an external concentric ridge, which limits the genal field. Plan curvature very strong and fairly uniform, but in profile the visual surface is almost flat and inclined at about 80° to the horizontal. In the 'natural attitude' (text-fig. 7 *b*, *e*). the upper rim is oblique to the horizontal, and the eye appears to slope forwards and downwards, though the 'horizontal' lens-rows actually lie in a horizontal plane.

The narrow (*tr*) palpebral lobe is almost uniformly curved in plan and consists of a narrow strip with a shallow concentric groove running parallel with the facial suture. It plunges steeply adaxially to the palpebral furrow, which lies a short distance below the upper rim of the eye. The tuberculate palpebral area declines with increasing steepness towards the axial furrow.

There are 34 dorso-ventral files in which the lenses are disposed as follows:

467 899 10 9*10* 10*11*10* 11*10*11* 10*11*10 11 10 10 10 10 9 988 788 765 2; Max. 11; Total 294 (* In the regions where the eye surface is covered by polyzoa, the number of lenses in the other eye have been counted.)



TEXT-FIG. 7. *Dalmanites vulgaris* (Salter). SM A 28635. *a*, *c*, Stereogram and visual surface of right eye (×5). The blank circles and the corresponding enclosed areas on the stereogram represent lenses covered by polyzoa. The equivalent lenses and lens-axes of the left eye are substituted here. *b*, Left eye in 'natural orientation' showing a horizontal row (*hr*) and one of the dorso-ventral files (*dvf*), which in this attitude appears vertical. *d*, Limits of binocular vision shown by the bearings of the upper (*bvu*) and lower (*bvl*) lenses of the first and last files. *e*, Profile view of the cephalon showing limits of binocular vision with respect to the upper surface of the head. Apparent angular bearings are shown here (apparent latitude $= \tan\theta\cos\phi$ where θ is the latitudinal and ϕ is the longitudinal bearing of the lens-axis in question).

Apart from the first and last three dorso-ventral files, which are parallel, the files diverge ventrally at a very high angle (the highest observed so far in any Phacopina). Within the files the lenses are closely packed together. In the lower part of the visual surface the lenses of adjacent files are quite widely spaced owing to the high downward divergence of the files so that there is about the distance of a lensar radius between them; but in the median and upper parts of the eye they are almost contiguous. The distance between the lenses within the files gradually increases upwards. The largest lenses (diam. 0·3 mm.) occur in the central region of the visual surface. On the periphery of this region they are smaller and all round the borders of the visual surface lenses of diameter less than 0·2 mm. are present. Hence the lowest two or three ascending and descending diagonal rows contain small lenses.

Minute lenses are found in the centre of the upper horizontal row and in an incipient accessory upper horizontal row which is present at the top of files 26, 28, and 30.

Interlensar sclera is indistinguishable in the region of the large closely packed lenses, but is visible at the bottom of the eye, and is tuberculate. Each lens here is surrounded by an irregular polygon of fine points.

Character of visual field. The maximum range of vision is 265° longitudinally, and 12–34° latitudinally. The visual fields of the two eyes overlap anteriorly and posteriorly and, as in all dalmanitids, the lenses covering the overlapping parts are small. The axes of the top and bottom lenses of the first files have slightly different longitudinal bearings (40 and 35°) and meet just in front of the glabella and the anterior margin of the cephalon respectively. Lens-axes of the last file likewise have different bearings (—35 and 45°) and meet at some distance behind the occipital ring clearing it by a fair angle (text-fig. 7 *d*, *e*). The upper limit is largely latitudinal, as is the lower over the anterior region, but posteriorly there is a shallow lacuna.

As in *Acaste downingiae* the strong differential curvature of the visual surface results in the arrangement of the lens-axes of the files into very distinct visual strips. Within the strips axial separations are usually less than 2° and never more than 4°. Between strips axial angles are about 6–7° though axial separations twice this figure occur between files 19 and 20, just posterior to the polar meridian. A unique feature of this eye is that all the visual strips slant the same direction and the top lens-axis in each file has about the same angular bearing as the bottom lens-axis of the preceding file. This condition may be contrasted with that in *A. downingiae*, where the strips follow a radial pattern, and that in *Chasmops odini* where they are curved. It may be considered as an adaptation whereby the whole longitudinal field of view is covered, with maximum economy of lenses.

In the overlapping parts of the visual field the separation of the visual strips is rather more variable.

Dalmanites caudatus (Brünnich 1781)

Plate 75, figs. 5, 6; text-fig. 8 *a–*,

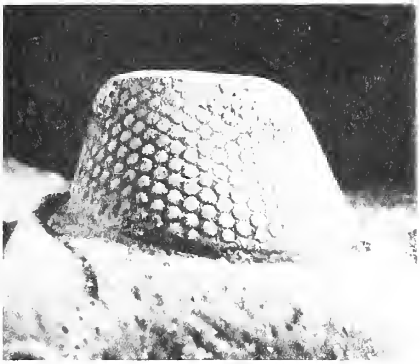
1781 *Trilobus caudatus* Brünnich, p. 392.
1839 *Asaphus longicaudatus* Murchison, p. 656, pl. 14, figs. 11–14.

EXPLANATION OF PLATE 75

Figs. 1–4. *Dalmanites vulgaris* (Salter). SM A 28635. Wenlock Limestone, Silurian, Dudley, England. 1, 2, 4, Right eye in lateral, dorsal, and dorso-lateral aspects. ×7·5. 3, Lenses near the lower rim of the visual surface. ×20.

Figs. 5, 6. *Dalmanites caudatus* (Brünnich). SM A 28644. Wenlock Limestone, Silurian, Dudley, England. Left eye in lateral and dorsal aspects. ×5.

Figs. 7–11. *Chasmops odini* (Eichwald). SM A 53427. C_2 Kukruse shale or C_3 Itfer shale, Caradocian, Estonia. 7, Right eye, lenses near the lower rim of the visual surface. ×25. 8–11, Right eye in lateral, frontal, dorso-lateral, and dorsal aspects. ×5.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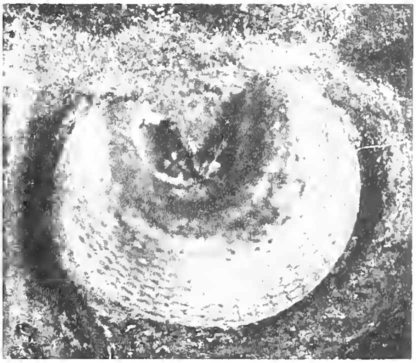
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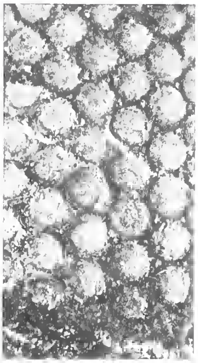
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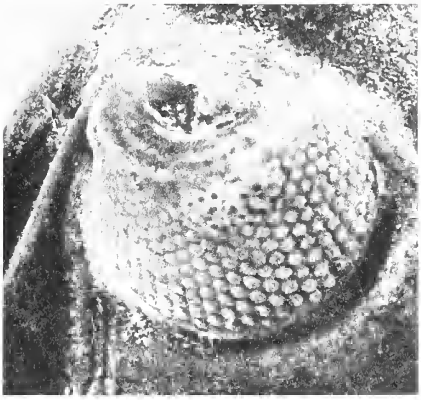
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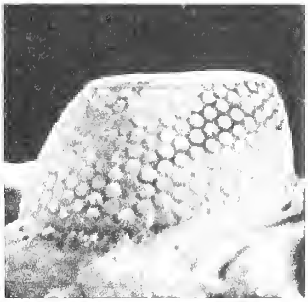
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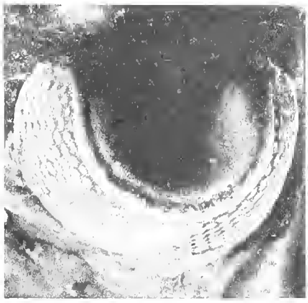
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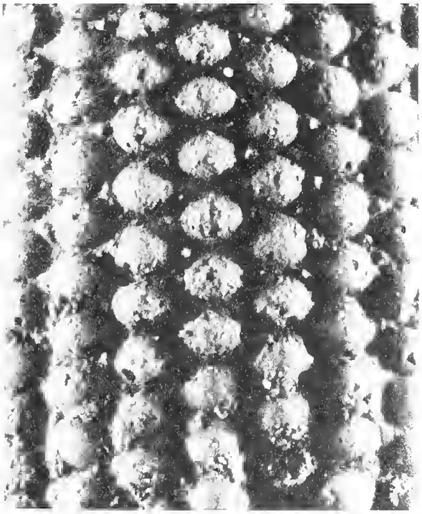
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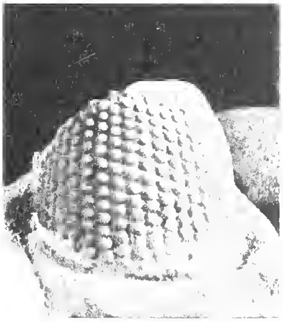
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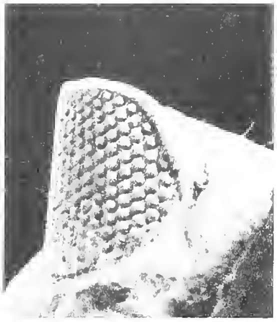
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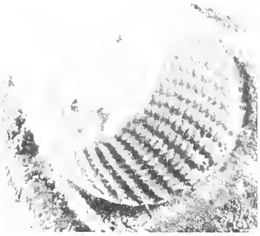
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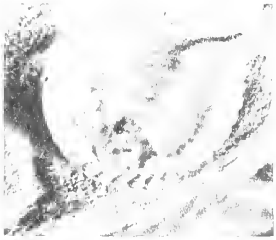
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CLARKSON, Schizochroal eyes in phacopid trilobites

1845 *Dalmannia longicaudata* (Murchison); Emmerich, p. 40.
1849 *Phacops caudatus* (Brünnich) var. *longicaudatus* (Murchison); Salter, pp. 1–6 (pars), pl. 1, figs. 13–14.
1864 *Phacops* (*Odontochile*) *longicaudatus* Murchison; Salter, pp. 55–56, pl. 3, figs. 19–28. (= *Dalmanites longicaudatus* of later authors.)
1935 *Dalmanites caudatus* (Brünnich); Delo, pp. 424–6, pl. 48, figs. 6, 7.

The fullest previous descriptions of this Wenlock Limestone species are those of Salter (1849, 1864). He made only brief reference to the eye.

Many specimens have been examined but only one eye-variant has been distinguished. SM A 28644 is well preserved, though the lensar surfaces have in some cases been planed off. Both eyes are identical.

Eye morphology (left eye SM A 28644). Dimensions of eye: L. (max.) 5 mm. (min.) 3·5 mm.; W. (max.) 3·5 mm. (min.) 3 mm.; H. 3 mm., where cephalic length is 13 mm. and width 20 mm.

The form and situation of the eye resembles that of *D. vulgaris*; the major differences lie in the degree of curvature, the character of the palpebral lobe, and the number and arrangement of the lenses. The visual surface is very strongly and regularly curved in plan, whereas in profile the degree of curvature of the anterior part of the visual surface is considerable but lessens posteriorly so that in the region of the last few files the eye is almost flat. The palpebral lobe is extremely narrow (*tr*), and plunges very steeply to the U-shaped palpebral furrow, which lies well below the upper rim of the eye.

Lenses disposed as follows in 32 files:

457 889 899 999 989 899 999 988 888 776 52; Max. 9; Total 249.

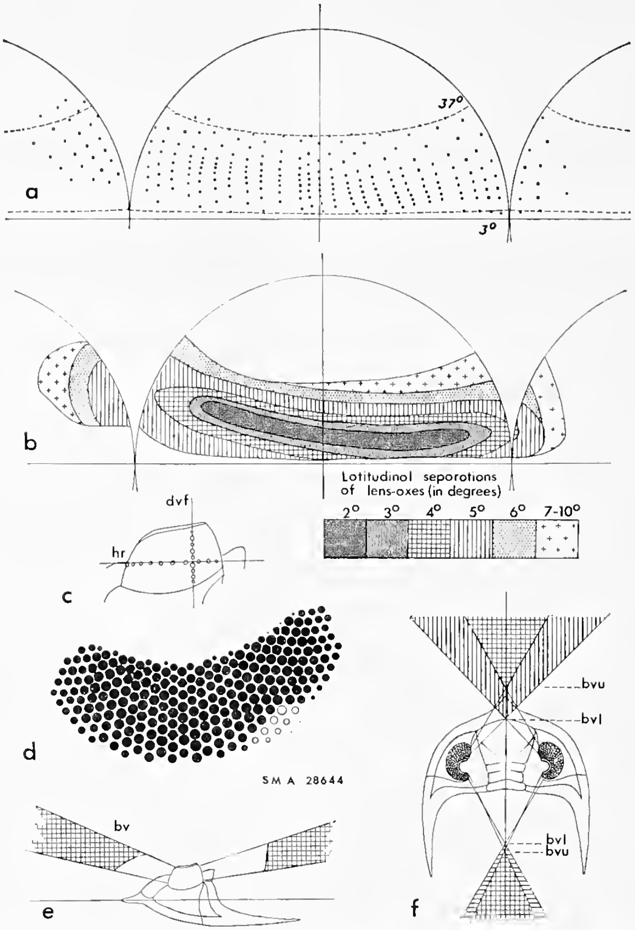
The outer files converge ventrally, but the central ones diverge at quite a high angle. Within files lens spacing increases ventrally. In the upper regions they are so closely packed as to be hexagonal, elsewhere they are rounded. The largest lenses (0·25 mm.) occur in a wide crescent running through the upper anterior, lower central, and upper posterior parts of the visual surface. Outside this crescent lie smaller lenses (0·175 mm.). In SM A 28644 the central lenses of the upper horizontal row have failed to develop. Three minute lenses at the top of files 25, 27, and 29 represent an incipient accessory upper horizontal row.

The lenses are so closely packed that no interlensar sclera can be seen.

Character of visual field. The maximum range of vision is 254° longitudinally, 3–37° latitudinally. There is an overlap of the visual fields of the two eyes comparable with that of *D. vulgaris* (text-fig. 8 *e*, *f*), though there is a greater difference (15°) between the longitudinal bearings of the top and bottom lenses of file 1, which seems to be associated with the relatively longer distance between the front of the glabella and the anterior point.

Lens-axes of the dorso-ventral files form visual strips which are separated by angles of 5–8°. Some of these strips are longitudinal, others, particularly those associated with the more posterior files, are divergent. Although the strips are quite regularly spaced they are quite unlike those of *D. caudatus* because of the strong differentiation in profile curvature of the eye from front to rear. On the contoured stereogram (text-fig. 8*b*) this change in curvature is shown by a band of closely spaced lens-axes which traverses the visual field diagonally in the anterior part of the visual field, and lies almost horizontally posteriorly. Within this band latitudinal axial separations average 2–3°, outside it they may be as high as 10°, and normally approximate the longitudinal separations.

The elevation of the lens-axes within the horizontal rows declines gradually backwards, but as the three small lenses of the accessory upper horizontal rows have elevations of 37°, the upper visual limit is unbroken.



TEXT-FIG. 8. *Dalmanites caudatus* (Brünnich). SM A 28644. *a*, *d*, Stereogram and visual surface of left eye (×5). *b*, Contoured stereogram showing latitudinal separations of lens-axes. The diagonal band containing the lowest separations is distinct. Longitudinal separations average 6–8°. *c*, Left eye in natural orientation. *e*, *f*, Limits of binocular vision, notation as in text-fig. 7.

Chasmops odini (Eichwald 1840)

Plate 75, figs. 7–11; text-fig. 9 *a*, *b*

1840 *Calymene odini* Eichwald, p. 62.
1851 *Chasmops odini* (Eich. sp.); M'Coy, p. 164, pl. 1*g*, figs. 22, 23.
1881 *Chasmops odini* (Eichwald); Schmidt, p. 101, tab. 2, figs. 1–13.
1937 *Chasmops odini* (Eichwald); Öpik, p. 77, tab. 9, figs. 5, 6, text-figs. 23–25.

In Eichwald's original description of this species little reference was made to the eye, but Schmidt gave a very detailed account, noting about 240 lenses in 20–22 files, and about 12 lenses per file. His excellent figures (1881, figs. 2, 8, 9) showed the almost flat visual surface. No new information was recorded by Öpik.

The material studied was a single cephalon, SM A 53427, from the Caradocian of Estonia (C_2 Kukruse shale or C_3 Itfer shale (after Öpik)). It is preserved in full relief and both eyes are present. The upper surface of the left eye is broken, but the right is undamaged apart from the posterior upper rim and a few of the topmost lenses which have been broken off.

Eye morphology (right eye SM A 53427). Dimensions of eye: L. (max.) 5·5 mm. (min.) 5·0 mm.; W. (max.) 4·5 mm. (min.) 4·0 mm.; H. 5·5 mm., where cephalic length (sag.) is 16 mm. and breadth 30 mm.

Eye very prominent and set high on the cephalon forming a high truncated cone, which if projected to form a cone would have a height/base ratio of 10:1. The anterior edge is situated almost exactly half way between the anterior border and the occipital ring, on a level with glabellar furrow (3p), and the posterior edge lies some way (2 mm.) anterior to the posterior marginal furrow. Both the anterior and posterior edges of the eye lie almost in the same exsagittal plane, the former being separated from the axial furrow by the highly inflated fixigena. The visual surface reaches almost to the antero-lateral border.

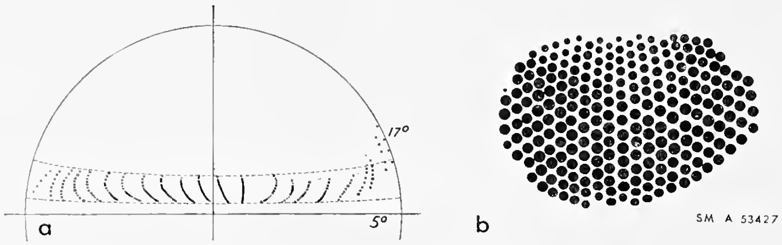
A deep lunate depression surrounds the base of the eye, external to which lies the narrow genal field from which the librigena plunges vertically. In plan the visual surface is strongly curved and parabolic about the transverse line but in profile it is almost flat with only the slightest curvature. The prominent outer rim of the palpebral lobe surrounds the whole of the upper edge of the visual surface and projects outwards over it, becoming thicker where it plunges downwards subparallel with the anterior and posterior dorso-ventral file. Adaxially to the rim the inner face of the palpebral lobe slopes to meet the palpebral furrow, which in its central part is very sharply reflexed so as to be almost V-shaped (the point of the V being directed outwards). At the base of the eye the palpebral furrow joins with the deep groove surrounding the bottom of the visual surface, so that the whole eye is encircled by one continuous furrow. The palpebral area is inflated and open to front and rear.

There are 22 dorso-ventral files, with the following lens distribution:

5 7 10 11 12 13 14 14 14 14 14 14 14 13 12 12 11 10 9 7 5 4; Max. 14; Total 239.

In all other phacopids which have been investigated the dorso-ventral files are straight, but here only the central files are straight and the outer files are curved outwards, the degree of flexure increasing in opposite directions away from the centre. (In text-fig. 9 the curvature of these files is shown as accurately as possible, but in representing the distance apart of the outer lenses there is some inevitable distortion.) Thus the files diverge from the top downwards at a moderate angle from each other and just below the median plane they being to converge again. All the lenses are quite closely packed, but there is a gradual upward increase in the distance between the lenses in the dorso-ventral files, hence the lowest lenses are elliptical and almost contiguous, whereas the smaller upper lenses are rounded and are nearly their own diameter apart. In certain files elliptical lenses occur near the top of the eye but generally they are round. Between the lenses of adjacent dorso-ventral files the separation is generally greater than the vertical distance between lenses within a file.

The lenses of the lower central and outer parts of the visual surface are the largest (0·3 mm.) and are of relatively uniform diameter. In the central files the lenses become progressively smaller upwards from the median region, decreasing to 0·15 mm. diam. Those of the upper horizontal row are of about the same diameter, and only increase slightly in size away from the centre. The interlensar sclera is flat but furnished with small round tubercles in the interstices of the lenses which form irregular polygons surrounding each lens. At the base of the visual surface these tubercles are very numerous and completely cover the lower rim.



TEXT-FIG. 9. *Chasmops odini* (Eichwald). SM A 53427. *a*, *b*. Stereogram and visual surface of right eye (× 5).

Characters of visual field. The maximum range of vision is 180° longitudinally, 5–17° latitudinally. Both visual limits are latitudinal, except at their posterior extremities, where the elevation of the lenses of the last few files increases greatly.

The pattern of lens-axis dispersal, as shown on the stereogram, is one of the most remarkable observed in any phacopid. The axes of the numerous lenses in the dorso-ventral files are accommodated within the visual field in very distinct, widely separated, and peculiarly curved visual strips. The curved appearance of these strips obviously relates to the curving files themselves; both are bowed outwards in opposite directions away from the central file, whose equivalent strip has a bearing of about 105° long. Within strips the latitudinal axial separations of the lens-axes may be as low as $\frac{1}{2}$°, though towards the extremities it increases to 2° or 3°. Longitudinal separations between strips may be as high as 15°. Apart from those in the last few files, where there is a sudden increase in elevation, all the lens axes of the horizontal rows have approximately constant bearings.

SUMMARY

This paper, together with my previous one (Clarkson, 1966*a*) describes the relationship between eye-form and the spatial and angular characteristics of the lenses, in a number of typical schizochroal trilobite eyes. Full physiological interpretations of this and other information relating to trilobite vision are to be made in a later paper but a brief concluding summary of observations to date can be given.

External morphology of eyes

(i) Lenses upon the visual surface are normally arranged in a regular pattern of hexagonal close packing. Breakdown in regularity occurs in a few cases.

(ii) During postlarval ontogeny there is an increase in lens number until full maturity is reached. The adult lens-number within species is approximately constant, though in some species there are apparently two distinct adult eye-variants, which may reflect a sexually dimorphic condition. In the present state of taxonomic confusion it is not yet possible to elucidate this matter further.

(iii) Within the visual surface of individual specimens of the Phacopina there is normally considerable variation in lens-size. Small lenses are always found in the upper central region, and the newly emplaced lenses at the lower ends of the dorso-ventral files are likewise small. The pattern is distinct in all the species investigated except *Chasmops odini.*

(iv) Lens size, number, and spacing vary greatly within the Phacopina as a whole. Eyes with very large lenses, e.g. *Phacops rana crassituberculata*, normally only have a limited lens number. In some eyes increased lens number has been achieved by the close packing of the lenses so that they become hexagonal. Characteristic patterns of the arrangement of lenses upon the visual surface relate to systematic categories and presumably reflect evolutionary relationships.

(v) Variation in lens-size within the visual surface of individuals is normally independent of differential surface curvature.

(vi) The lenses are not always set normal to the visual surface but owing to their large size their axial directions may readily be inferred from the external morphology of the eyes.

Characters of visual fields. Three main patterns of the arrangement and dispersal of lens-axes are found within Phacopina, largely as a result of distinct modes of curvature of the visual surface. In species with two adult eye-variants the visual fields of both may be of similar extent, although the lens-axes may have a slightly different arrangement. These patterns are as follows:

(i) Visual fields of wide (*c.* 30–40°) latitudinal extent, normally associated with eyes of 100 lenses or less, in which the plan curvature is rarely more than twice the profile curvature. The upper visual limit is normally latitudinal, though a deep triangular postero-ventral lacuna is commonly present which truncates the equatorial lower limit. This device apparently prevents occlusion of vision in this region by the high posterior cephalic border. Axial separations are high though some of the lens-axes may be clustered together in the lower anterior part of the visual field. Examples are *Phacops rana milleri*, *P. rana crassituberculata*, *P. latifrons*, *P. fecundus*, *P. batracheus*, *P. musheni* (see Clarkson, 1966*b*), *Acastoides constricta.*

(ii) Visual fields of narrow (10–20°) latitudinal extent usually relating to eyes with upwards of 100 lenses, curving very much more in plan than in profile. Both visual limits are generally latitudinal; if there is a lacuna it is shallow. The lower visual limit lies at 10° or more above the equator. Such eyes are highly astigmatic, as the lens-axes are dispersed in visual strips which are present from a very early stage in postlarval development. These strips cross the visual field from top to bottom and may be disposed either radially as in *Acaste downingiae*, diagonally in *Dalmanites vulgaris*, or may themselves be curved, e.g. *Chasmops odini.*

(iii) Visual fields which combine many of the features of (i) and (ii). The number of lenses in the eye is variable. Both visual limits are latitudinal, the lower normally lying a few degrees above the equator (12° in *P. breviceps*). Incomplete visual strips are developed which run in a band normally parallel with the visual limits (apart from *Dalminites caudatus*) but which do not extend the full latitudinal width of the visual field. In *P. breviceps* and *P. boecki* this band of partial visual strips lies at the base of the visual field; in *Acaste downingiae macrops* it is above this level; and in *D. caudatus* it runs diagonally across the anterior part of the visual field and posteriorly runs parallel to and just above the lower limit.

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TWO CRISTATE MEGASPORES FROM THE LOWER CARBONIFEROUS OF SCOTLAND

by K. L. ALVIN

ABSTRACT. A new megaspore described under the name *Triletes pannosus* sp. nov. resembles in its crest of anastomosing hairs *T. subpalaeocristatus* Alvin from the same locality. A new specimen of this latter species has yielded further details of its structure. Comparison is made between the two species.

SOME fifteen specimens of a new megaspore were obtained from samples of shale collected at Oxroad Bay, East Lothian. The shale contains abundant seed megaspore membranes, microspores, and fragmentary carbonized plant remains. It was collected and macerated in the hope that it might yield whole specimens of a megaspore described recently from petrified material from the same locality under the name *Triletes subpalaeocristatus* Alvin (1965). This latter spore was so closely associated with the cone of the lycopod *Oxroadia gracilis* Alvin that it was almost certainly borne by this plant. It was described only from serial peel sections and was of interest because of its unusual morphology in possessing a crest of hairs along the lips of the trilete ridge. Oddly enough the new megaspore also possesses a crest, but appears genuinely distinct.

A new specimen of *T. subpalaeocristatus* has been found in the original block containing *Oxroadia*. This has been macerated out from the matrix and has yielded some new information about this species for which an emended diagnosis is now given.

SYSTEMATIC DESCRIPTIONS

Genus TRILETES Bennie and Kidston ex Zerndt

Triletes pannosus sp. nov.

Plate 76, figs. 1–6; text-fig. 1 A–D

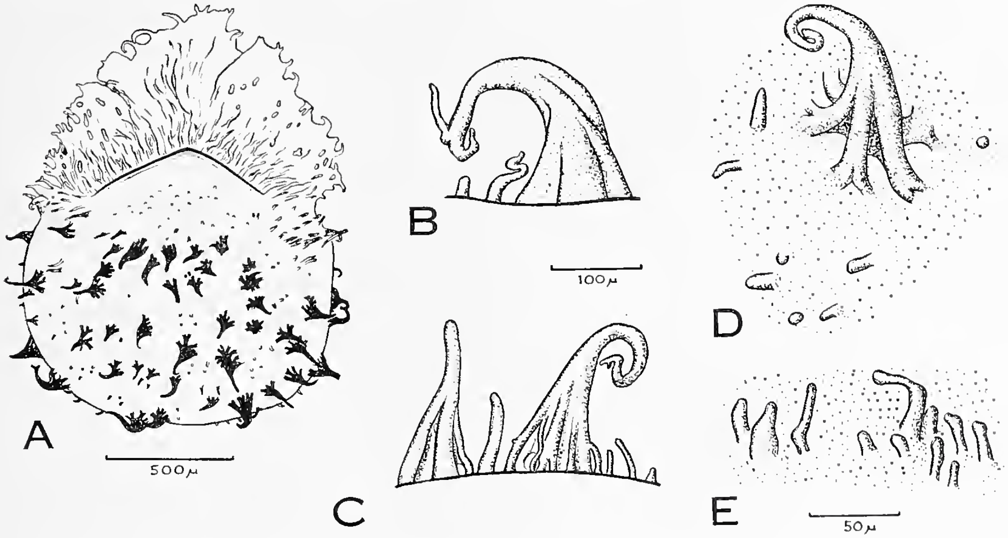
Diagnosis. Megaspore spheroidal; mean equatorial diameter 1,360 μ (range for nine spores measured 1,180–1,580 μ); mean height (excluding crest) 1,260 μ (range for ten spores measured 1,100–1,440 μ). Wall about 30–50 μ thick. Arms of trilete ridge extending about three-quarters the radius of the spore. Wall (except for contact areas) bearing numerous spines about 200 μ long, sometimes up to 400 μ and up to 200 μ wide at the base. Spines simple or forked near the tip, straight or commonly curved; base expanded and buttressed; buttresses often forming separate 'legs'. Papillae and simple hairs up to 100 μ long also present among the spines. Papillae, 10–20 μ in diameter, usually present on contact areas. Lips of trilete ridge bearing a prominent crest up to 660 μ high at the apex (mean height for twelve spores 525 μ), diminishing to about half this at the ends of the trilete arms. Crest resembling a series of anastomosing hairs, but sometimes forming a more or less continuous membrane with free teeth distally; hairs or teeth of very varied thickness, generally 5–20 μ.

[Palaeontology, Vol. 9, Part 3, 1966, pp. 488–91, pl. 76.]

Locality and horizon. Oxroad Bay, East Lothian, Scotland. Cementstone Group (Upper Tournaisian), Calciferous Sandstone Series, Lower Carboniferous.

Holotype. British Museum (Natural History), Palaeontology Department, V52016a. The specific name is derived from the ragged appearance of the crest.

Discussion. The new spore most closely resembles *Triletes echinoides* Chaloner (1954), a species described originally from the Beaver Bend Limestone of the Mississippian of Indiana, but one which has since been recorded from a number of localities including Britain where it has been found in the sporophyll known as *Lepidostrobophyllum fimbriatum* (Kidston) (Allen 1951; Lacey 1962). Since the publication of the original description, the range in the equatorial diameter for the species has been extended to 1·2–4·0 mm., though the two original specimens were 2·66 mm. and 2·00 mm. The wide range virtually covers that for the new Scottish spore. The spines of *T. echinoides* are up to about 1 mm. long (Winslow 1959), whereas the maximum length in *T. pannosus* is only less than half this. The chief difference between the two species lies in the crest: in *T. echinoides* this has the form of a continuous fluted membrane with no indication of hairs or teeth or even of perforations.



TEXT-FIG. 1. A–D, *Triletes pannosus* sp. nov. E, *Triletes subpalaeocristatus* Alvin. A, Specimen showing the general features. The crest, part of which is shown in Plate 76, fig. 6, shows an especially high degree of fusion among the hairs so as to form a more or less continuous membrane. Slide V52016e. B, C, Spines, short hairs, and papillae in profile. Slide V52016 f, g. D, Part of the spore wall in surface view showing a single buttressed spine and papillae. Slide V52016e. E, Part of the wall in surface view. Slide V51513z.

In the general character of the ornamentation of the distal face, the new spore resembles a number of other Carboniferous spores, especially perhaps *T. crassiaculeatus* (Zerndt). However, this spore differs in the quite different form of the apical prominence.

The trilete crest of *T. pannosus*, in resembling a series of anastomosing hairs arising from the lips of the ridge, may be compared with that of *T. subpalaeocristatus* Alvin

(1965). Indeed, when the new spore was discovered it was thought that it might be identical with this species which had been based on specimens from a block of petrified plant material from the same locality. A new specimen of this spore has now been macerated from the original block and the following emended diagnosis incorporates the new information that this has yielded.

Triletes subpalaeocristatus Alvin 1965

Plate 76, figs. 7, 8; text-fig. 1E

Emended diagnosis. Megaspore nearly spherical; mean diameter 1,450 μ (range for four spores 1,250–1,750 μ); height (excluding crest) only about 50 μ less than equatorial diameter. Wall about 35–45 μ thick. Arms of trilete ridge extending the whole radius of the spore. Distal face and contact areas bearing scattered papillae and short hairs up to about 50 μ long. No distinct arcuate ridge, but contact areas delimited distally by a narrow zone of relatively dense papillae and hairs. Lips of trilete ridge bearing a crest of branched anastomosing hairs (3·5–) 6·5 (–13·0) μ thick; maximum height of crest at apex up to 405 μ, height diminishing to about half this at the ends of the trilete arms.

Discussion. This species, on the evidence of the new specimen, is rather less like *T. palaeocristatus* Chaloner than was originally believed. It differs in possessing an ornamentation of short hairs and papillae scattered over the surface and in the delimitation of the contact areas by arcuate zones of denser ornamentation. The new specimen, in being somewhat larger than the original specimens, extends the size range so that this approaches more closely that for *T. palaeocristatus.*

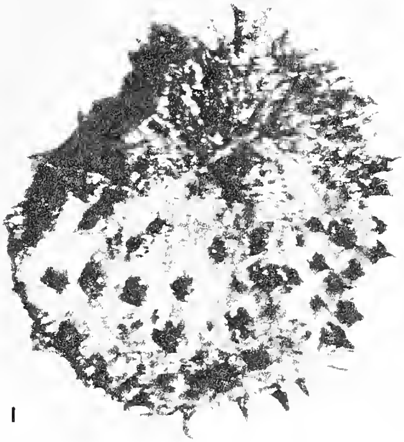
GENERAL DISCUSSION

The similarity in certain characters, most notably the presence of an apical crest of hairs, between *T. subpalaeocristatus* and *T. pannosus* is remarkable, especially as these are the only known megaspores from Oxroad Bay. Since the two species are based on material preserved in a different manner, the question immediately arises as to whether the difference between them might not be due either to the modes of preservation or even to the techniques used in preparing clean specimens. *T. pannosus* (Pl. 76, figs. 1–6; text-fig. 1A–D), coming as it does from the shale, is always compressed, but although some specimens are split open, the preservation is excellent. These spores were obtained by first breaking down shale samples in nitric acid and potassium chlorate, neutralizing and picking out the spores, and then freeing them from adhering mineral particles in hydrofluoric acid. The specimen of *T. subpalaeocristatus* obtained free of matrix (Pl. 76, figs. 7, 8; text-fig. 1E) was etched from the block slowly in acetic acid and subsequently freed from siliceous material in hydrofluoric acid and from pyrite in nitric acid.

EXPLANATION OF PLATE 76

Figs. 1–6. *Triletes pannosus* sp. nov. 1, Holotype; Slide V52016a, ×35. 2, Slide V52016b, ×35. 3, Spines and papillae in profile; Slide V52016c, ×80. 4–6, Portions of the crest of three different specimens showing variation in form; Slides V52016 c, d, e, ×80.

Figs. 7, 8. *Triletes subpalaeocristatus* Alvin. 7, New specimen isolated from the nodule; Slide V51513z, ×35. 8, Portion of the crest of the same spore, ×80.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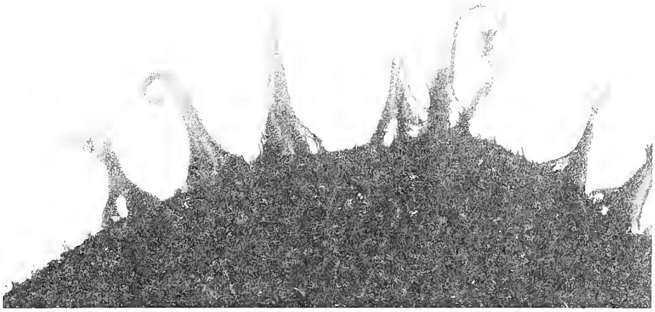
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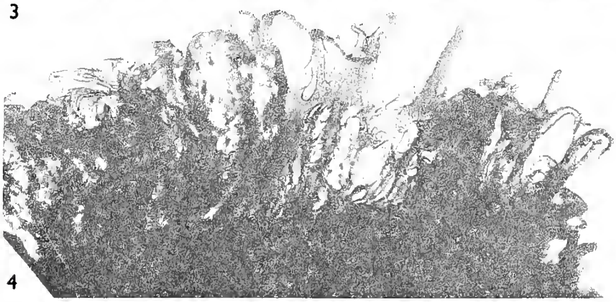
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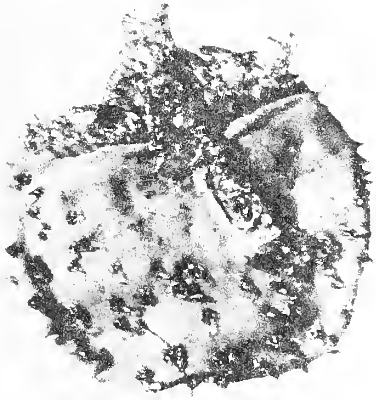
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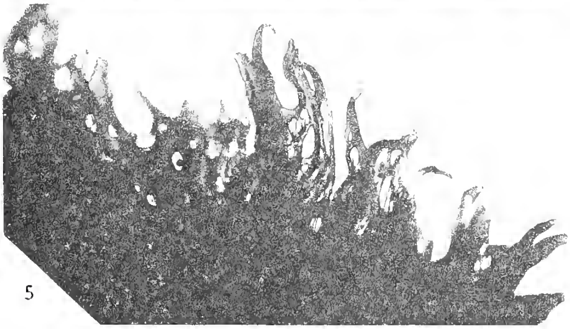
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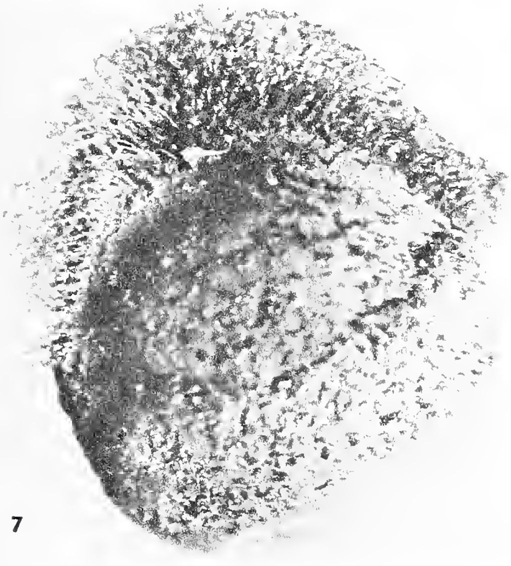
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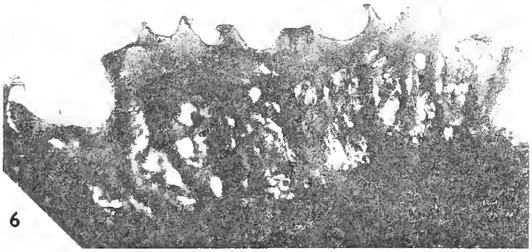
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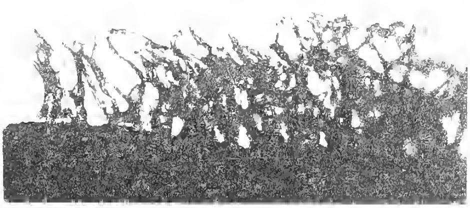
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ALVIN, Lower Carboniferous megaspores

It was carefully examined at every stage and the only structural damage that was observed was that some hairs protruding through patches of pyrite on the surface came away when this was dissolved at the final stage.

The most obvious difference between the two species is the presence in *T. pannosus* of large buttressed spines and their apparently complete absence in *T. subpalaeocristatus*. It has been noticed that the spines are frequently broken (Pl. 76, fig. 3, middle) and also that touching them with a needle often causes them to break away cleanly from the surface. Abrasion of the spore prior to preservation could conceivably have removed all the spines in the spores from the nodule. However, if abrasion sufficient to have removed all the spines had occurred, the short delicate hairs scattered over the wall and the hairs of the trilete crest would probably not have survived as they have. Moreover, all the known specimens of *T. subpalaeocristatus*, including the new one, were lying in close proximity to the cone of *Oxroadia* which probably bore them.

Disregarding the spiny character, there are other differences between these two kinds of spores which seem quite sufficient to indicate that they are genuinely distinct species. These are: (1) the greater length of the arms of the trilete ridge in *T. subpalaeocristatus*; (2) the finer hairs of the crest and the lesser degree of fusion among them; (3) the arcuate zones of papillae and hairs of which there is no indication in *T. pannosus*; (4) the presence of some short hairs on the contact areas, particularly near the tips of the ridge which again are entirely lacking in the species from the shale where in fact the lips are very sharply delimited from the contact areas.

The coincidence at the same locality of these two spores sharing the very unusual character of a trilete crest of anastomosing hairs is remarkable. The fact that one is apparently confined to the shale bands and the other is known only from a nodule may be of no significance. On the other hand, it may indicate an ecological difference between the two plants, possibly related lycopods, that they represent. Nothing is yet known of the composition of the microfossil flora of the shales, and of the nodule flora, only a small number of macrofossil species have been described.

Acknowledgement. My thanks are due to Mr. A. Horne for photographic assistance.

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UPPER CRETACEOUS FORAMINIFERA FROM THE BALLYDEENLEA CHALK, COUNTY KERRY, IRELAND

by F. T. BARR

ABSTRACT. Twenty-three species of Upper Cretaceous foraminifera have been recovered from the newly discovered (Walsh 1960) Ballydeenlea Chalk of County Kerry, Ireland. These are the first Upper Cretaceous foraminifera reported from the Republic of Ireland and the westernmost Upper Cretaceous fauna found in Europe. This faunal assemblage shows that the Ballydeenlea Chalk can be correlated with part of the Upper Chalk (Senonian) of England and Northern Ireland. The presence of *Bolivinoides decorata* (Jones) in this fauna indicates further that the Ballydeenlea Chalk is, at least in part, Upper Campanian in age and equivalent to the *Belemnitella mucronata* zone of the British Isles and Western Europe.

IN 1960, while systematically mapping the Upper Palaeozoic rocks of the Killarney District, County Kerry, Dr. P. T. Walsh discovered a small pocket of hard white chalk within the typical dark Palaeozoic shale and limestone of the area. This chalk was exposed in a disused quarry in Ballydeenlea townland, six miles north of Killarney, and had been quarried for perhaps over a century until 1930. The exposure may have been known to geologists in the past, but until Walsh's (1960) initial investigation, there is no record in the literature that any geological significance had ever been attributed to this exposure. Walsh collected material from this quarry and soon both megafossils and microfossils suggestive of an Upper Cretaceous age were recognized. The megafossils consisted chiefly of fragments of *Inoceramus sp.* and fragments of unidentifiable echinoids. Foraminifera were observed in thin section and although specific identifications could not be made, generic determinations suggested that the Ballydeenlea Chalk was Upper Cretaceous in age. This was the first recognition of Cretaceous rocks in the Republic of Ireland.

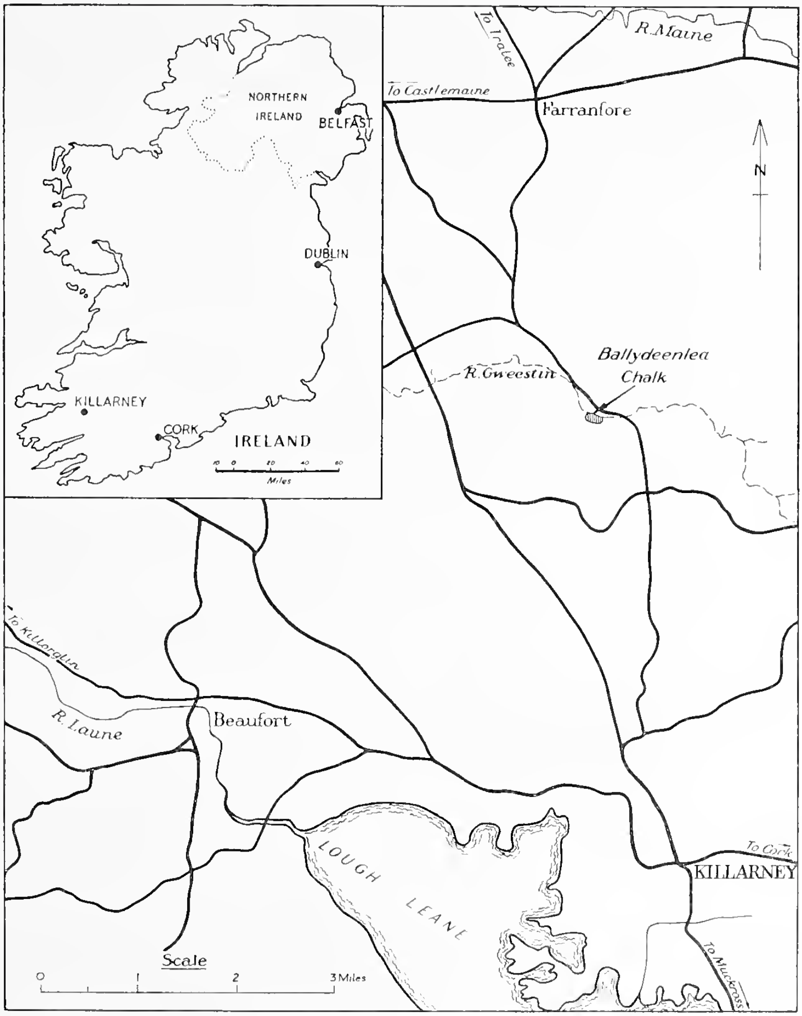
The Ballydeenlea Chalk is a pocket-like mass surrounded by Palaeozoic rocks. The minimum dimensions of this deposit are approximately 130 ft. by 300 ft. and the thickness is about 100 ft. The Ballydeenlea Chalk shows no bedding and consists chiefly of a hard white limestone. Flint nodules typical of the Upper Cretaceous Chalk of England and Northern Ireland are common. Angular fragments of brecciated dark shale are also abundant throughout most of the deposit. These fragments vary in size from a few millimetres to pieces several feet across. This shale has so far been found to be unfossiliferous.

Walsh (1966) gives a detailed description of the Ballydeenlea Chalk and several other deposits in the Killarney district which may possibly be related. He concludes that the Ballydeenlea Chalk represents a karst collapse deposit. Prior to Upper Cretaceous times, a large cavern formed in the Carboniferous limestone. During the late Cretaceous, an arm of the sea transgressed over this area, probably from the west, depositing a marine sequence of white chalk over the Killarney district. Soon afterwards, the roof of the limestone cavern collapsed and the cavern was filled by the overlying Upper Cretaceous Chalk along with fragments of dark Palaeozoic shales from the roof. The Ballydeenlea

[Palaeontology, Vol. 9, Part 3, 1966, pp. 492–510, pls. 77–79.]

Chalk was thus protected from later erosion, whereas the great bulk of Upper Cretaceous sediments deposited over this part of Ireland was removed by Cenozoic erosion.

The preservation of this small deposit of Upper Cretaceous Chalk is indeed fortunate.



TEXT-FIG. 1. Map showing location of the Ballydeenlea Chalk in Co. Kerry, south-western Ireland.

Its presence has considerably changed some of the fundamental ideas about the palaeogeography of Ireland during the Upper Cretaceous. The purposes of this present study are: (1) to date the Ballydeenlea Chalk more exactly, which should add to the precision of palaeogeographic reconstruction; (2) to show that earlier suggestions (Walsh 1960, p. 113) that the Ballydeenlea Chalk was equivalent to the Middle Chalk (Turonian) are incorrect; and (3) to describe and document the first Upper Cretaceous foraminifera found in the Republic of Ireland, and which also constitute the westernmost Upper Cretaceous fauna in Europe.

Acknowledgements. I thank Dr. P. T. Walsh for supplying the material from the Ballydeenlea Chalk on which this study is based, and discussing various problems related to this deposit; Miss Elizabeth R. Hill, Mr. Wilf Austin, and Mr. John Smith for help with the manuscript; and my wife, Melza, for preparing the illustrations of foraminifera.

Deposition of types. All specimens illustrated in this paper and additional material from the Ballydeenlea Chalk are deposited in the British Museum (Natural History).

PALAEONTOLOGY AND AGE OF THE BALLYDEENLEA CHALK

The Ballydeenlea Chalk is predominantly a hard white limestone which was found difficult to disaggregate. First attempts to obtain foraminifera in a free form from this well-indurated rock were unsuccessful. Consequently, foraminifera were first observed only in thin section. Thin sections of the Ballydeenlea Chalk characteristically exhibit fairly common foraminifera in addition to abundant small fossil fragments. On the basis of these foraminifera, Dr. F. T. Banner and Dr. W. H. Blow (British Petroleum Co.) expressed the opinion that this Irish chalk was equivalent to the Middle Chalk (Turonian) (Walsh 1960, p. 113).

I subsequently experimented with various techniques to disaggregate this tough limestone and obtain specimens of foraminifera in a free state, and met with partial success using the following method:

1. The limestone was crushed down to fine pebble size.
2. This material was then heated in a dilute solution of hydrogen peroxide for several hours.
3. The residue was then washed through a 200-mesh sieve.
4. The remaining fraction was then placed in an ultrasonic vibrator for 30 to 45 minutes.

This is rough treatment for delicate foraminifera and no doubt many specimens were destroyed or damaged. Nevertheless, by using large amounts of material and repeating this process many times, a large, although generally poorly preserved, fauna was finally obtained. In addition to the foraminifera recovered, molluscan and echinoid fragments were common, siliceous sponge spicules were abundant, fish teeth were rare, and a single ostracod was found. The following foraminifera are recorded from the Ballydeenlea Chalk:

Ammodiscus cretacea (Reuss)
Glomospira cf. *gordialis* (Jones and Parker)
Textularia sp.
Trochamminoides sp.
Haplophragmoides sp.
Ataxophragmium variablis (d'Orbigny)
Arenobulimina cf. *sphaerica* Marie
Lagena acuticosta Reuss
Nodosaria limbata (?) d'Orbigny
Dentalina cf. *communis* (d'Orbigny)
Lenticulina sp.
Praebulimina obtusa (d'Orbigny)
Bolivinitella eleyi (Cushman)
Bolivinoides decorata (Jones)

Heterohelix globulosa (Reuss)
Gyroidinoides umbilicata (d'Orbigny)
Eponides cf. *concinna* Brotzen
Globigerinelloides aspera (Ehrenberg)
Rugoglobigerina sp.
Gavelinella lorniana (d'Orbigny)
Gavelinella thalmanni (Brotzen)
Gavelinella sp.
Cibicides beaumontiana (d'Orbigny)

It is not certain how well this list of foraminifera represents the complete fauna. By analogy with faunas usually obtained from the Upper Cretaceous Chalk of southern England, one would suspect that this list represents only a fraction of the complete fauna. The methods used to disaggregate the limestone probably introduced a considerable bias in the fauna obtained.

Nevertheless, the foraminifera recovered from the Ballydeenlea Chalk can be used to date this deposit precisely. It must be pointed out that it is possible that the Ballydeenlea Chalk may consist of a mixture of sediments of several different ages. However, all the species recovered can occur together within a faunal assemblage of a single age. Many of the species range in the British Isles and Western Europe throughout most of the Senonian (see text-fig. 2); other species have a stratigraphic range of Middle Senonian to Maestrichtian. The bulk of the fauna, therefore, indicates that the Ballydeenlea Chalk is a time equivalent to part of the Upper Chalk (Senonian) of England, not the Middle Chalk (Turonian) as was previously suggested. Furthermore, about twelve specimens of *Bolivinoides decorata* (Jones) were recovered. This species is restricted to the *Belemnitella mucronata* Zone (Upper Campanian) of England, Northern Ireland, and Western Europe in general (Barr 1966), and its presence therefore indicates that the Ballydeenlea Chalk, at least in part, is Upper Campanian in age and a time equivalent to the *B. mucronata* Zone of England and Northern Ireland.

SYSTEMATIC PALAEONTOLOGY

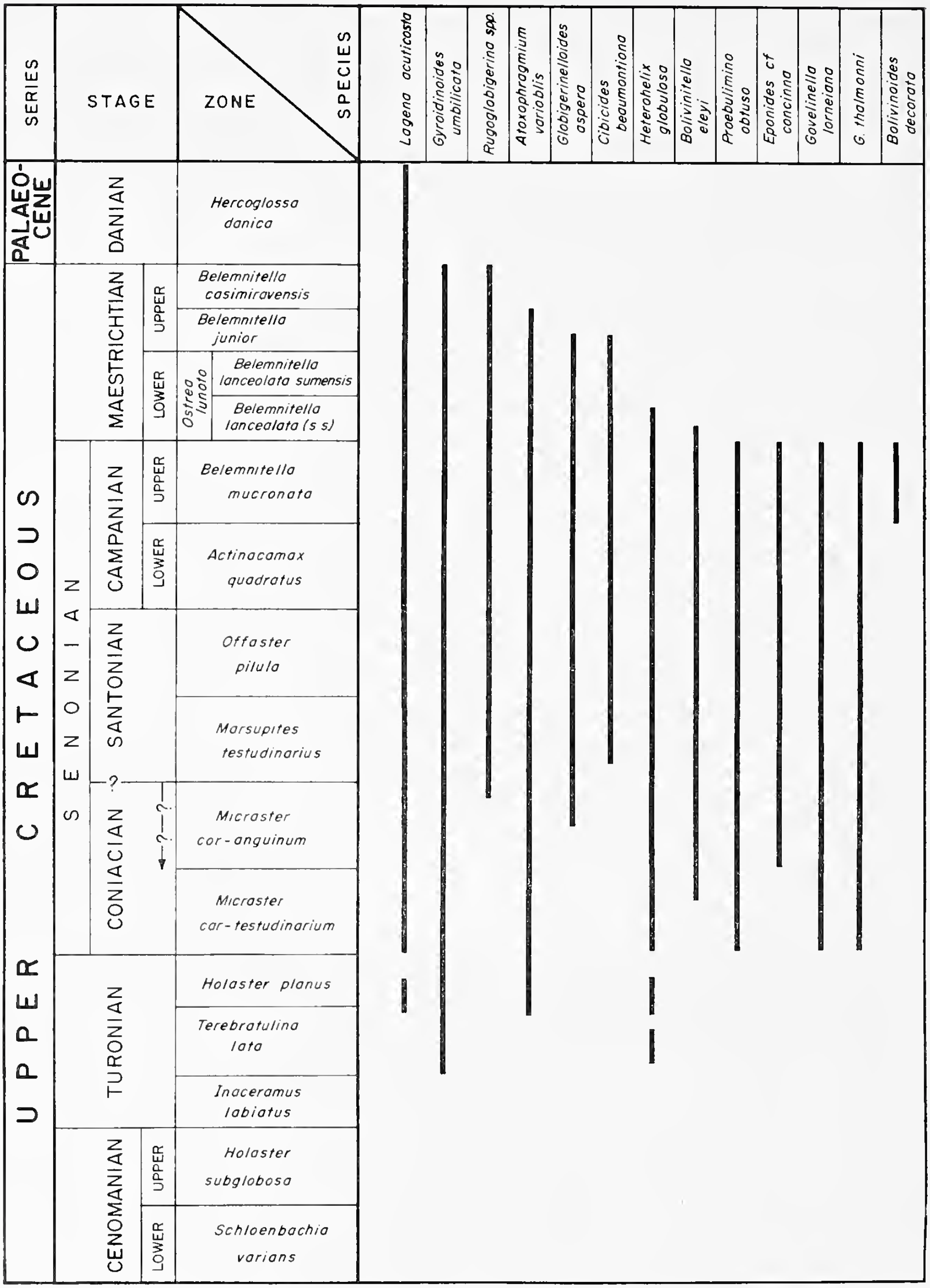
Family AMMODISCIDAE Reuss 1862
Subfamily AMMODISCINAE Reuss 1862
Genus AMMODISCUS Reuss 1862

Ammodiscus cretacea Reuss

Plate 77, fig. 2

Operculina cretacea Reuss 1845, p. 35, pl. 13, figs. 64, 65.
Cornuspira cretacea Reuss; Reuss 1860, p. 177, pl. 1, fig. 1.
Ammodiscus gaulticus Berthelin; Brotzen 1936, p. 31, pl. 1, figs. 3 *a*, *b*.
Ammodiscus cretacea (Reuss); Marie 1941, p. 18, pl. 1, figs. 5–6.
Ammodiscus cretaceus (Reuss); Cushman 1946, pp. 17, 18, pl. 1, fig. 35 (see synonymy).
Ammodiscus cretaceus (Reuss); Hagn 1953, pp. 4, 5, fig. 3.
Involutina cretacea (Reuss); Belford 1960, pp. 22, 23, pl. 6, fig. 1.

Occurrence. Rare distorted specimens of *A. cretacea* were recovered from the Ballydeenlea Chalk. This species, although usually rare, has a wide geographic distribution and ranges throughout much of the Upper Cretaceous.



TEXT-FIG. 2. Chart showing the stratigraphic ranges in the British Isles and Western Europe of some of the Foraminifera recovered from the Ballydeenlea Chalk. Based chiefly on Barr (1961, 1962, 1966).

Genus GLOMOSPIRA Rzehak 1885
Glomospira cf. *gordialis* (Jones and Parker)

Trochammina squamata var. *gordialis* Jones and Parker 1860, p. 304.

Trochammina squamata var. *gordialis* Jones and Parker; Parker and Jones 1865, p. 408, pl. 15, fig. 32.

Glomospira gordialis Jones and Parker; Cushman 1946, pp. 18, 19, pl. 1, figs. 38–40 (see synonymy).

Occurrence. A single specimen was recovered from the Ballydeenlea Chalk; it appears to be identical to specimens illustrated by Cushman (1946, p. 18, pl. 1, figs. 38–40). Cushman (op. cit., p. 19) recorded *G. gordialis* from the Austin Chalk, Taylor Marl, and Velasco Shale of the Gulf Coastal Area of the U.S.A. and Mexico.

Family ATAXOPHRAGMIIDAE Schwager 1877
Subfamily ATAXOPHRAGMIINAE Schwager 1877
Genus ATAXOPHRAGMIUM Reuss

Ataxophragmium variablis (d'Orbigny)

Bulimina variablis d'Orbigny 1840, p. 40, pl. 4, figs. 9–11.

Ataxogyroidina variablis (d'Orbigny); Barnard and Banner 1953, pp. 205, 206, pl. 9, figs. 6 *a*, *b*; text-figs. 7 *a–l* (see synonymy).

Remarks. There is considerable variation in the general test shape, configuration of apertural face, and in shape of aperture. Barnard and Banner (1953, text-figs. 7 *a–l*) illustrated much of this variation.

Occurrence. Rare specimens of *A. variablis* were recovered from the Ballydeenlea Chalk. This species is abundant in the Senonian Chalk of southern England, the Paris Basin, and other parts of Western Europe.

Subfamily GLOBOTEXTULARIINAE Cushman 1927*a*
Genus ARENOBULIMINA Cushman 1927*a*

Arenobulimina cf. *sphaerica* Marie

Arenobulimina sphaerica Marie 1941, p. 49, pl. 4, figs. 36 *a–e*.

Remarks. Three specimens of a small *Arenobulimina* recovered from the Ballydeenlea Chalk closely resemble *A. sphaerica* Marie in most respects. The poor preservation of these specimens, however, does not allow a positive identification.

A. sphaerica was originally described from the *B. mucronata* Zone of the Paris Basin.

Family LITUOLIDAE de Blainville 1825
Subfamily HAPLOPHRAGMOIDINAE Maync 1952
Genus TROCHAMMINOIDES Cushman 1910

Trochamminoides sp.

Plate 77, figs. 1 *a*, *b*

Description. Test planispiral, loosely coiled, evolute, biumbilicate, often distorted; periphery in side view circular; 6–9 indistinct chambers in final whorl, uniformly and rapidly increasing in size; sutures indistinct, weakly depressed, slightly curved, radial; wall finely arenaceous.

Remarks. This species is similar to *Trochamminoides velascoensis* Cushman in some respects, but can easily be distinguished by its larger size, greater and rapidly increased thickness, and less compressed test.

Occurrence. This species is rare in the Ballydeenlea Chalk. Specimens of an unnamed species of *Trochamminoides* have been observed in the Campanian of the Sacramento Valley, California, and appear to be conspecific with this Irish form.

Family NODOSARIIDAE Ehrenberg 1838
Subfamily NODOSARIINAE Ehrenberg 1838
Genus NODOSARIA Lamarck 1812

Nodosaria limbata (?) d'Orbigny

Nodosaria limbata d'Orbigny 1840, p. 12, pl. 1, fig. 1.
Nodosaria limbata d'Orbigny; Franke 1928, p. 42, pl. 3, figs. 27, 28.
Nodosaria limbata d'Orbigny; Cushman and Jarvis 1932, p. 32, pl. 10, fig. 5.
Nodosaria concinna Reuss; Cushman and Jarvis 1932 (*non* Reuss), pp. 31, 32, pl. 10, fig. 4.
Nodosaria limbata d'Orbigny; Cushman 1946, p. 74, pl. 27, figs. 1, 2 (see synonymy).
Dentalina concinna (Reuss); Hagn 1953 (*non* Reuss), pp. 43, 44, pl. 4, fig. 18.
Nodosaria limbata d'Orbigny; Said and Kenawy 1956, p. 133, pl. 2, fig. 32.
Dentalina catenula catenula Reuss; Pożaryska 1957 (*non* Reuss), pp. 76, 77, pl. 9, fig. 8.
Nodosaria limbata d'Orbigny; Belford 1960, pp. 38, 39, pl. 11, figs. 7–9.

Occurrence. Rare broken specimens of *Nodosaria* were recovered from the Ballydeenlea Chalk. These fragments appear to be identical to the specimens of *N. limbata* in the d'Orbigny Collection in Paris; however, because of the incompleteness of the only specimens recovered, there is still some uncertainty as to this identification. I have also found specimens of *N. limbata* in the *B. mucronata* Zone (Upper Campanian) of southern England and in the *B. lanceolata* Zone (Lower Maestrichtian) at Sidestrand, Norfolk. D'Orbigny (1840, p. 12) originally described this species from the *B. mucronata* Zone at Meudon in the Paris Basin.

Genus LAGENA Walker and Jacob 1798

Lagena acuticosta Reuss

Plate 77, figs. 7, 8

Lagena acuticosta Reuss 1862, p. 305, pl. 1, fig. 4.
Lagena acuticosta Reuss; Egger 1899, p. 106, pl. 5, fig. 12.

EXPLANATION OF PLATE 77

All specimens are from the Ballydeenlea Chalk, ×125.

Fig. 1. *Trochamminoides sp.* 1*a*, side view; 1*b*, end view; P45707.
Fig. 2. *Ammodiscus cretacea* Reuss, side view; P45710.
Fig. 3. *Praebulimina obtusa* (d'Orbigny); P45702.
Figs. 4, 5. *Bolivinoides decorata* (Jones). 4, side view, final chamber broken; P45693. 5*a*, side view; 5*b*, end view; P45692.
Fig. 6. *Bolivinitella eleyi* (Cushman). 6*a*, side view; 6*b*, edge view; P45698.
Figs. 7, 8. *Lagena acuticosta* Reuss. 7, P45699. 8, P45700.

BARR, Foraminifera from Ballydeenlea Chalk

Lagena isabella (d'Orbigny); Franke 1925 (*non* d'Orbigny), p. 60, pl. 4, fig. 40.
Lagena isabella (d'Orbigny); Franke 1928, p. 87, pl. 8, fig. 1.
Lagena acuticosta Reuss; Cushman 1931*a*, p. 308, pl. 35, fig. 12.
Lagena acuticosta Reuss; Cushman 1932, p. 337, pl. 50, fig. 13.
Lagena isabella (d'Orbigny); Brotzen 1936 (*non* d'Orbigny), pp. 111, 112, pl. 7, fig. 5; text-fig. 37.
Lagena cayeuxi Marie 1941, pp. 74, 75, pl. 9, figs. 82, 83.
Lagena amphora Reuss; Schijfsma 1946, p. 54, pl. 2, fig. 17.
Lagena acuticosta Reuss; Cushman 1946, p. 94, pl. 39, figs. 14, 15.
Lagena acuticosta Reuss; Visser 1951, pp. 234, 235, pl. 2, fig. 1.
Lagena acuticosta Reuss; Frizzell 1954, p. 102, pl. 14, figs. 1, 2.
Lagena cf. *cayeuxi* Marie; McGugan 1957, p. 339, pl. 31, fig. 22.
Lagena acuticosta Reuss; Martin 1964, p. 61, pl. 5, figs. 2*a*, *b*.

Occurrence. Six specimens of *L. acuticosta* Reuss were found in the Ballydeenlea Chalk. This species has a long stratigraphical range and great geographical distribution; it ranges from the *M. cor-testudinarium* Zone (Coniacian) to the top of the *B. mucronata* Zone (Upper Campanian) on the Isle of Wight. I have also found this species in the Lower Maestrichtian of Norfolk, the Lower Maestrichtian of southern Limberg, and the Upper Maestrichtian of Stevns Klint, Denmark. Cushman (1946, p. 94) reported that *L. acuticosta* had a wide distribution in the Gulf Coastal area of the U.S.A., occurring in strata of Austin to Navarro age.

Family TURRILINIDAE Cushman 1927*a*
Subfamily TURRILININAE Cushman 1927*a*
Genus PRAEBULIMINA Hofker 1953

Praebulimina obtusa (d'Orbigny)

Plate 77, fig. 3

Bulimina obtusa d'Orbigny 1840, p. 39, pl. 4, figs. 5, 6.
Bulimina laevis Beissel 1891 (part), p. 66, pl. 12, figs. 42, 43 (*non* figs. 39–41).
Bulimina elegans d'Orbigny; Chapman 1892 (*non* d'Orbigny), p. 516 (list), pl. 15, fig. 9.
Bulimina elegans d'Orbigny; Heron-Allen and Earland 1910, p. 409, pl. 6, fig. 11.
Bulimina ovulum Reuss; Franke 1925, p. 25, pl. 2, fig. 17.
Bulimina ovulum Reuss; Franke 1928, p. 157, pl. 14, fig. 14.
Buliminella carseyae Plummer; Dain 1934 (*non* Plummer), p. 37, pl. 4, fig. 38.
Buliminella laevis (Beissel); Cushman and Parker 1936, p. 6, pl. 2, figs. 3*a–c*.
Buliminella obtusa (d'Orbigny); Brotzen 1936, p. 131, pl. 8, figs. 2*a*, *b*.
Buliminella obtusa (d'Orbigny) forma typica; Marie 1941, p. 198, pl. 30, figs. 291*a–f*.
Buliminella obtusa (d'Orbigny) *inflata* Marie 1941, p. 199, pl. 30, figs. 192*a–e*.
Buliminella obtusa (d'Orbigny) *laevis* (Beissel); Marie 1941, p. 199, pl. 30, figs. 293*a–e*; pl. 31, figs. 294*a–e*.
Buliminella obtusa (d'Orbigny); Schijfsma 1946, p. 80, pl. 4, fig. 9.

Description. Test free, tapering, approximately $1\frac{1}{2}$ times longer than wide, consisting of 4 to 5 whorls each containing 3 to 4 weakly inflated chambers rapidly and uniformly increasing in size; spiral sutures depressed; chamber sutures curved, flush or weakly depressed; aperture slit-like or loop-shaped opening along inner margin of final chamber, often also extending up into chamber face bordered by thin narrow lip; tooth plate simple, narrow, attached to inner side of aperture and extending into penultimate aperture; wall calcareous, smooth, finely perforate.

Remarks. *P. obtusa* occurs commonly throughout the Senonian chalk of southern England. In the middle and upper parts of the *B. mucronata* Zone, it becomes progressively larger, more inflated and more ovate, and eventually evolves into a distinctively larger form which is indicative of the latest Campanian and Maestrichtian in Western Europe.

Occurrence. D'Orbigny (1840, pp. 39, 40) originally described this species from the Upper Cretaceous localities at Meudon and Saint-Germain in the Paris Basin. Marie (1941, pp. 197–9) reported three varieties of this species from the *B. mucronata* Zone of the Paris Basin, and Schijfsma (1946, p. 80) records *P. obtusa* from the Campanian of southern Limberg, Netherlands. *P. obtusa* is common in the Ballydeenlea Chalk.

Family BOLIVINITIDAE Cushman 1927*a*
Genus BOLIVINOIDES Cushman 1927*a*

Bolivinoides decorata (Jones)

Plate 77, figs. 4, 5

Bolivinoides decorata (Jones); Barr 1966, pp. 220–43, pl. 34, figs. 2–6, 12; pl. 35, figs. 6–9; pl. 36, figs. 1–5. Full synonymy.

Remarks. *B. decorata* (Jones), a species common to the *B. mucronata* Zone of southern England and Northern Ireland, has recently been described in detail (Barr 1966). A lectotype was established from a series of syntypic specimens in the Joseph Wright Collection, which is located in the Queen's University, Belfast (op. cit. pp. 231–4, pl. 36, figs. 1 *a*, *b*). *B. decorata* was shown to have exceptional value as an index fossil of the Upper Campanian.

The direct ancestor of *B. decorata* appears to be *B. hiltermanni* Barr. The latter gave rise to *B. decorata* at the beginning of the Upper Campanian (base of the *B. mucronata* Zone). The *A. quadratus* Zone–*B. mucronata* Zone (Lower Campanian–Upper Campanian) contact in southern England can be located with some accuracy at the stratigraphic position where *B. hiltermanni* is replaced by *B. decorata* (s.s.). *B. decorata* differs from its ancestor, *B. hiltermanni*, by having a larger, more flaring test with a small length/breadth ratio (usually 1·5 to 1·8 compared with 1·9 to 2·3 which is most usual for *B. hiltermanni*). The surface sculpture is more distinct on *B. decorata* and there are more lobes on the final chambers, most often 4 or 5, whereas *B. hiltermanni* usually possesses 3 on its latest chambers.

Bolivinoides miliaris Hiltermann and Koch is similar to *B. decorata* (Jones) in many respects and appears to have been derived from *B. decorata* during the late *B. mucronata* Zone. *B. decorata* is distinguished from *B. miliaris* by having a slightly greater length/breadth ratio and a more elongate, less rhomboidal lateral outline. The maximum breadth of *B. decorata* is closer to the apertural end, whereas the maximum breadth of *B. miliaris* is nearer the mid-point of the test. The surface lobes of *B. miliaris* are less regular than those of *B. decorata* and there is more of a tendency for them to fuse with the lobes on the earlier chambers.

Edgell (1954, pp. 71, 72) described a new subspecies which he named *B. decorata* (Jones) *australis*. This subspecies is a form transitional between *B. decorata* (Jones) and *B. gigantea* Hiltermann and Koch. Barr (1966) re-examined type specimens of *B. decorata australis* and concluded that this form was closer morphologically to *B. gigantea* and was quite distinct from *B. decorata* (s.s.). *B. australis* appears to have evolved from

B. decorata (s.s.) at the beginning of the Maestrichtian. It can be distinguished from *B. decorata* by: (1) having a smaller length/breadth ratio; (2) having more surface lobes on the final chambers (5 to 7 on the final chamber compared with 4 or 5 for *B. decorata* s.s.); (3) possibly being more commonly ornamented near its initial end; and (4) sometimes having a more rhomboidal outline.

Occurrence. Approximately twelve specimens of *Bolivinoides decorata* were recovered from the Ballydeenlea Chalk. However, most of these specimens were broken or damaged to varying degrees.

B. decorata occurs in abundance throughout the *B. mucronata* Zone in southern England and appears to be restricted to this zone (Barr 1966). The type locality for this species is at Keady Hill, County Derry, Northern Ireland, which is probably in the upper part of the *B. mucronata* Zone.

B. decorata also occurs in the Ballycastle Pellet Chalk of Northern Ireland (McGugan 1957, p. 339, pl. 32, figs. 10–15; Barr 1966). However, it appears that this formation was derived by Tertiary erosion of an Upper Cretaceous land surface (Charlesworth 1963, p. 369) and that the contained foraminifera were also derived from the nearby Upper Cretaceous Chalk.

Genus BOLIVINITELLA Marie 1941

In 1854, Ehrenberg proposed the generic name *Loxostomum*, but unfortunately neither gave a description of this new genus nor designated a type species. However, he listed seven new Upper Cretaceous species which he considered to belong to this genus: *Loxostomum aculeatum*, *L. anglicum*, *L. curvatum*, *L. rostratum*, *L. subrostratum*, *L. tumens*, and *L. vorax*. None of these species was described and the only illustrations were of specimens mounted in balsam and viewed by transmitted light. Consequently, there have been few attempts to use Ehrenberg's species of *Loxostomum* and most of them must be considered *nomina dubia*.

Cushman (1927*b*) subsequently fixed the type species of the genus *Loxostomum* as *L. subrostratum* Ehrenberg. In various editions of Cushman's classification (e.g. 1955, p. 269, pl. 27, figs. 30–32), he described *Loxostomum* as follows: 'Test in early stages similar to *Bolivina*, adult tending to become uniserial; aperture terminal.—Cretaceous to Recent.' Cushman included *Bolivina plaita* Carsey in the genus *Loxostomum*. Subsequent authors have considered this species typical of the genus and have based their concept of *Loxostomum* on this and similar forms.

Marie (1941, pp. 189, 190) erected the genus *Bolivinitella* and designated the well-known species *Bolivinita eleyi* Cushman as the type species. Marie (op. cit., p. 191, pl. 29, figs. 282 *a–c*) illustrated a typical specimen of *B. eleyi* from the *B. mucronata* Zone (Upper Campanian) at Montereau, and listed the occurrence of this species from numerous other localities in the Paris Basin in the *B. mucronata* Zone, including Meudon (one of the two localities from which Ehrenberg (1854) originally recovered his specimens of *Loxostomum subrostratum*).

Following suggestions made by Hofker (1952), Loeblich and Tappan (1962, pp. 110, 111) placed *Bolivinitella* Marie and *Loxostomum* Ehrenberg in synonymy. They suppressed *Bolivinitella* as a junior synonym of *Loxostomum* and erected a new genus, *Coryphostoma*, in which they placed many species previously referred to *Loxostomum* (e.g. *Bolivina plaita* Carsey). Loeblich and Tappan pointed out that Marie (1941) recorded *Bolivinitella* forma typica from Meudon, a locality from which Ehrenberg originally described *Loxostomum subrostratum*. They concluded: 'the specimens illustrated as *B. eleyi* by Marie (1941, pl. 29, figs. 282 *a–c*) are typical of *L. subrostratum* and the two "species" are not only congeneric, but almost certainly conspecific.'

At best the suppression of *Bolivinitella* as a junior synonym of *Loxostomum* is premature. Ehrenberg never described *L. subrostratum* and the only illustration is a drawing of a specimen viewed by transmitted light. Consequently, *L. subrostratum* is not well enough known to be recognized with any assurance. Furthermore, I have collected material from the Upper Cretaceous Chalk at Meudon with M. Pierre Marie which indeed contains numerous specimens of *Bolivinitella eleyi*; however, there are a number of other biserial forms present (e.g. *Bolivina plaita*) which might conceivably belong to the true *Loxostomum subrostratum*. Therefore, at least until Ehrenberg's original specimens can be re-examined, it would seem best to continue the usage of *Bolivinitella* as a valid genus.

Bolivinitella eleyi (Cushman)

Plate 77, figs. 6 *a, b*

Textularia obsoleta Reuss; Eley 1859 (*non* Reuss), p. 202, pl. 8, fig. 11*c*.
Bolivina obsoleta Eley; Jones 1872, p. 124 (list).
Bolivinita eleyi Cushman 1927*a*, p. 91, pl. 12, figs. 11 *a, b*.
Bolivinita eleyi Cushman; Cushman 1931*b*, p. 39, pl. 5, figs. 8 *a, b*.
Bolivinita eleyi Cushman; Cushman 1932, p. 338, pl. 51, figs. 7 *a, b*.
Bolivina quadrilatera (Schwager); Macfadyen 1932, pp. 492, 493, pl. 35, figs. 21 *a, b*.
Bolivinita quadrilatera (Schwager); Dain 1934, pp. 34, 35, pl. 3, fig. 35.
Bolivinita eleyi Cushman; Brotzen 1936, p. 122, pl. 9, figs. 5 *a, b*, text-fig. 41.
Bolivinitella eleyi (Cushman); Marie 1941, p. 190, pl. 29, figs. 282 *a, b*.
Bolivinita eleyi Cushman; Cushman 1946, p. 114, pl. 48, figs. 18–20.
Bolivinitella eleyi Cushman; Schijfsma 1946, pp. 72, 73, pl. 6, fig. 10.
Bolivinita eleyi Cushman; Hagn 1953, p. 76, pl. 6, fig. 24.
Bolivinitella eleyi (Cushman); Frizzell 1954, p. 112, pl. 16, figs. 23 *a, b*.
Bolivinitella eleyi (Cushman); McGugan 1957, p. 340.
Bolivinitella eleyi (Cushman); Montanaro Gallitelli 1957, p. 150, pl. 34, figs. 14–17.
Bolivinitella eleyi (Cushman); Belford 1960, p. 62, pl. 15, figs. 20, 21.
Bolivinitella eleyi (Cushman); Akimets 1961, pp. 192, 193, pl. 19, figs. 9 *a, b*.
Bolivinita eleyi Cushman; Kaptarenko-Chernousova *et al.* 1963, p. 113, pl. 19, figs. 7 *a, b*.
Bolivinitella eleyi (Cushman); Graham and Church 1963, p. 51, pl. 5, figs. 25 *a, b*.

Description. Test elongate, compressed, sometimes twisted, rectangular in cross-section, with up to 16 chambers arranged biserially, almost becoming uniserial in final stage; sides nearly parallel or gradually tapering; lateral sides flat or slightly concave, chambers reniform, arched, overlapping; sutures distinct, limbate, flush or very slightly raised, fusing at edges, forming a thin longitudinal keel along each edge; wall calcareous, very finely perforate, surface smooth; aperture a thin terminal slit; approximate length 0·56 mm.; breadth 0·20 mm.; thickness 0·09 mm.

Occurrence. *B. eleyi* is fairly common in the Ballydeenlea Chalk. It is common in southern England, where it ranges from the base of the *M. cor-anguinum* Zone to the top of the *B. mucronata* Zone. *B. eleyi* also occurs in lowermost Maestrichtian strata of Western Europe and North Africa. The holotype is from the upper Brownstone Marl of Arkansas.

Family HETEROHELICIDAE Cushman 1927*a*
Subfamily HETEROHELICINAE Cushman 1927*a*
Genus HETEROHELIX Ehrenberg 1843

Heterohelix globulosa (Ehrenberg)

Plate 78, figs. 5, 6

Textularia globulosa Ehrenburg 1840, p. 135, pl. 4, figs. 2, 4, 5, 7, 8.
Textilaria globulosa Ehrenburg; Ehrenburg 1854, pl. 21, fig. 87.
Textularia globulosa Ehrenberg; Eley 1859, pp. 194, 202, pl. 2, fig. 9; pl. 9, fig. 9.
Textilaria globifera Reuss 1860, p. 232, pl. 13, figs. 7, 8.
Textularia decurrens Chapman 1892, p. 515, pl. 15, fig. 6.
Gümbelina globulosa (Ehrenberg); Egger 1899, p. 32, pl. 14, fig. 43.
Textularia globifera Reuss; Franke 1925, p. 11, pl. 1, fig. 13.
Textularia globulosa Ehrenberg; Franke 1928, p. 134, pl. 12, fig. 11.
Pseudotextularia globulosa (Ehrenberg); Macfadyen 1932, pl. 35, fig. 22.
Gümbelina globulosa (Ehrenberg); Morrow 1934, p. 194, pl. 29, figs. 18*a*, b.
Gümbelina globifera (Reuss); Loetterle 1937, p. 34, pl. 5, fig. 3.
Gümbelina globulosa (Ehrenberg); Cushman 1946, pp. 105, 106, pl. 45, figs. 9–15 (see synonymy).
Gümbelina globulosa (Ehrenberg); Williams-Mitchell 1948, p. 99, pl. 9, fig. 2.
Gümbelina globulosa (Ehrenberg); Loeblich 1951, p. 108, pl. 12, figs. 4, 5.
Gümbelina globulosa (Ehrenberg); Hagn 1953, p. 73, pl. 6, figs. 16, 17.
Gümbelina globulosa (Ehrenberg); Frizzell 1954, p. 109, pl. 15, figs. 24–27.
Heterohelix globulosa (Ehrenberg); Montanaro Gallitelli 1957, pl. 31, figs. 12–15.
Gümbelina globulosa (Ehrenberg); Belford 1960, p. 59, pl. 15, figs. 10, 11.
Heterohelix globulosa (Ehrenberg); Said and Kerdany 1961, p. 331, pl. 2, fig. 1.
Heterohelix globulosa (Ehrenberg); Graham and Church 1963, pp. 61, 62, pl. 7, figs. 11*a*, *b*.
Heterohelix globulosa (Ehrenberg); Barr and Cordey 1964, pp. 306, 307, pl. 49, fig. 4.
Heterohelix globulosa (Ehrenberg); Takayanagi 1965, pp. 195, 196, pl. 20, figs. 1*a*, *b* (see synonymy).

Remarks. *H. globulosa* is distinguished by its tapering test, lobulate periphery, and smooth globular chambers. Specimens of *H. globulosa* are fairly common in the Ballydeenlea Chalk, but most are somewhat smaller than typical specimens of this species.

Occurrence. *H. globulosa* occurs in abundance throughout the Senonian of southern England. Williams-Mitchell (1948, pl. 10) recorded the range of this species in the Chalk of England as *I. labiatus* Zone (Lower Turonian) to the *B. mucronata* Zone. *Textularia decurrens* Chapman (= *H. globulosa*) was originally described from the phosphatic chalk at Taplow, Buckinghamshire, which is referred to the *M. testudinarius* Zone (Santonian) (Barr and Cordey 1964, pp. 306, 307).

Family PLANOMALINIDAE Bolli, Loeblich, and Tappan 1957
Genus GLOBIGERINELLOIDES Cushman and ten Dam 1948

Globigerinelloides aspera (Ehrenberg)

Plate 78, figs. 4*a*, *b*

Rotalia aspera Ehrenberg 1854, p. 24, pl. 27, figs. 57, 58; pl. 28, fig. 42; pl. 31, fig. 44.
Phanerostomum asperum Ehrenberg 1854, p. 23, pl. 30, figs. 26*a*–*b*.

Rotalia aspera Ehrenberg; Beissel 1891, p. 73, pl. 14, figs. 1–6.
Globigerina aequilateralis (*non* Brady); Chapman 1892, p. 517, pl. 15, fig. 14.
Globigerina aequilateralis (*non* Brady); Heron-Allen and Earland 1910, p. 424, pl. 8, figs. 11, 12.
Globigerinella aspera (Ehrenberg); Brotzen 1936, p. 170, pl. 13, fig. 2.
Globigerinella aspera (Ehrenberg); Schijfsma 1946, pp. 94–96, pl. 6, fig. 8.
Globigerinella aspera (Ehrenberg); Bandy 1951, p. 508, pl. 75, fig. 3.
Globigerinella aspera (Ehrenberg); Belford 1960, p. 91, pl. 25, figs. 4–6.
Planomalina aspera (Ehrenberg); Barr 1962, pp. 561, 563, pl. 69, figs. 4*a*, *b*.
Planomalina (*Globigerinelloides*) *aspera aspera* (Ehrenberg); van Hinte 1963, p. 97, pl. 12, figs. 2*a*, 3.
'*Globigerinella*' *aspera* (Ehrenberg); Graham and Church 1963, pp. 64, 65, pl. 7, figs. 17*a–c*.
Globigerinelloides aspera (Ehrenberg); Barr and Cordey 1964, p. 309.
Globigerinelloides asper (Ehrenberg); Takayanagi 1965, pp. 201, 202, pl. 20, figs. 9*a–c*.

Occurrence. Approximately twelve specimens of *G. aspera* were recovered from the Ballydeenlea Chalk, and additional specimens were observed in thin section. *G. aspera* appears to be the most common planktonic species found in this chalk; it has a wide geographic distribution, occurring in most areas of the world where Senonian planktonic faunas are found. Barr (1962) recorded *G. aspera* in abundance from the Isle of Wight, ranging from the lower *M. cor-anguinum* Zone to the upper *B. mucronata* Zone. It is also found in the lower and middle Maestrichtian of continental Europe. Barr and Berggren (1965) recorded specimens of *G. aspera* from the Palaeocene Thanet Formation of eastern Kent. These specimens, along with other Upper Cretaceous species found in the Thanet Formation, were undoubtedly derived from the nearby Campanian Chalk.

Family GLOBOTRUNCANIDAE Brotzen 1942
Genus RUGOGLOBIGERINA Brönnimann 1952

Rugoglobigerina sp.

Plate 78, figs. 2, 3

Remarks. Several small specimens of *Rugoglobigerina* were recovered from the Ballydeenlea Chalk. The chambers of these forms were coarsely hispid and arranged in a very low trochospiral. These specimens could not be specifically identified, but are generally similar to several species that occur in the Campanian chalk of western Europe.

EXPLANATION OF PLATE 78

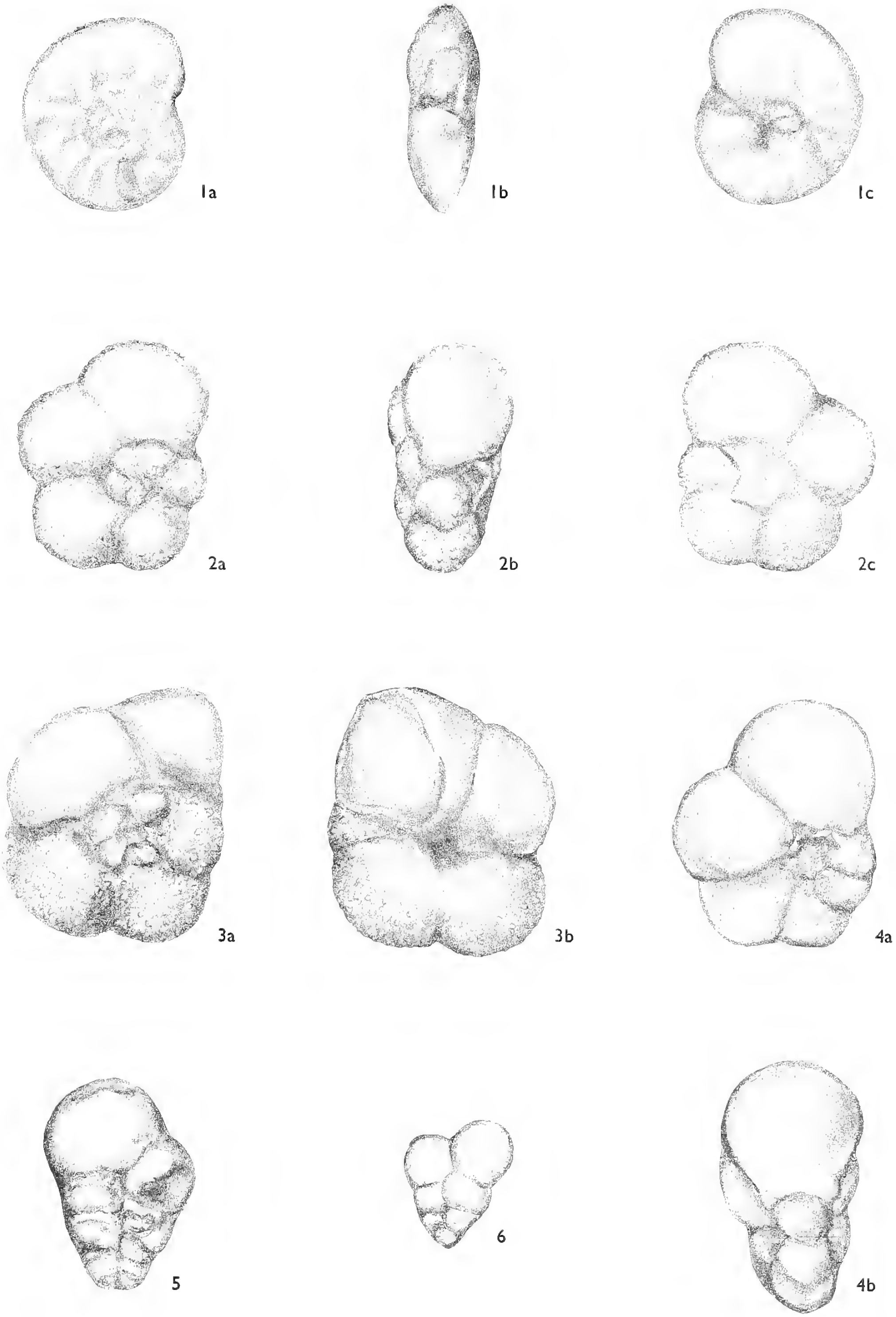
All specimens are from the Ballydeenlea Chalk, × 175.

Fig. 1. *Gavelinella thalmanni* (Brotzen). 1*a*, dorsal view, juvenile specimen; 1*b*, end view; 1*c*, ventral view; P45703.

Figs. 2, 3. *Rugoglobigerina sp.* 2*a*, dorsal view; 2*b*, end view; 2*c*, ventral view; P45709. 3*a*, dorsal view; 3*b*, ventral view, showing final chamber broken; P45708.

Fig. 4. *Globigerinelloides aspera* (Ehrenberg). 4*a*, lateral view; 4*b*, end view; P45701.

Figs. 5, 6. *Heterohelix globulosa* (Ehrenberg). 5, lateral view, initial end missing; P45704. 6, lateral view of exceptionally small specimen; P45705.



BARR, Foraminifera from Ballydeenlea Chalk

Family EPONIDIDAE Hofker 1951
Genus EPONIDES de Montfort 1808

Eponides cf. *concinna* Brotzen

Plate 79, figs. 2*a–c*

Epionides concinna Brotzen 1936, p. 167, pl. 12, figs. 4*a–c*.

Description. Test trochoid, consisting of about 3 whorls, biconvex; dorsal side weakly convex, nearly evolute, early whorls somewhat obscured by thin smooth mass of hyaline calcite; ventral side convex, involute, umbilicate; periphery in side view circular, weakly lobulate, with slight keel; chambers weakly inflated, ventrally overlapping, 9 to 12 in final whorl, uniformly and gradually increasing in size; ventral sutures distinct, depressed, dorsal sutures indistinct on early whorls, distinct on final whorl, limbate, flush, slightly curved, oblique; aperture narrow slit at base of final chamber, extending from umbilicus to periphery, bordered by thin, narrow lip; umbilicus small, shallow, often partially filled by low umbilical plug; wall calcareous, finely perforate, surface smooth.

Remarks. The morphology of the umbilical area of specimens referred to *Eponides* cf. *concinna* varies considerably. The umbilicus varies from a shallow simple form through ones containing a slightly raised plug to umbilici almost completely filled by a well-developed umbilical plug. The original illustration of the holotype of *E. concinna* shows a small shallow umbilicus with no umbilical plug. Although the specimens in the present study are similar in most respects to the type specimen from Sweden, there is still some uncertainty as to their relationship. On the other hand, the Ballydeenlea specimens appear to be identical to specimens from the Upper Cretaceous Chalk of southern England which range from the base of the *M. cor-anguinum* Zone to the upper part of the *B. mucronata* Zone.

Family OSANGULARIIDAE Loeblich and Tappan 1964
Genus GYROIDINOIDES Brotzen 1942

Gyroidinoides umbilicata (d'Orbigny)

Plate 79, figs. 3*a–c*

Rotalina umbilicata d'Orbigny 1840, pl. 3, figs. 4–6.
Rotalina nitida Reuss; Beissel 1891, p. 71, pl. 14, figs. 14–16.
Rotalia soldanii umbilicata (d'Orbigny); Franke 1927, p. 692.
Gyroidina umbilicata (d'Orbigny); Cushman 1931*b*, p. 43, pl. 6, fig. 3.
Gyroidina umbilicata (d'Orbigny); Macfadyen 1932, p. 489 (list), pl. 35, figs. 27*a*, *b*.
Gyroidina nitida (Reuss); Brotzen 1936, pp. 157–9, pl. 11, figs. 3*a–c*; text-fig. 58.
Gyroidina umbilicata (d'Orbigny); Marie 1941, pp. 219, 220, pl. 34, figs. 318*a–c*.
Gyroidina nitida (Reuss); Schijfsma 1946, pp. 85, 86, pl. 5, figs. 1*a–c*.
Gyroidina nitida (Reuss); Williams-Mitchell 1948, p. 97, pl. 8, figs. 6*a–c*.
Gyroidina umbilicata (d'Orbigny); McGugan 1957, p. 342, pl. 33, fig. 4.

Description. Test trochoid, planoconvex, composed of 3 to $3\frac{1}{2}$ whorls; dorsal side flat, evolute, ventral side strongly convex, involute, umbilicate, periphery in side view broadly rounded; chambers weakly inflated, 7 to 8 chambers in final whorl, uniformly and gradually increasing in size; ventral sutures straight, radial, flush; early dorsal sutures on final whorl depressed, slightly curved, nearly radial, dorsal spiral suture in early whorls flush, indistinct, in final whorl distinct, depressed; aperture narrow slit at base of final chamber, extending from ventral umbilicus on to dorsal side, bordered by thin narrow lip; umbilicus narrow, shallow, sometimes partially covered by apertural lip; wall calcareous, finely perforate, surface smooth.

Occurrence. G. umbilicata is common in the Ballydeenlea Chalk. This species has a long stratigraphic range in Western Europe. In southern England, *G. umbilicata* ranges from the Upper Turonian to the top of the Campanian. It is also abundant in the Lower Maestrichtian chalk at Sidestrand, Norfolk.

Family ANOMALINIDAE Cushman 1927*a*
Subfamily ANOMALININAE Cushman 1927*a*
Genus GAVELINELLA Brotzen 1942

Gavelinella lorneiana (d'Orbigny)

Plate 79, figs. 1 *a–c*

Rosalina lorneiana d'Orbigny 1840, p. 36, pl. 3, figs. 20–22.
Anomalina (*Rosalina*) *lorneiana* (d'Orbigny); Egger 1909, p. 45, pl. 4, figs. 10–12.
Anomalina clementiana (d'Orbigny); Cushman 1931*b*, p. 46, pl. 6, figs. 10*a–c*.
Discorbis lorneiana (d'Orbigny); Marie 1941, pp. 214–16, pl. 33, figs. 314*a–c*.
Anomalina clementiana (d'Orbigny); Cushman 1946 (part), p. 155, pl. 63, figs. 13*a–c* (*non* figs. 12 *a–c*).
Gavelinella lorneiana (d'Orbigny); Loeblich and Tappan 1964, p. 759, figs. 621 (6*a–c*).

Occurrence. Rare specimens of *G. lorneiana* were recovered from the Ballydeenlea Chalk. I have found this species in abundance at Culver Cliff, Isle of Wight, where it ranges from the *M. cor-testudinarium* Zone (Coniacian) to the lower part of the *B. mucronata* Zone. D'Orbigny (1840, p. 37) originally described this species from the Upper Campanian localities of St. Germain and Meudon in the Paris Basin, where he recorded it in abundance, and from Sens (Lower Campanian) and England, where he found only rare specimens. Marie (1941, p. 215) also reported *G. lorneiana* from various localities in the *B. mucronata* Zone (Upper Campanian) of the Paris Basin.

Gavelinella thalmanni (Brotzen)

Plate 78, figs. 1 *a–c*

Cibicides thalmanni Brotzen 1936, pp. 190, 191, pl. 14, figs. 7*a–c*.

Description. Test flatly trochoid, nearly planispiral, consisting of about $2\frac{1}{2}$ tightly coiled whorls; dorsal side weakly convex, semi-evolute, umbilicate; ventral side flat, involute,

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EXPLANATION OF PLATE 79

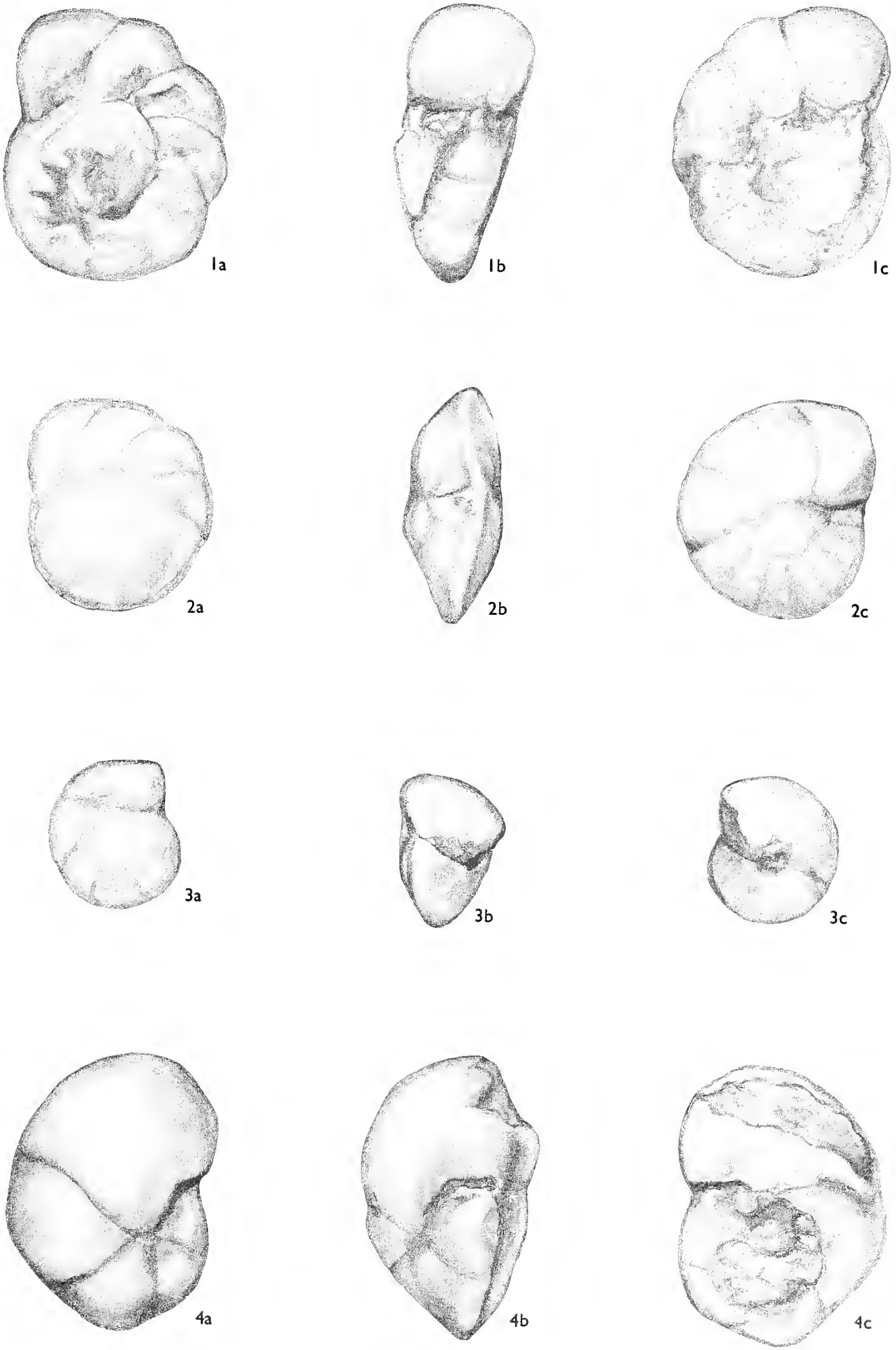
All specimens are from the Ballydeenlea Chalk.

Fig. 1. *Gavelinella lorneiana* (d'Orbigny), ×95. 1*a*, dorsal view; 1*b*, end view; 1*c*, ventral view, umbilicus obscured by matrix; P45694.

Fig. 2. *Eponides* cf. *concinna* Brotzen, ×125. 2*a*, dorsal view; 2*b*, end view; 2*c*, ventral view; P45697.

Fig. 3. *Gyroidinoides umbilicata* (d'Orbigny), ×125. 3*a*, dorsal view; 3*b*, end view; 3*c*, ventral view; P45695.

Fig. 4. *Cibicides beaumontiana* (d'Orbigny), ×125. 4*a*, ventral view; 4*b*, end view; 4*c*, dorsal view, final chamber broken, umbilical area obscured by matrix; P45696



BARR, Foraminifera from Ballydeenlea Chalk

weakly umbilicate; periphery in side view circular, in end view rounded; chambers uninflated, 11–12 in final whorl, uniformly and gradually increasing in size; dorsal sutures indistinct, weakly depresssed, gently curved, nearly radial, bordered by low, broad septal ridges which become less raised toward periphery; ventral sutures weakly depressed, usually obscured by low, very broad, gently curved, nearly radial septal ridges, composed of opaque, white, shell material which merges into thickened carinal band; septal ridges most prominent in early chambers of final whorl becoming less raised in final chambers; primary aperture low arch at base of final chamber with slit extending to ventral umbilicus, bordered by thin narrow lip, umbilical portion of apertures of successive chambers appear to remain open as relict apertures; dorsal umbilicus broad, fairly deep; ventral umbilicus narrow, shallow; wall calcareous, coarsely perforate.

Remarks. Specimens of *G. thalmanni* from the Ballydeenlea Chalk are very similar to Brotzen's (1936, pl. 14, figs. 7 *a–c*) figures of the holotype, although his illustrations do not show the early whorls dorsally, which are usually apparent on the Irish specimens. *G. thalmanni* is easily distinguished from *G. pertusa* (Marsson), *G. costata* Brotzen, *G. bullata* Brotzen, and most other species of *Gavelinella* by having a dorsal umbilicus.

Occurrence. G. thalmanni is common in the Ballydeenlea Chalk. I have also found this species in the Chalk of southern England, ranging from the *M. cor-testudinarium* Zone to the upper part of the *B. mucronata* Zone. The holotype of *G. thalmanni* is from the Senonian strata of southern Sweden.

Family CIBICIDIDAE Cushman 1927*a*
Subfamily CIBICIDINAE Cushman 1927*a*
Genus CIBICIDES de Montfort 1808

Cibicides beaumontiana (d'Orbigny)

Plate 79, figs. 4*a–c*

Truncatulina beaumontiana d'Orbigny 1840, p. 35, pl. 3, figs. 17–19.
Truncatulina lobatula (d'Orbigny); Marsson 1878, p. 167, pl. 5, figs. 38 *a–f*.
Truncatulina convexa Reuss; Egger 1899, p. 149, pl. 18, figs. 25–27.
Truncatulina lobatula (Walker and Jacob); Franke 1925 (*non* Walker and Jacob), p. 83, pl. 7, fig. 7.
(?) *Cibicides excavata* Brotzen 1936, p. 189, pl. 13, figs. 7, 8.
Cibicides ribbingi Brotzen 1936, pp. 186–9, pl. 13, figs. 5, 6, text-figs. 67, 68.
Cibicides beaumontiana (d'Orbigny); Marie 1941, pp. 249, 250, pl. 37, figs. 352–4.
Cibicides excavata Brotzen; Schijfsma 1946, pp. 100, 101, pl. 6, figs. 7 *a–c*.
Cibicides ribbingi Brotzen; Williams-Mitchell 1948, p. 103, pl. 9, figs. 5 *a*, *b*.
Cibicides beaumontianus (d'Orbigny); McGugan 1957, p. 344, pl. 32, figs. 24 *a–c*.

Remarks. Cibicides beaumontiana exhibits considerable variation in shape of test. The dorsal surface may be slightly concave, flat, or convex. The dorsal side of attached forms reflects the shape of the surface to which the foraminifer had attached itself. Non-attached forms exhibit more inflated, slightly convex dorsal surfaces.

Brotzen (1936, pp. 186–90, pl. 13, figs. 5–8) described two new species, *Cibicides ribbingi* and *C. excavata*, from the Senonian chalk of southern Sweden. It is possible that both of these forms are variants of *C. beaumontiana. C. ribbingi* is the more compressed form which was attached to a flat or convex surface, while *C. excavata* is a more inflated form which was only partially attached, or not attached at all. Both Brotzen's species, although superficially quite different, appear to be within the range of variation of *C. beaumontiana.*

Occurrence. C. beaumontiana is common in the Senonian chalk of southern England, where it ranges from the *M. testudinarius* Zone (Santonian) to the top of the *B. mucronata* Zone. It also occurs in abundance in the *B. lanceolata* Zone (Lower Maestrichtian) of Sidestrand, Norfolk. D'Orbigny originally described *C. beaumontiana* from the Chalk (*B. mucronata* Zone) of Meudon, and from unspecified localities in England.

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PODOCNEMIS SOMALIENSIS, A NEW PLEURODIRAN TURTLE FROM THE MIDDLE EOCENE OF SOMALIA

by C. A. WALKER

ABSTRACT. A new pleurodiran turtle, *Podocnemis somaliensis*, is described from the Middle Eocene of Somalia.

BETWEEN 1928 and 1930 the fragments of a fairly complete turtle shell were collected by W. A. Macfadyen and J. A. Hunt from the Middle Eocene of Somalia (then British Somaliland), along with numerous nautiloids. The specimen was presented to the Sedgwick Museum, Cambridge, and was then sent to the British Museum (Natural History) for repair and description, but it has remained undescribed until now.

The geology of the area concerned was dealt with in detail by Macfadyen (1933, 1952) and, to some extent, by Haas and Miller in their description of the nautiloids (1952).

Family PELOMEDUSIDAE
Subfamily PELOMEDUSINAE
Genus PODOCNEMIS Wagler 1830

Podocnemis somaliensis sp. nov.

Plate 80

Diagnosis. Nuchal large and broad; its lateral sutures not straight but rather sigmoid; notch in anterior border probably absent (or, if present, very small). Carapace almost as broad as long, widest part just behind bridge. Six neurals, behind which 6th–8th pairs of pleurals meet in mid-line. Anterior lobe of plastron wide, with blunt anterior edge; entoplastron broader than long; xiphiplastral symphysis longest.

Holotype. The unique specimen, Sedgwick Museum C 54.276: an almost complete carapace and plastron.

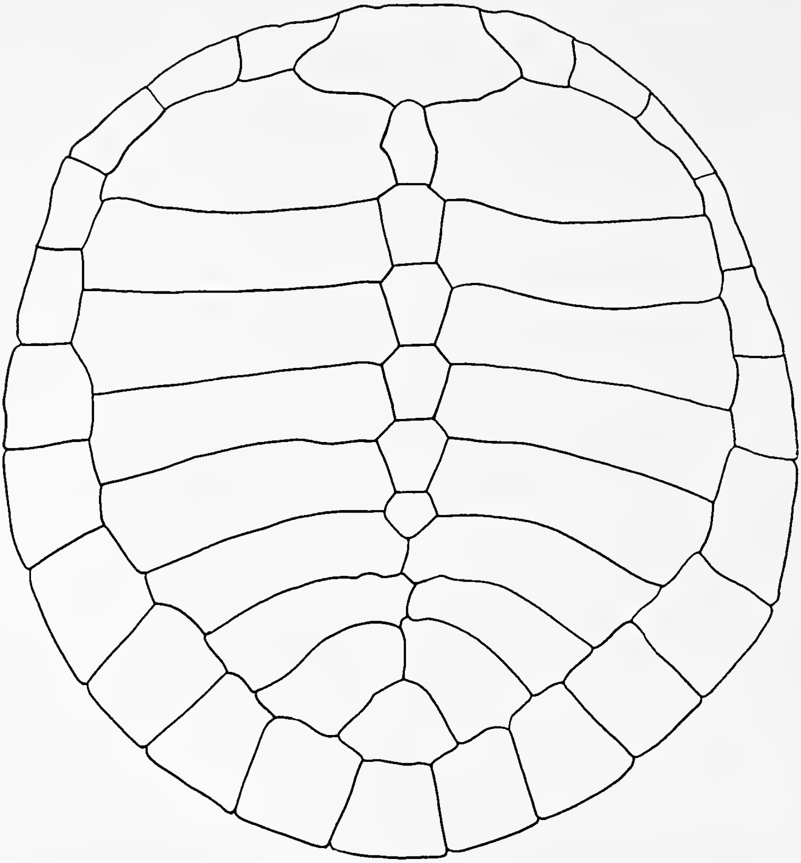
Occurrence. Lower half of the Nautilus Beds, Lower Daban Series, Middle Eocene (Lutetian); Bijo Gora River, near Las Daban (10° 22′ N., 45° 14′ E.), some 25 km. ESE. of Berbera, Somalia.

State of preservation. The shell has suffered some crushing. The outline of the carapace is distorted a little at both ends. The plastron has been damaged to a greater degree, and many of the sutures have been obscured, especially on the outer surface where plaster has been used to fill in eroded areas of bone. There are no shield furrows visible.

The nuchal lacks a portion from the leading edge backwards. All the neurals are present, but the suture between the first and second cannot be distinguished. All the pleurals, except the seventh and eighth pairs and the first right, are distorted to some extent.

[Palaeontology, Vol. 9, Part 3, 1966, pp. 511–16, pl. 80.]

The plastron has suffered slight distortion in such a way that the sagittal suture no longer forms a straight line, its front part being bent to the right. The sutures of the entoplastron are obscured on the left side by plaster; the sagittal suture and the posterior suture of the right epiplastron have been covered by plaster on the outer surface but remain visible in places on the visceral side. On the left side the mesoplastron is almost entirely absent and large sections of the hyoplastron and hypoplastron are also missing. The mesoplastron can be seen on the right, but there has been distortion and its inner

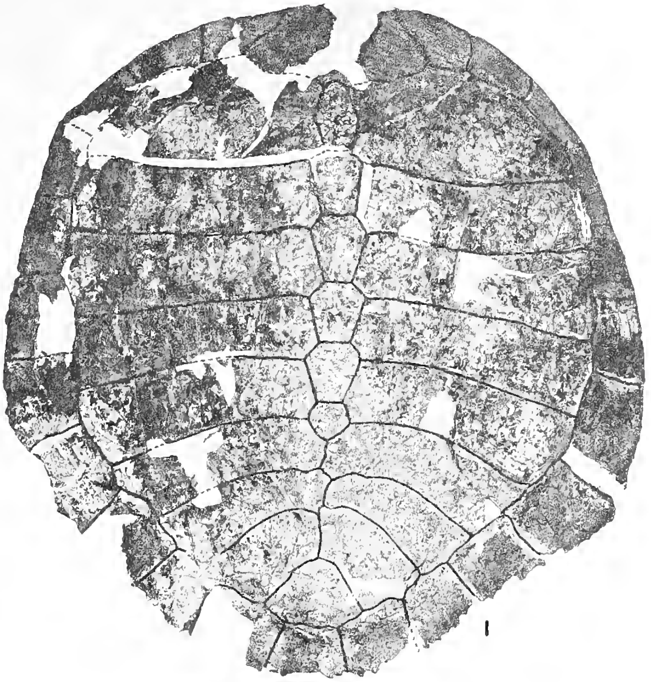


TEXT-FIG. 1. *Podocnemis somaliensis* sp. nov., reconstruction of the carapace in dorsal view, Sedg. Mus. C 54.276. ×$\frac{1}{4}$.

EXPLANATION OF PLATE 80

Podocnemis somaliensis sp. nov., holotype, Sedgwick Museum C 54.276. Middle Eocene of Somalia.

Fig. 1. Dorsal view of carapace. (Nuchal, first neural, and suprapygal are foreshortened.)
Fig. 2. Right lateral view of whole shell.
Fig. 3. Visceral view of plastron.
Fig. 4. Ventral view of plastron, with carapace in position.
Magnification $\frac{1}{5}$ natural size.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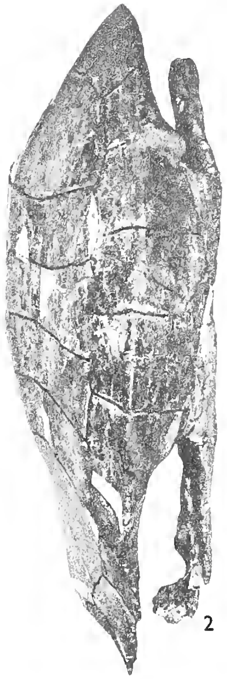
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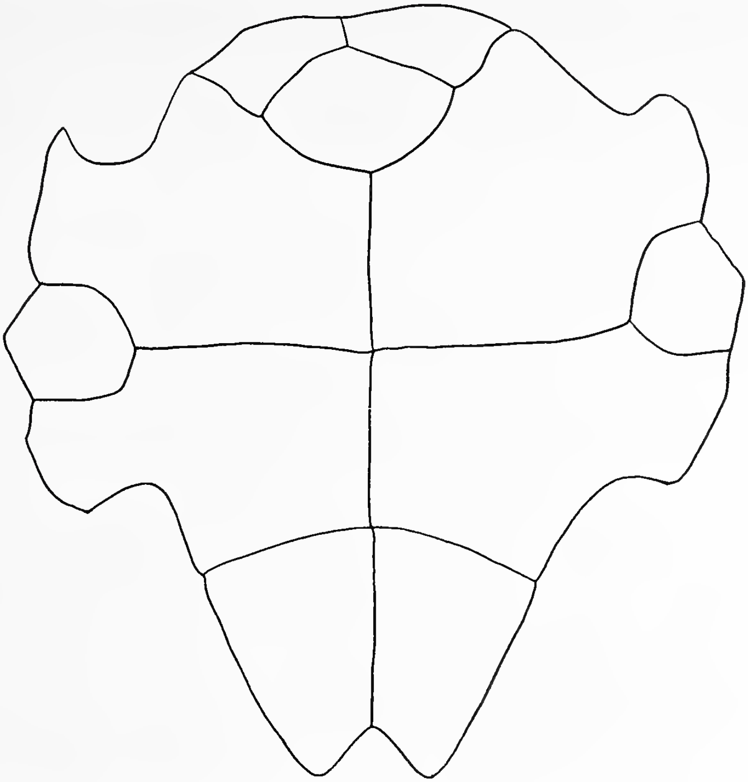
3


4

WALKER, Eocene pleurodiran turtle

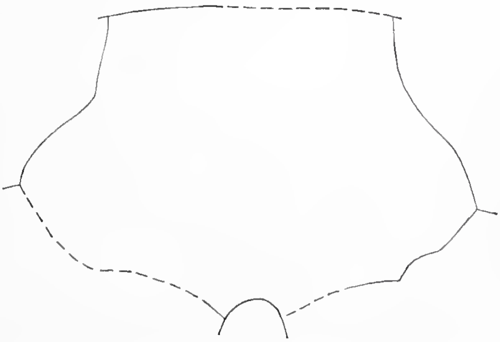
edge is imperfect. The xiphiplastra are broken off in front of the notch and their lateral margins are chipped.

Of the two sets of buttresses the right is more perfect than the left. Short stumps of the ilia are fused to the carapace and of the pubes and ischia to the plastron.



TEXT-FIG. 2. *P. somaliensis* sp. nov., reconstruction of the plastron in ventral view, Sedg. Mus. C 54.276. × ¼.

Description. Carapace. The carapace is almost as wide as long, with its greatest width just behind the bridge. The nuchal is relatively large, being broader than long, and its lateral sutures are slightly sigmoid rather than straight (text-fig. 3). The first neural, which butts on to the nuchal, forms an elongated hexagon widest in the middle; neurals 2–5 are also hexagonal and almost equal in size, but the greatest width of each is near its anterior end; neural 6 is smaller, pentagonal, and wedged between pleurals 5 and 6. The suprapygal is roughly pentagonal



TEXT-FIG. 3. *P. somaliensis* sp. nov., dorsal view of the nuchal. × ½.

with wide angles and is considerably broader than long. The pygal, although incomplete, does not seem to be enlarged. There are 8 pairs of pleurals, the first being the largest and the others becoming successively smaller towards the suprapygal; pleural 2 is concave anteriorly, 3 is biconcave, while 4–8 are convex in front and concave behind. The axillary and inguinal buttresses are located under the first and fifth pleural plates, the axillary being the larger (as is usual in *Podocnemis*). The visceral surface is not well preserved; the iliac scars occupy a position on either side of the mid-line under the seventh and eighth pleurals. Of the 11 pairs of peripherals nos. 4–7 are connected with the bridge.

Plastron. The anterior lobe is wide with a straight anterior edge. The suture separating the two epiplastra in the mid-line is short; from its posterior end the margin of the epiplastron runs obliquely outwards and backwards, separating it from the entoplastron, and then outwards and forwards, separating it from the hyoplastron. The entoplastron appears short and wide on the outer surface, but on the inner surface its outline is different (text-figs. 4, 5). Only one mesoplastron is preserved; it is badly crushed and the sutures are difficult to see, but it is wider than long. The sutures between the hyoplastra and hypoplastra are straight, but those between the hypoplastra and xiphiplastra are slightly curved, concave towards the rear. The xiphiplastra form the longest part of the sagittal suture but are incomplete posteriorly, thus making it impossible to give any true indication as to the size and shape of the notch. The pubic and ischial scars are well represented, with the ischia probably meeting in the mid-line, although some breakage has occurred at this point.

Measurements. (E) = estimated, (R) = right side, (V) = visceral, (O) = outer.

Carapace

Length				450 mm. (E)
Maximum width				424 mm.
		Length	*Maximum Width*	*Anterior Width*
Nuchal		76·5	120	74 mm.
Neurals	1.	56·5	29·5	15 mm.
	2.	41·5	33·5	17 mm.
	3.	41·5	35·5	21·5 mm.
	4.	38	35	18 mm.
	5.	38	35	20 mm.
	6.	25·5	27	17 mm.
Suprapygal		48	64	—
Pygal		50 (E)	34·5	65 mm. (E)

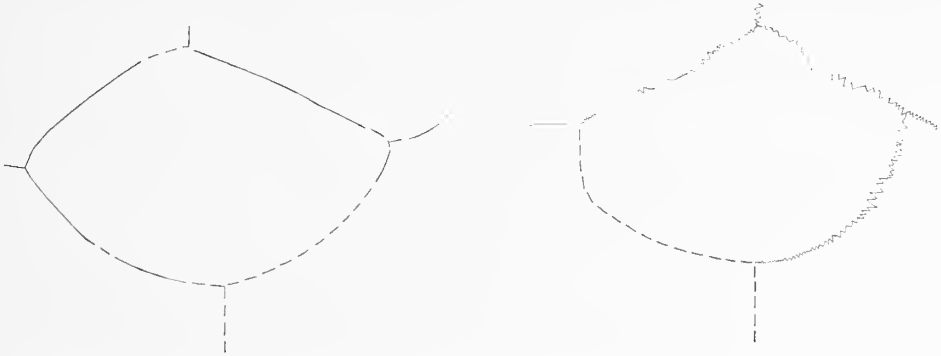
		Inner length	*Outer length*
Peripherals (R)	1.	27	55 mm.
	2.	41	49 mm.
	3.	44	57·5 mm (E)
	4.	51·5	55 mm. (E)
	5.	45·5	51·5 mm.
	6.	47	58·5 mm.
	7.	59	73 mm. (E)
	8.	50 (E)	62 mm. (E)
	9.	48	49 mm. (E)
	10.	38	60 mm. (E)
	11.	46	50 mm. (E)

Plastron

Sagittal length		377 mm. (E)
Sagittal length of anterior lobe		68 mm.
Sagittal length of bridge		177 mm.
Sagittal length of posterior lobe		132 mm. (E)
Length of epiplastral symphysis		18 mm. (V) 19·5 mm. (O)
Length of entoplastron		62 mm.
Length of hyoplastral symphysis	98 (R)	93 mm. (EV) 94 mm. (O)
Length of hypoplastral symphysis	94 (R)	90 mm. (EV) 90 mm.
Length of xiphiplastral symphysis	103 (R)	111 mm. (EV) 106 mm. (EO)
Length of mesoplastron		64 mm. (RO)
Width immediately anterior to bridge		254 mm.
Width immediately posterior to bridge		225 mm.
Width of entoplastron		87 mm. (V) 98 mm. (O)
Width of mesoplastron		68 mm. (EO)

Comparisons. The presence of small, laterally placed mesoplastra and of only six neurals indicates that the species should be placed in the sub-family Pelomedusinae (see Zangerl 1948, pp. 48 *et seq.*). Reference to *Podocnemis* is suggested by the exact pattern of bones in the carapace (with the nuchal and 1st neural in direct contact, *not* separated by the 1st pair of pleurals) and by the absence of a central fontanelle between hyo- and hypoplastra.

Podocnemis somaliensis is the largest species of the genus yet discovered in Africa. Although no shield furrows are visible in this specimen, it may be differentiated from other contemporary African species of the genus by the size, shape, and proportions of the nuchal, the carapace as a whole and the entoplastron. These species include only *P. antiqua* Andrews 1903 and *P. stromeri* Reinach 1903, both from the Middle Eocene of Egypt (see also Dacqué, 1912).



TEXT-FIGS. 4, 5. *P. somaliensis* sp. nov., ventral and visceral views of the entoplastron. ×½.

P. antiqua resembles the new species in the shape of the carapace, but it is much smaller and differs considerably in its anatomy. The nuchal contrasts with that of *P. somaliensis* in having straight lateral sutures and, behind it, a pair of foramina on either side of the 1st neural which are certainly absent in the new form. The suprapygal differs also in being much broader than long.

P. stromeri and its variety *major* both have oval shells, the proportions of which are like those of the Recent *P. madagascariensis* Grandidier but unlike those of *P. somaliensis*, in particular their nuchals and entoplastra are of different proportions. The xiphiplastral symphyses are not the longest in the mid-line, as they are in the Somalian species.

Remarks. It would be unwise to draw any conclusions as to the relationships of *P. somaliensis* with other species of *Podocnemis* until more material becomes available; it would be especially useful to have knowledge of its shield furrows and to compare it first hand with other African forms. However, the specimen is obviously specifically distinct and sufficiently well preserved to merit designation as the holotype of a new species.

Acknowledgements. I thank Dr. A. J. Charig for criticizing the manuscript; the Sedgwick Museum, Cambridge, for the further loan of the specimen; and Mr. A. Tanner who took the photographs.

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SOME LATE SILURIAN BRYOZOA FROM THE CANADIAN ARCTIC ISLANDS

by THOMAS E. BOLTON

ABSTRACT. One new species of trepostome *Diplotrypa franklini*, and two species of cyclostome *Fistulipora(?) mutabilis* Hennig and *Cyclotrypa silurica* Hennig originally described from the Ludlovian rocks of Gotland are characteristic of the Early Ludlovian shelly faunas scattered throughout the Canadian Arctic Islands.

BRYOZOA form only a small part of the Silurian shelly faunas collected from various islands in the Canadian Arctic Archipelago. However, some species are rather widespread and through their similarity with precisely dated fauna on the Island of Gotland assist in the regional correlation of the associated rock units.

In North America, Llandoverian and Wenlockian bryozoan faunas have been detailed by Bassler (1906, 1928) and Perry and Hattin (1960) but, with the exception of the Bryozoa of the Tonoloway Formation of West Virginia (Bassler 1923), Ludlovian Bryozoa are little known. In contrast, the Silurian Bryozoa of the Soviet Republic of Tuva have been studied in great detail by Astrova (1959, 1965), and recently the Ludlovian Bryozoa of Great Britain have been discussed by Owen (1960, 1962). Certain elements of both these faunas, especially among the Cyclostomata, are closely related to the Canadian Arctic bryozoan faunas. A still closer relationship is evident, however, between the Canadian species and forms described by Hennig (1905, 1906, 1908) from the Island of Gotland. Several species or closely related forms characteristic of the Early and Middle Ludlovian Hemse and Hamra Groups (Hede 1960) have been identified in the '*Atrypella schei* faunas' of the Read Bay Formation on Somerset, Cornwallis, and south-western Devon Islands and of the Douro Formation on north-western Devon Island (text-fig. 1). The most abundant form is the trepostome *Diplotrypa franklini* sp. nov., mainly from Early Ludlovian rocks, but in addition identified in Late Silurian or Early Devonian strata in east-central Ellesmere Island. Associated with this species are the cyclostomes *Fistulipora(?) mutabilis* Hennig and *Cyclotrypa silurica* Hennig, the cryptostome *Fenestella sp.*, and poorly preserved trepostomes of the genus *Eridotrypa.* Among the latter is a specimen (GSC No. 20430, Read Bay Formation, Cornwallis Island) with zooecia 0·25–0·3 mm. in diameter and rare diaphragms that is closer to *Eridotrypa umbonensis* Owen (1962, p. 203) from the Lower Bringewood Beds of the Welsh borderland than to *E. ramea* Hennig (1908, p. 38) with its more numerous diaphragms found within the Hemse Group.

SYSTEMATIC DESCRIPTIONS

Order TREPOSTOMATA Ulrich 1882
Genus DIPLOTRYPA Nicholson 1879

Type species. Favosites petropolitanus Pander 1830

[Palaeontology, Vol. 9, Part 3, 1966, pp. 517–22, pls. 81–82.]

Diplotrypa franklini sp. nov.

Plate 81, figs. 1–6; Plate 82, fig. 4

1958 *Mesotrypa sp.* cf. *M. suprasilurica* Hennig; Thorsteinsson, pp. 49, 50, 52, 67.
1963 *M. suprasilurica* Hennig; Fortier *et al.*, pp. 132, 205.
1963 *M.* cf. *M. suprasilurica* Hennig; ibid., p. 240.
1965 *M. sp.* cf. *M. suprasilurica* Hennig; Bolton, p. 12.

TEXT-FIG. 1. Late Silurian bryozoan localities Canadian Arctic Archipelago. 1. Cape Admiral M'Clintock, Somerset Island. 2. Resolute Bay area, Cornwallis Island. 3. Goodsir Creek, Cornwallis Island. 4. Radstock Bay, Devon Island. 5. Colin Archer Peninsula, Devon Island. 6, Darling Peninsula, Ellesmere Island.

EXPLANATION OF PLATE 81

Figs. 1–6. *Diplotrypa franklini* sp. nov. 1. Longitudinal section multilaminate colony, paratype GSC 20425, × 23. 2. Tangential section showing large mesopores, paratype GSC 20423, *c.* × 32. 3, 5, 6. Tangential and longitudinal sections, holotype GSC 20421, *c.* × 32 and × 100. 4. Tangential section, paratype GSC 20422, *c.* × 32.

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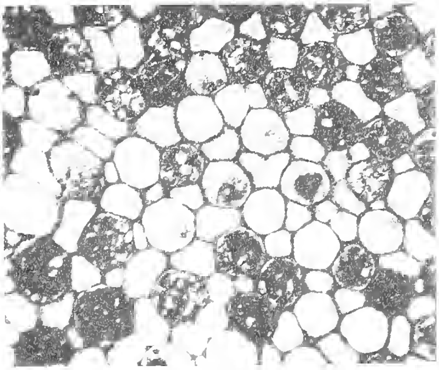

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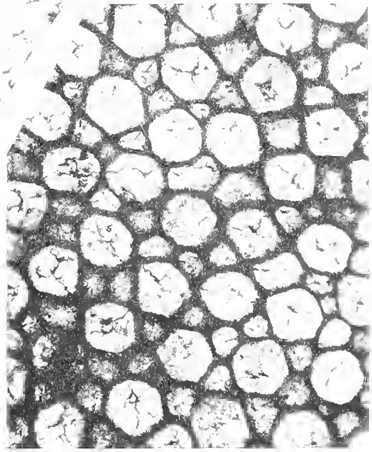

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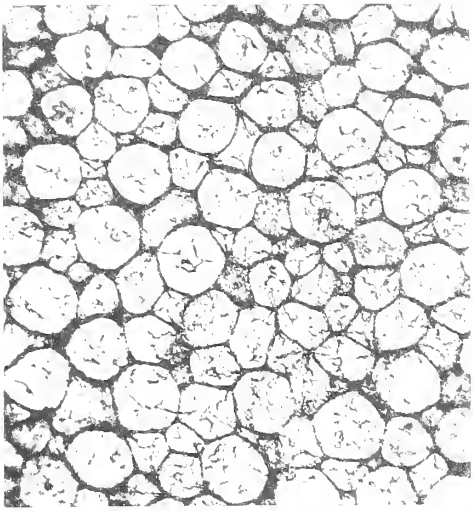

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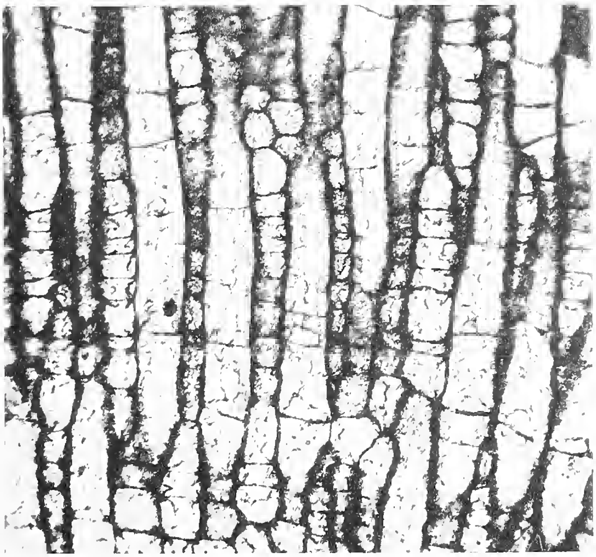

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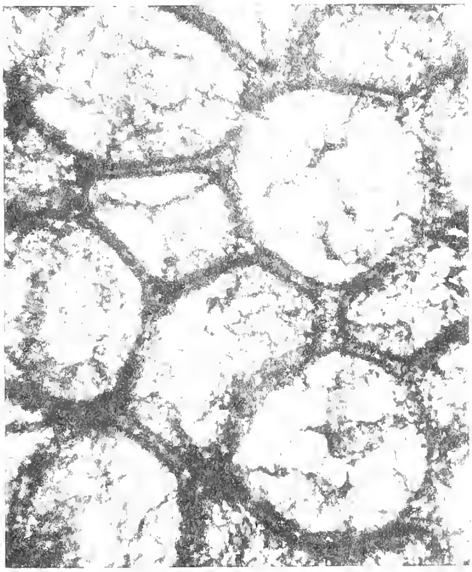

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BOLTON, Silurian Bryozoa from Canada

Description. Zoaria vary from small, cylindrical to subhemispherical to shallow conical mounds, some concentric layered; largest is 45 mm. wide and 30 mm. high; suggestion of a few low small monticules.

In tangential section, the zooecia are polygonal to subrounded, the openings slightly more oval where the zooecial walls are thicker (paratype 20425), 0·20–0·22 mm. in diameter, with a minimum of 0·15 mm. and a maximum of 0·28 mm. Generally eight to ten zooecia are present in 2 mm. Single rows of subtriangular to rectangular mesopores completely isolate, form a half circle, or are lacking from between zooecial openings, the arrangement varying within one complete colony horizontally and vertically, as well as between layers within a multilaminate colony (paratype 20425). Diameter of mesopores normally 0·1 to 0·15 mm., but some of the more rectangular mesopores extend up to 0·3 mm. (Pl. 81, fig. 2). Walls between mesopores and zooecial openings clear, amalgamate (?), thin (Pl. 81, fig. 6). Rare megacanthopore-like structures are confined to thickened walls at zooecial junctions, localized in paratype 20422, larger and more numerous in paratype 20426; absent from most colonies.

In longitudinal sections of multilaminate colonies, the normally erect zooecia and mesopores both may be inclined for a very short distance along the basal laminae. Thin diaphragms are present throughout the length of the zooecial tubes, horizontal to slightly oblique, but abruptly bending up at the boundary of the zooecial wall, 0·2 to 0·3 mm. apart (four to six per 1 mm.) with a minimum of 0·15 mm. and a maximum of 0·45 mm. (paratype 20423). Diaphragms much closer in mesopores, 0·1 mm. apart normally (ten to eleven per 1 mm.). Mesopores are continuous throughout zoaria, walls often curved inward at diaphragms. Walls clear, skeletal microstructures not preserved, of equal thickness throughout length of tubes.

Discussion. This new species is assigned to *Diplotrypa* rather than to *Mesotrypa* because of the absence or rarity of acanthopores and cystiphragms, despite amalgamate (?) walls characteristic of the latter genus. *Diplotrypa franklini* differs from *D. nummiformis* (Hall), from the Rochester and Osgood Formations (Niagaran) of New York and Indiana States, in that the latter discoidal species has more closely spaced, more inclined diaphragms and normally six to seven zooecia in 2 mm. (Bassler 1906, p. 27; Perry and Hattin 1960, p. 707). *D. walkeri* Bassler (1906, p. 47) from the Rochester Formation of Ontario and New York State and *D. neglectoformis* Astrova (1959, p. 26) from the Wenlockian both have larger zooecia, discontinuous mesopores, and fewer diaphragms.

Mesotrypa suprasilurica Hennig (1908, p. 30, text-figs. 35–37), principally from the Late Llandoverian (Hede 1921, p. 31) but also recorded from the Early Ludlovian of Gotland, with which this new species was originally compared, is identical in zoarial form. It differs in that the species has more distinct acanthopores, some with rounded lumen often projecting into the hollow of the zooecial tubes and more oblique or funnel-shaped diaphragms. '*Prasopora*' [= *Diplotrypa?*] *gotlandica* Hennig (1908, p. 28) from the Early Ludlovian Hemse Group of Gotland has smaller zoaria and some cystiphragm-like and closer diaphragms. Astrova (1959, p. 29) has suggested that some of the species assigned to *Mesotrypa* that lack cystiphragms and acanthopores might be included in her Wenlockian genus *Mesotrypella*. This genus characteristically has branched colonies, with rounded or subrounded zooecial openings, oblique or flexed diaphragms, and very undulating walls of constant thickness throughout the entire colony, whereas *Diplotrypa* has massive colonies and straight or slightly flexed walls. Specimens of *D. franklini* lacking acanthopores nevertheless have many features in common with *Mesotrypella alashensis* Astrova.

Distribution and types. D. franklini is most abundant in the Lower Ludlovian Member A of the Read Bay Formation, 459 to 731 ft. (holotype 20421; paratypes 20422, 20423) and at 1,365 ft. below the top on Goodsir Creek on the central-east coast of Cornwallis Island. Additional specimens have been identified 22 ft. above the base of Upper Ludlovian Member C of the Read Bay Formation at the same locality and in Member A near Resolute Bay, central-south coast of Cornwallis Island; upper beds of the Read Bay Formation, Cape Admiral M'Clintock, north coast of Somerset Island (paratype 20424) and the west side of Radstock Bay, south-western Devon Island (paratype 20425); lower beds of the Douro Formation, Colin Archer Peninsula, north-western Devon Island; and 3,380 to 3,400 ft. above base of undifferentiated Allen Bay–Read Bay Formation (Late Silurian or Early Devonian) on Darling Peninsula, east-central Ellesmerc Island (paratype 20426).

Order CYCLOSTOMATA Busk 1852

Genus FISTULIPORA M'Coy 1850

Type species. Fistulipora minor M'Coy 1850

Fistulipora (?) *mutabilis* Hennig 1908

Plate 82, figs. 2, 5, 7, 8

1908 *Fistulipora mutabilis* Hennig, p. 19, pl. 2, figs. 1–7; pl. 7, figs. 3, 4; text-figs. 21–23.
1958 *F. sp.* cf. *mutabilis* Hennig; Thorsteinsson, pp. 50, 59.

Description. Zoaria thin small expansions, largest over 13 mm. long and 26 mm. thick.

In tangential section, the zooecial openings are oval, 0·2–0·25 mm. in diameter ranging between 0·18 to 0·3 mm., four to five zooecia in 2 mm. Lunaria are poorly developed, broadly arched to slightly indenting zooecial cavities, lacking or obscure on most zooecia. Vesicles subpolygonal or polygonal, variable in size and number, at least one between adjacent zooecia.

In longitudinal section, zooecia are recumbent near the base of a colony, erect with thin walls throughout the remainder of the zoarium. Diaphragms are rare, thin, horizontal. Zooecia are separated by single polygonal tubes, 0·1 mm. in diameter with closely spaced horizontal diaphragms, by interlocking tubes of varying diameter and horizontal or convex diaphragms, or by vesicles; the latter structures are particularly well developed in early stages of growth (Pl. 82, fig. 7). Thickness of these compound zones ranges between 0·4 and 0·7 mm.

Discussion. Similar species include *F. strawi* Owen, but with fewer intervening vesicles, and certain forms of *F. promiscua* Perry and Hattin with barely discernible lunaria. As

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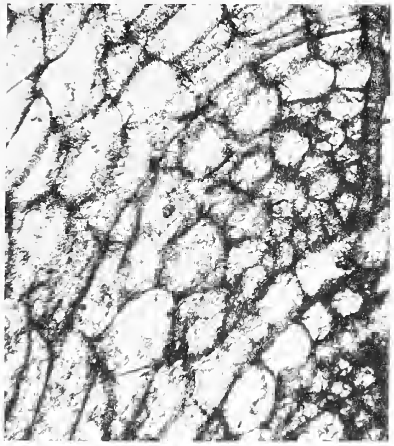
EXPLANATION OF PLATE 82

Figs. 1, 3. *Cyclotrypa silurica* Hennig. Longitudinal and tangential sections, GSC 20429, ×23.

Figs. 2, 5, 7, 8. *Fistulipora* (?) *mutabilis* Hennig. 2, 7. Tangential and longitudinal sections, GSC 20427, ×25. 5, 8. Longitudinal section showing complete colony and enlargement of upper right corner, GSC 20428, ×10 and ×23.

Fig. 4. *Diplotrypa franklini* sp. nov. Tangential section showing a few acanthopores, paratype GSC 20426, ×23.

Fig. 6. *Cheilotrypa ostiolata* (Hall). Longitudinal section to show irregular axial canal, GSC 20431, ×10.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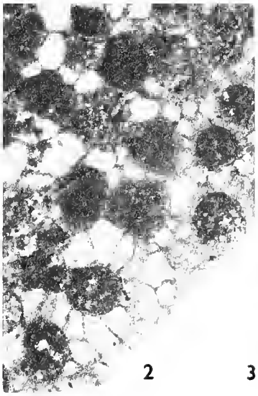
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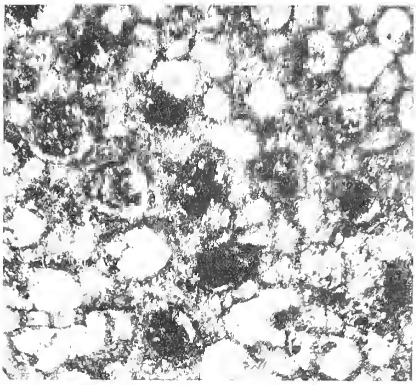
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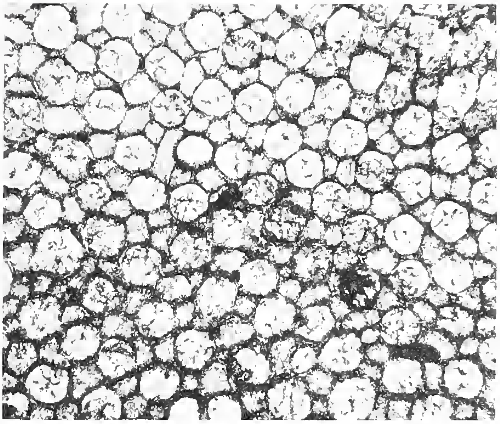
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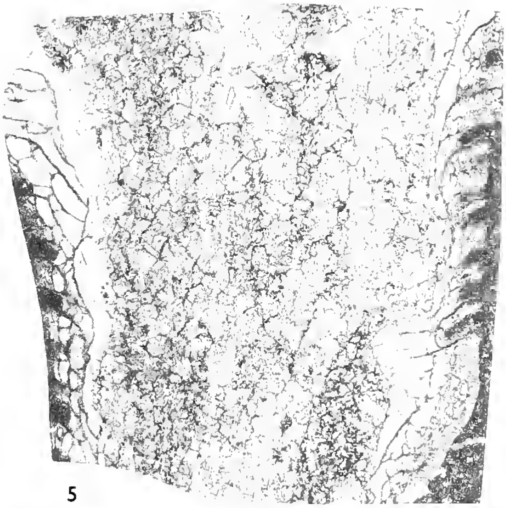
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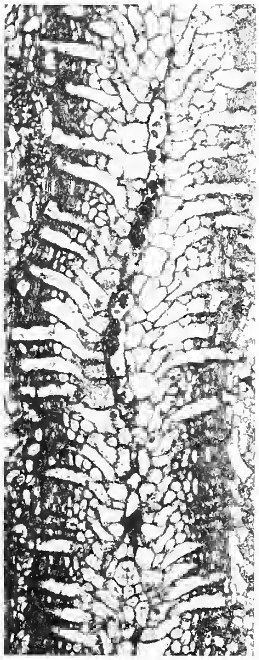
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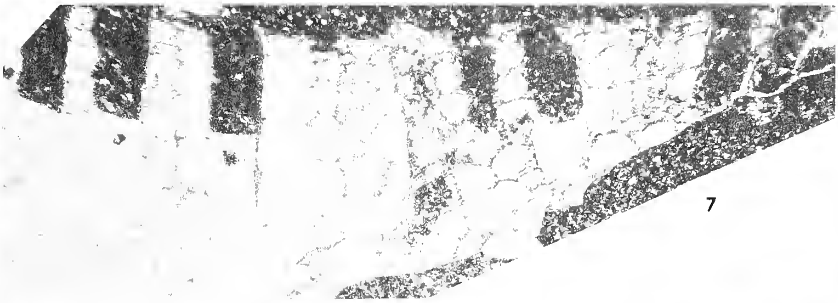
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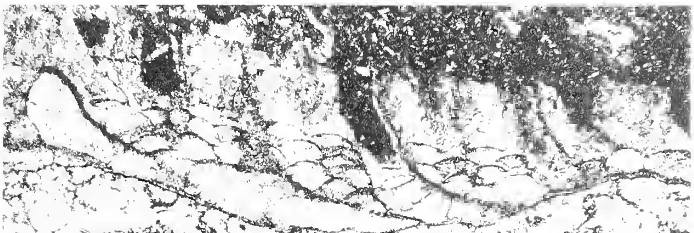

BOLTON, Silurian Bryozoa from Canada

many zooecia of *F. mutabilis* apparently lack lunaria, or where developed the lunaria are inconspicuous, this species might equally be assigned to *Cyclotrypa* Ulrich 1896. Specimen No. 20428 (Pl. 82, figs. 5, 8) with its dense stereom (?) and pseudo-ramose habit is strikingly similar in both tangential and longitudinal sections to *Cheilotrypa? opinabilis* Astrova (1965, p. 156, pl. 13, figs. 2*a*, *c*) from the Lower Ludlovian. The irregular central filling is 3·4 to 4·6 mm. thick in the Canadian specimen and between 0·18 and 2·8 mm. thick in the Russian specimen. In neither specimen is a true irregular axial canal or adjacent non-tabulated vertical zooecia characteristic of *Cheilotrypa* (*C. ostiolata* (Hall) from the Rochester Formation at De Cew Falls, Southern Ontario, Pl. 82, fig. 6) evident in the central filling; accordingly the Canadian form is interpreted as an encrusting form of *Fistulipora mutabilis*.

Distribution and types. Lower Ludlovian Member A of the Read Bay Formation, 618 and 698 ft. below the top (GSC Nos. 20427, 20428), Goodsir Creek on central-east coast, and upper beds of the Read Bay Formation near Resolute Bay, central-south coast of Cornwallis Island. The syntypes were from the Early Ludlovian Hemse Group (Hede 1921, p. 57), but the species was recognized by Hennig throughout the Late Llandoverian to Middle Ludlovian strata of Gotland.

Genus CYCLOTRYPA Ulrich 1896

Type species. *Fistulipora communis* Ulrich 1890.

Cyclotrypa silurica Hennig 1908

Plate 82, figs. 1, 3

1908 *Cyclotrypa silurica* Hennig, p. 24, pl. 1, fig. 19; pl. 4, figs, 8, 9; text-figs. 26–29.
1958 *C. sp.* cf. *C. silurica* Hennig; Thorsteinsson, pp. 49, 50.

Description. Zoarium cylindrical, branching, up to 12 mm. in diameter.

In tangential section, zooecia are thin walled, oval, 0·2 mm. in diameter with a maximum of 0·28 mm., five zooecia in 2 mm. Lunarium undeveloped. Adjacent zooecia nowhere in contact, separated by at least one polygonal vesicle; interzooecial distance ranges from 0·1 mm. to more than 0·4 mm.

In longitudinal section, zooecia open obliquely to the zoarial surface, thin walled, with a few thin, horizontal diaphragms in both axial and peripheral regions up to 0·8 mm. apart. The interzooecial tissue normally is vesicular; in single tubes the cystiphragm-like diaphragms are 0·1 to 0·3 mm. apart, closest in the peripheral regions.

Discussion. The branching form and cystiphragm (?) structure of *C. silurica* allies it with the Ludlovian species *Fistuliramus sinensis* Astrova (1965, p. 153, pl. 12, figs. 2*a*–*d*; pl. 13, figs. 1*a*, *b*), but it lacks the lunaria and heavy concentration of 'cystiphragms' in the peripheral zone characteristic of that genus.

Distribution and types. This species was identified from collections 331 (GSC No. 20429) and 618 ft. below the top of the Lower Ludlovian Member A of the Read Bay Formation, Goodsir Creek, central-east coast of Cornwallis Island. The syntypes were from the Middle Ludlovian Hamra Group (Hede 1921, p. 76) but the species also was recognized by Hennig in the Late Llandoverian, Wenlockian, and Early Ludlovian strata of Gotland.

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THE SILURIAN BRACHIOPOD *EOCOELIA HEMISPHAERICA* (J. DE C. SOWERBY) AND RELATED SPECIES

by A. M. ZIEGLER

ABSTRACT. The atrypacean *Eocoelia* occurs widely in the Upper Llandovery and is now known from the lower Wenlock. It shows evolutionary trends in the progressive suppression of ribs and in the modification and strengthening of the articulatory mechanism. These trends are used to define four successive species, *Eocoelia hemisphaerica* (J. de C. Sowerby) of C_1–C_2 age, *E. intermedia* (Hall) of C_3–C_4 age, *E. curtisi* sp. nov. of C_5 age, and *E. sulcata* (Prouty) of C_6–Wenlock age. The taxa *Eocoelia hemisphaerica sefinensis* (Williams) and *Eocoelia quebecensis* Amos and Boucot are relegated to the synonymy of *Eocoelia hemisphaerica*. Because of the abundance of *Eocoelia* at some localities, the term *Eocoelia* Community seems appropriate; this community probably occurred in a near-shore environment. Brachiopod lineages, such as the *Eocoelia* lineage, provide a reliable basis for fine-scale correlation.

THE small costate atrypacean *Eocoelia* is a characteristic element of Upper Llandovery and low Wenlock shelly deposits in Great Britain, eastern North America, and Siberia. It is also known from Norway and South America (Harrington 1950). Differences, considered to be evolutionary in nature, have been noticed in *Eocoelia* by Williams (1951) and Amos and Boucot (1963), and make the fossil an important one for correlation purposes. Material for the present investigation was collected from the southern part of the Welsh Borderland (Gloucestershire, Herefordshire, and Worcestershire) where *Eocoelia* occurs in profusion and can be obtained from many stratigraphic levels ranging in age from C_1 (early Upper Llandovery) to early Wenlock.

The type species of *Eocoelia*, *Atrypa hemisphaerica*, was originally described by J. de C. Sowerby in Murchison's *The Silurian System* (1839, p. 637, pl. 20, fig. 7). Unfortunately the locality of the figured specimen was not specifically stated. There is a specimen in the Geological Survey Museum labelled 'Sil Syst Pl. 20, f. 7.'; it resembles the figure only in being a block containing many specimens. However, the block may be accepted tentatively as the type specimen with the theory that the figure is an artist's interpretation of this block. The label on the block is Ankerdine Hill (an area in Worcestershire at the southern end of the Abberley Hills), one of the two localities mentioned by Sowerby for his species. Davidson (1866, pl. XIII, fig. 23) was probably wrong in stating the locality of Sowerby's specimen to be May Hill, a locality that was not mentioned in the first edition of *The Silurian System* (1839).

Davidson further confounded the issue by figuring specimens from several localities and inadvertently giving greater prominence to specimens which, on close examination, are quite distinct from the type. Thus, he showed enlargements of specimens from Penwhapple Glen, Ayrshire (1866, pl. XIII, figs. 29*a*, 30*a*), which, in contrast with the type, do not have discrete dental lamellae and which have relatively weak ribbing. It has been assumed by subsequent workers, namely Williams (1951, pp. 113–14), and Amos and Boucot (1963, pp. 445–7), that specimens like Davidson's Penwhapple Glen specimens are identical with the type; in each case these workers have erected new names

[Palaeontology, Vol. 9, Part 4, 1966, pp. 523–43, pls. 83, 84.]

to describe species which, in reality, are identical with the type of *Eocoelia hemisphaerica*. These names, *Coelospira hemisphaerica sefinensis* Williams and *Eocoelia quebecensis* Amos and Boucot, must be relegated to the synonymy of *E. hemisphaerica*. However, the important fact is that Williams, and Amos and Boucot, showed that the form with strong ribs and dental lamellae is definitely earlier in date than the other, and Williams, working in the type area of Llandovery, established this date as C_1 of the Upper Llandovery.

A second species of *Eocoelia*, conspecific with the type of Hall's (1860, p. 147) *E. intermedia*, occurs in C_4 beds at Llandovery. Specimens of *E. intermedia* are similar to *E. hemisphaerica*, but possess relatively weaker ribs and display intermediate stages in the disappearance of the umbonal chambers of the pedicle valve, with the consequent disappearance of the dental lamellae as distinct entities.

The complete disappearance of the umbonal chambers as well as a further reduction in rib strength is seen in a third species, here named *Eocoelia curtisi*. Davidson's Penwhapple Glen specimens mentioned above are of this type, which occurs abundantly in the basal Damery beds of the Tortworth Inlier.

The highest Llandovery and lowest Wenlock beds of Tortworth, May Hill, and the Malvern Hills contain an *Eocoelia* with mere vestiges of ribs; the ribs occur only as faint traces in the early growth stages of the shell, that is, in the beak region. This form occurs in North America and has been described as *Eocoelia sulcata* (Prouty) (Prouty and Swartz 1923, p. 466).

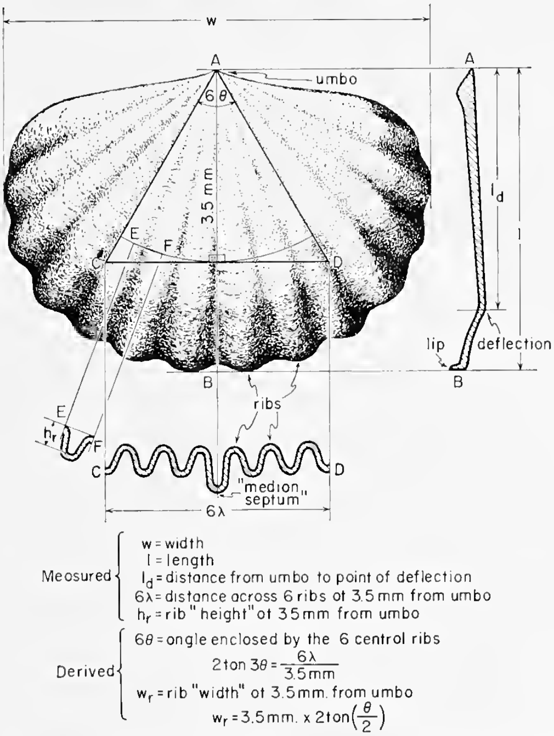
Four species of *Eocoelia*, *E. hemisphaerica*, *E. intermedia*, *E. curtisi*, and *E. sulcata* may thus be recognized. All four occur on both sides of the Atlantic and their stratigraphic succession may be demonstrated in localities as widely separated as Maryland, Nova Scotia, and the Welsh Borderland.

In the present investigation bulk collections were made from forty-five localities in the southern part of the Welsh Borderland and thirty-two of these contained specimens of *Eocoelia*. Numbers of *Eocoelia* range up to 272 in a collection, and the fourteen largest collections have been treated statistically (Appendix; for a description of other localities see Ziegler 1963). Collections from Llandovery and Ireland have also been examined, as well as eighty-one collections from a variety of regions in eastern North America. Such dimensions as length, width, distance between ribs at a set distance from the umbo, and height of ribs at the same distance from the umbo, were measured (text-fig. 1); also, the number of ribs was noted, as was the presence or absence of such features as the umbonal cavities and the cardinal process.

Acknowledgements. I would like to thank Dr. W. S. McKerrow who supervised the research, which was part of a D.Phil. thesis at Oxford University; Mr. J. M. Edmonds (University Museum, Oxford), who housed the thesis collections; Dr. A. J. Boucot (California Institute of Technology), who made available for study his extensive collections of North American and European material; Dr. M. L. K. Curtis (City Museum, Bristol), and Dr. L. R. M. Cocks (British Museum (Natural History)), who conducted the writer to localities at Tortworth, Gloucestershire, and Norbury, Shropshire, respectively. The research was supported in part by a grant from the Burdett-Coutts Fund, Oxford University.

ASSEMBLAGE ANALYSIS AND INTERPRETATION

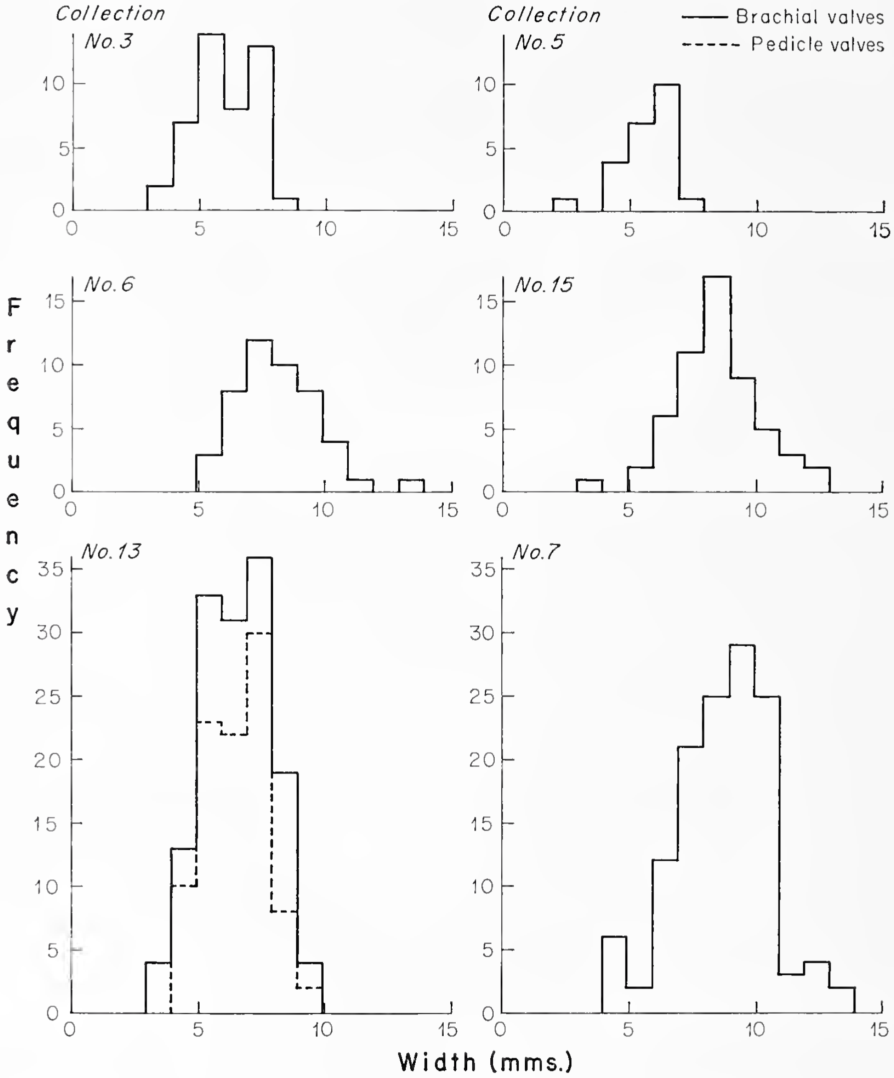
The extent to which a fossil sample is representative of the original population is a problem which should be considered by any taxonomist who deals with closely related species. Differences between samples cannot be used for taxonomic discrimination unless it can be shown that the samples were unaffected by current activity capable of selectively removing portions of the assemblage. Recently many techniques have been suggested for detecting preburial alteration of fossil assemblages (Fagerstrom 1964), and some of these are applicable to the *Eocoelia* assemblages preserved in the Upper Llandovery sandstones and shales of the Welsh Borderland.



TEXT-FIG. 1. Brachial valve of *Eocoelia* showing the parameters measured.

It should be noted that the fossils of the Upper Llandovery rocks are typically confined to the bottom of some of the beds, and not evenly distributed throughout the rock either vertically through several beds or horizontally along one bed, so the activity of currents in concentrating the shells may be inferred. Furthermore, most of the valves are disarticulated; of a total of 704 brachial valves collected, only 6 remain attached to pedicle valves. This consideration is not very significant since *Eocoelia* did not possess completely locking valves, and so these would become disarticulated easily once the soft parts had disappeared. Of more concern is the fact that the ratio of opposing valves may be as high as 1 : 1·5. On the other hand, less than 1% of all the valves collected show signs of wear or abrasion and what little breakage exists may be largely attributed to post-burial compaction of the sediment.

The character of the size-frequency distributions has been used by some workers to distinguish sorted assemblages. Boucot (1953) theorized that undisturbed assemblages should be highly skewed to the right due to high infant mortality, while current-sorted assemblages would have normal distributions. But Rudwick (1962) and Craig and Hallam (1963) showed that an undisturbed assemblage might very well have a modal peak in the large size range, as well as one in the very small range; this is because larvae, once established, may have very low mortality rates until mature. The *Eocoelia* assemblages (text-fig. 2) have modal peaks in the larger size ranges; there is no peak in the small range and it must be concluded that, owing to their very small size, the victims of high infant mortality were removed or destroyed by currents.



TEXT-FIG. 2. Size-frequency distributions. For localities see Appendix.

Size-frequency distributions may be used to better advantage in another way. Since the brachial valve of *Eocoelia* is flat, or nearly flat, and the pedicle valve quite convex, and since it is known that sphericity is an important hydrodynamic factor (Menard and Boucot 1951, p. 150), it is evident that the mean sizes of the valves would differ significantly if carried any distance by a current. The size-frequency distributions of the brachial and pedicle valves of sample 13 are compared in text-fig. 2. Although there are more brachial than pedicle valves, the shapes of the distributions correspond very closely, an indication that current sorting was at a minimum.

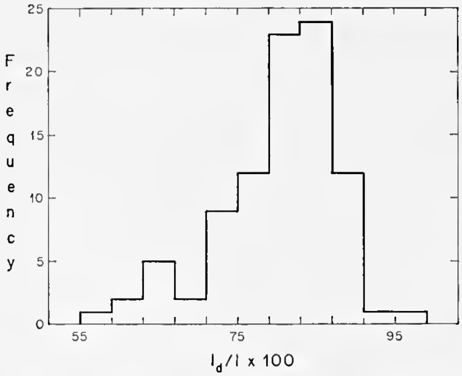
TABLE 1. *The relation of the Lip and Deflection to size in three collections*

Width	*Collection no. 13*		*Collection no. 11*		*Collection no. 15*	
(mm.)	*Present*	*Absent*	*Present*	*Absent*	*Present*	*Absent*
			LIP			
–4·5		4		2		1
4·6–5·5	3	17	1	5		0
5·6–6·5	6	25	3	3		4
6·6–7·5	15	15	3	10		5
7·6–8·5	12	22	8	9		18
8·6–9·5	2	3	3	1		10
9·6–10·5	1				1	4
10·6–						8
			DEFLECTION			
–4·5		5		2		1
4·6–5·5	17	5	2	5		0
5·6–6·5	27	7	3	4		4
6·6–7·5	23	5	10	6	1	4
7·6–8·5	31	4	9	8	7	11
8·6–9·5	5	1	4	1	8	3
9·6–10·5	1				2	5
10·6–					3	2

The examination of maturity indices may give useful information as to the relative ages represented in the samples. Two such indices, the 'lip' and 'deflection' (text-fig. 1) are present, at least in the two earlier species, *Eocoelia hemisphaerica* and *E. intermedia*. The relationship of lip and deflection to size in several samples is shown in table 1; the specimens with these structures tend to be larger, but the difference in size is by no means great and, in fact, in only the lip distribution of sample 13 is the association significant ($\chi^2 = 8{\cdot}87$, $p < 0{\cdot}003$). If, as seems likely, the lip is the final stage in the ontogeny of the animal, then several conclusions follow: (1) the wide size range exhibited by specimens with lips indicates that some individuals reached maturity at a considerably smaller size than others; (2) the large number of specimens with lips shows that many specimens actually lived to maturity; and (3) the fact that the specimens without lips are nearly as large as the ones with lips suggests that the former had nearly attained full maturity.

Unlike the lip, the deflection was formed some time before the animal finished growing. The distance from the umbo at which the deflection occurred (l_d) may be compared with the overall length of the valve (l) in the ratio $l_d/l \times 100$. Text-fig. 3 shows the distribution of this statistic for sample 13. The distribution has a sharp peak showing that most of the deflections occur at about 85% of the length of the valve. More important, there is no apparent correlation between l and $l_d/l \times 100$, i.e. smaller specimens have the deflection in the same relative position as larger specimens. As with the case of the lip, this suggests that the specimens were mostly mature at the time of their death.

In conclusion, most of the fossil beds studied are thought to be the result of some event, such as a storm, which stirred up the bottom, concentrating the shells lying on the sea floor, most of which were dead and disarticulated, and burying them with a layer of sediment. There is no clear indication that current sorting seriously affected the samples, except that the victims of high infant mortality appear to be unrepresented.



TEXT-FIG. 3. Histogram showing the percentage of the length at which the deflection occurs (l = length, l_d = distance from umbo to point of deflection). Measurements were made on the brachial valves of Collection 13.

SYSTEMATIC DESCRIPTIONS

Superfamily ATRYPACEA
Family LEPTOCOELIIDAE Boucot and Gill 1956
Genus EOCOELIA Nikiforova 1961

Type species. *Atrypa hemisphaerica* J. de C. Sowerby 1839, *in* Murchison, *The Silurian System*, p. 637, pl. 20, fig. 7.

Diagnosis. The valves of *Eocoelia* are plano-convex and effectively corrugated by prominent radial ribs. The plane of bilateral symmetry is emphasized by a strong median rib in the pedicle valve and a corresponding trough in the brachial valve; internally, this trough is a positive feature and supports a low, rounded median ridge. The articulation mechanism is developed so that, in addition to the normal tooth-socket relationship, the crural plates fit into well-defined grooves, or fossettes, on the internal surfaces of the teeth (text-fig. 4).

Comparison. *Leptocoelia* and *Australocoelia*, the two other genera of the Leptocoeliidae, always possess well-developed cardinal processes, whereas this structure, if developed at all in *Eocoelia*, is usually no more than a low inconspicuous ridge. Also, *Leptocoelia* and *Australocoelia* possess a sharply defined fold and sulcus involving two ribs of the brachial valve and one of the pedicle valve; the valves of *Eocoelia* are usually gently warped into a fold and sulcus, but this structure is not distinct enough to be defined in terms of number of ribs involved.

Discussion. Shape. The brachial valve is usually flat, but may be gently concave or gently convex. The pedicle valve is always convex and in some cases approaches a hemispherical shape. The width is slightly greater than the length. The beak of the pedicle valve is small and overhangs the brachial valve by approximately 0·2 mm. or 0·3 mm. in specimens about 1 cm. long. Young shells tend to be equidimensional but become slightly wider with respect to their length in their older growth stages.

TABLE 2. *Statistics of the allometry curves for the variates length* (l) *and width* (w)

For a discussion of the parameters a, σ_a, b, and r see Kermack and Haldane 1950, p. 40, or Imbrie 1956, p. 228

Species of Eocoelia	*Collection no.*	N	a	σ_a	b	r	$l/w_{w=7} \times 100$
E. sulcata	5	10	0·961	0·060	0·978	0·964	90·57
E. curtisi	9	8	1·113	0·053	0·719	0·977	89·71
	3	17	0·924	0·094	0·965	0·850	83·29
E. intermedia	15	16	0·817	0·042	1·218	0·972	85·29
	6	21	0·927	0·053	0·916	0·941	79·57
E. hemisphaerica	7	55	0·936	0·038	0·948	0·922	83·71
	11	27	1·060	0·050	0·740	0·931	83·14
	13	45	0·917	0·041	0·991	0·926	84·29
	14	11	0·851	0·100	1·159	0·890	86·71

The posterior margins form an obtuse angle at the umbo which varies from 165° to 145° as measured on the brachial valve. The delthyrium is small (from 0·2 to 0·4 mm. wide in adult specimens) and is uncomplicated by deltidial plates. The cardinal extremities are rounded. Interareas are not developed in *Eocoelia.*

Eocoelia possesses structures caused by a change in the direction of growth of the anterior margin of the shell. In one case, anterior growth ceased completely and the valves grew directly toward one another to form a 'lip' around the margin of each valve. This structure varies in height up to 0·32 mm., values of 0·1 mm. and 0·2 mm. being common (text-fig. 1). In another case, an inward 'deflection' occurs in the direction of growth of each valve (text-fig. 1). Abundant examples of the lip and deflection are to be found in the early populations of *Eocoelia,* that is, those that are grouped with *E. hemisphaerica* and *E. intermedia,* but the structures are rarely developed in the later populations, that is, *E. curtisi* and *E. sulcata.* The disappearance of these structures was gradual and is thought to represent an evolutionary trend.

There is usually a weak sulcus in the brachial valve of *Eocoelia* and a corresponding fold in the pedicle valve.

Ribs. Eocoelia possesses unbranching ribs which should be considered both from the standpoint of strength and number. The early species, *E. hemisphaerica,* has strong, rather angular ribs whereas the last species, *E. sulcata,* has ribs which are present only as vestiges and can be seen just in the area around the umbo, that is, in the young growth stages. The species which are intermediate stratigraphically have ribs of intermediate strength (Pl. 83).

The modal rib number varies considerably in *Eocoelia*; however, this feature does not appear to behave consistently with time (Tables 3, 4). The early species, *E. hemisphaerica*, has a moderate number of ribs with populations showing modes of 14 and 16 ribs. *E. intermedia* tends to have more ribs, the modes being 16 and 18. *E. curtisi* and *E. sulcata* have about 12 and 10 respectively, though the decrease in these cases is due as much to the progressive fading of ribs in the postero-lateral regions of the shell as to an increase in rib spacing.

TABLE 3. *Rib Number*

Species of Eocoelia	*Collection no.*	*N*	7–8	9–10	11–12	13–14	15–16	17–18	19–20
E. sulcata	8	5	2	2	1				
	2	3	1	1		1			
	4	5		2	1	1	1		
	5	21	3	7	9	2			
E. curtisi	9	7		2	4		1		
	10	8		3	2	2	1		
	3	25		1	17	6	1		
E. intermedia	15	18			1	12	4	1	
	6	15				1	8	5	1
E. hemisphaerica	7	81			2	37	36	6	
	11	8			2	5	1		
	13	79			9	52	16	2	
	14	31			9	19	3		
	12	11			2	7	2		
	*	8				7	1		

* Material from Williams's C_1 locality in the Llandovery District (1951, p. 114).

Articulation. Like most atrypids, the early species *E. hemisphaerica* possesses, in the brachial valve, a pair of blade-like hinge plates medianly bounding the sockets, and, in the pedicle valve, a pair of dental lamellae supporting teeth which are connected to the posterior margin of the shell by planareas. Lateral to the dental lamellae are umbonal chambers. However, in the later populations, these are not present and the teeth and dental lamellae are fused into one large tooth-like mass. The intermediate stage of the disappearance of these chambers is the characteristic feature of *E. intermedia* and they are never present in later populations, that is, *E. curtisi* and *E. sulcata* (Pl. 84).

The inner surfaces of the teeth of *Eocoelia* each have a groove, or fossette, into which fit the laterally directed crural plates of the brachial valve. Thus *Eocoelia* has an interlocking articulation mechanism which consists of the normal tooth-socket relationship

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EXPLANATION OF PLATE 83

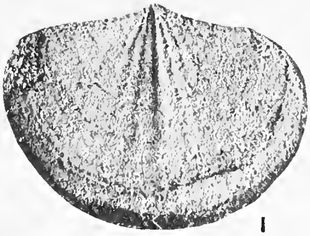
All specimens are rubber casts of external moulds of brachial valves, ×4. For localities see Appendix.

Figs. 1–6. *Eocoelia sulcata*. 1, 2, Collection 1, USNM 140431, 140432; 3, 4. Collection 8, OUM C6457*a*, C6454*a*; 5, 6, Collection 2, USNM 140433, 140434.

Figs. 7–8. *E. curtisi*. Collection 3, OUM C3198*b*, C3225*a*.

Figs. 9–12. *E. intermedia*. 9, 10, Collection 15, OUM C8050*b*, C8066*b*; Collection 6, OUM C1644*a*, C1669*a*.

Figs 13–16. *E. hemisphaerica*. 13, 14, Collection 7, OUM C1095*b*, C1012*a*; Collection 13, OUM C6857*b*, C6810*b*.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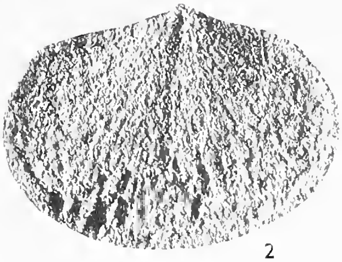
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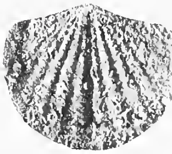
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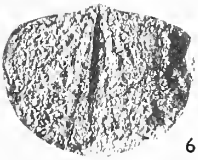
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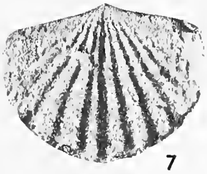
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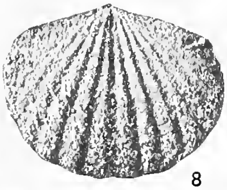
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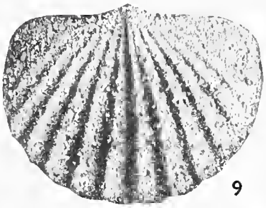
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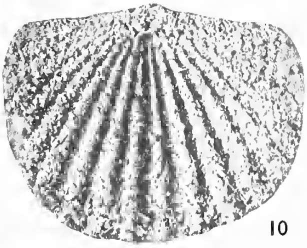
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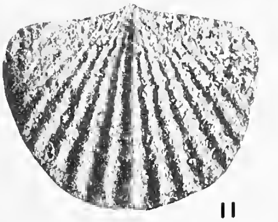
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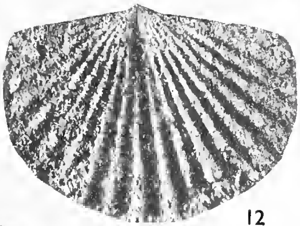
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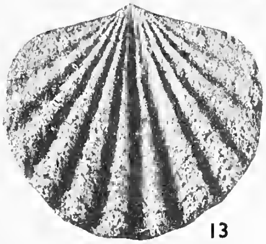
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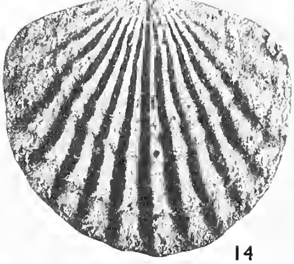
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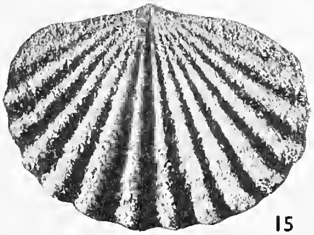
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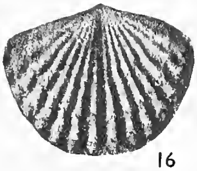
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ZIEGLER, Silurian atrypacean brachiopod *Eocoelia*

as well as the crural plate-fossette relationship. The fossettes, which are present in all species of *Eocoelia*, are more deeply impressed in the later species.

Lophophore support. Presumably the lophophore was attached to the anterior portions of the hinge plates. The existence of spires has been investigated by Nikiforova (Nikiforova and Andreeva 1961, p. 253), who sectioned many specimens without finding spires, although they were present in other atrypids in the same deposit. As has been mentioned, the crural plates served in the role of articulation as well as for lophophore support. They are rather blade-like and curved laterally. The bases of the crural plates bound the notothyrial cavity and diverge anteriorly and ventrally.

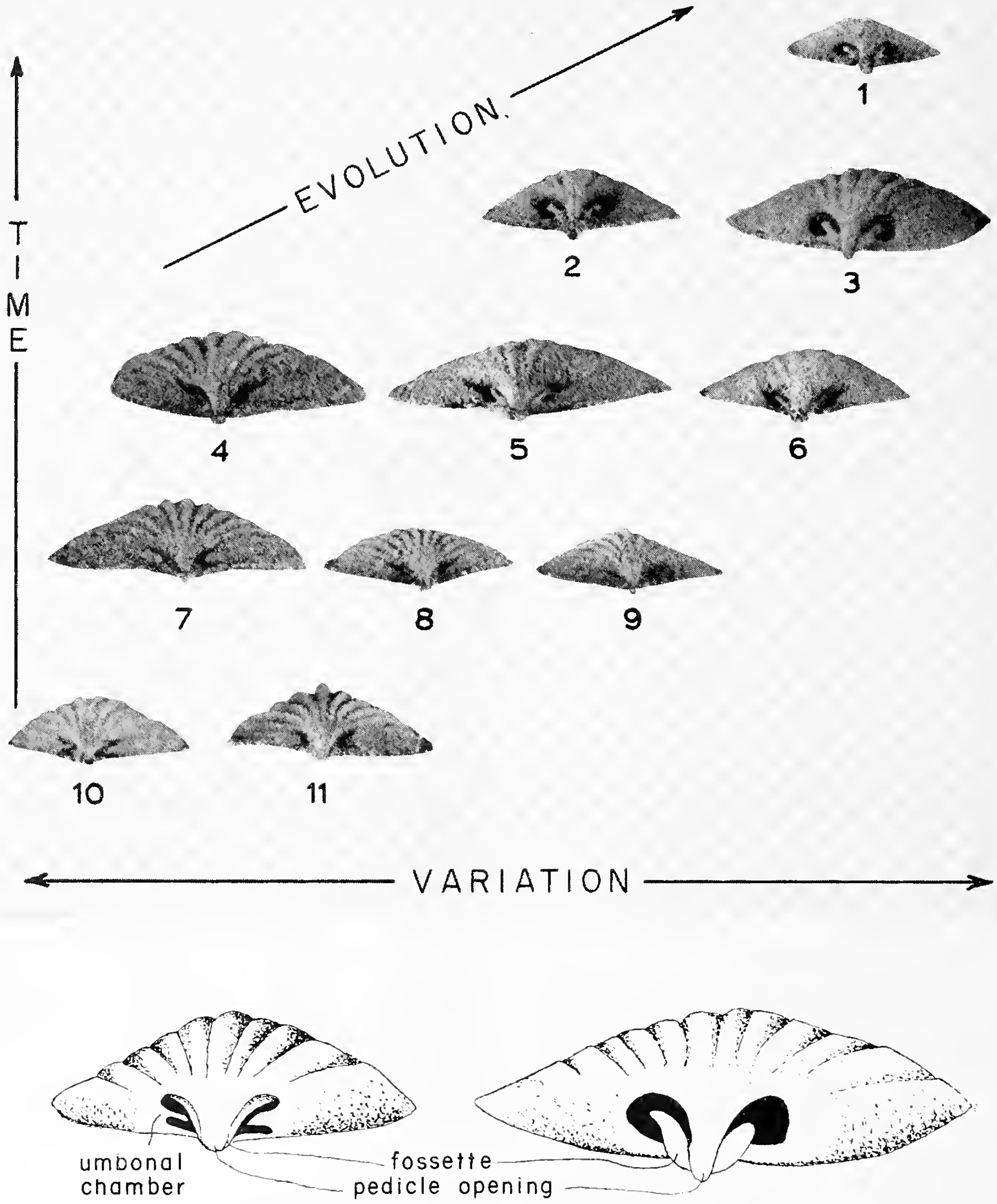
TABLE 4. *Statistics of 6θ, where 6θ = angle enclosed by six ribs*

Species of Eocoelia	*Collection no.*	*N*	*Lower confidence limit*	*Mean*	*Upper confidence limit*	*Standard deviation*	*Observed range*
E. sulcata	8	3	44·67	60·67	70·67	6·44	56–68
	2	4	54·44	61·50	68·56	4·44	58–68
	4	3	40·12	60·00	79·88	8·00	52–68
	5	12	58·16	61·33	64·50	4·50	50–66
E. curtisi	9	11	56·15	58·18	60·21	3·03	52–64
	10	12	57·68	60·50	63·32	4·44	56–70
	3	33	57·70	59·27	60·84	4·44	50–68
E. intermedia	15	47	55·55	56·72	57·89	3·94	48–66
	6	42	51·34	52·67	54·00	4·30	46–60
E. hemisphaerica	7	114	55·85	56·88	57·91	5·56	40–70
	11	50	57·61	59·08	60·55	5·19	48–70
	13	94	57·88	59·17	60·46	6·29	46–74
	14	29	57·74	60·48	63·22	5·85	52–76
	12	14	58·65	61·57	64·49	5·06	52–78

TABLE 5. *Statistics of the size (width)-frequency distributions*

Collection no.	*N*	*Number of fossil beds*	*Mean width (mm.)*	*Observed range (mm.)*	*Description of distribution*
8	6	1	6·02	4·7–7·2	—
2	9	many	6·23	5·6–7·3	—
4	7	2 or 3	7·03	5·9–8·0	—
5	23	1	5·71	2·8–7·4	skew, left
9	19	1	5·98	2·8–9·0	unimodal
10	15	several	6·68	3·0–8·6	skew, left
3	45	2	6·16	3·4–8·8	bimodal
15	56	1	8·63	3·9–12·6	skew, right
6	47	several	8·29	5·5–13·4	skew, right
7	129	many	8·87	4·2–13·8	skew, left
11	56	1	7·06	4·2–9·0	skew, left
13	141	2	6·72	3·7–10·2	bimodal
14	38	2 or 3	7·16	3·3–10·6	irregular
12	19	1	6·74	4·5–9·4	unimodal

Muscle attachment. In the brachial valve the adductor scars are faintly impressed immediately anterior to the crural plates and on either side of a low, rounded median



TEXT-FIG. 4. Changes in the posterior end of the pedicle valve. All specimens are internal moulds and all are × 4, with the exception of the line drawings, which are × 8. All the specimens are in the Oxford University Museum collections. For localities see Appendix. Top row, Collection 2, *Eocoelia sulcata*; 1, C3734*a*. Second row, Collection 3, *E. curtisi*; 2, C3240*b*; 3, C3241*a* (a diagram of the latter is shown in the bottom right of the figure). Third row, Collection 15, *E. intermedia*; 4, C8169*a*; 5, C8167*a*; 6, C8168*a*. Fourth row, Collection 6, *E. intermedia*; 7, C1719*a*; 8, C1702*b*; 9, C1699*b*. Bottom row, Collection 13, *E. hemisphaerica*; 10, C6937*b*; and 11, C7004*a* (a diagram of the former is shown in the bottom left of the figure).

ridge. The cardinal process (Pl. 84, fig. 5) is rarely distinct and not developed in all specimens; it is usually not more than a low ridge running along the notothyrial cavity.

In the pedicle valve, the paired diductor scars are oval with their long axes parallel to that of the valve and are sometimes impressed to such a depth that a distinct and very narrow ridge, or myophragm, is left between them (Pl. 84, fig. 4). Small elongate adductor muscle scars are often seen postero-medianly to the diductor scars.

Size. Eocoelia is typically small, shell widths usually being under 10 mm.; the largest recorded width is 13·4 mm. The size varies considerably from collection to collection (Table 5).

Species

Atrypa hemisphaerica J. de C. Sowerby, 1839, *in* Murchison, *The Silurian System*, p. 637, pl. 20, fig. 7.
Leptocoelia intermedia Hall, 1860, p. 147, fig. 5.
Eocoelia curtisi sp. nov.
Coelospira sulcata Prouty 1923, p. 466, pl. 27, figs. 6–8.

Species questionably assigned

Atrypina(?) *paraguayensis* Harrington 1950, p. 62, pl. 1, figs. 9, 10, 13–16.

Eocoelia hemisphaerica (J. de C. Sowerby)

Plate 83, figs. 13–16; Plate 84, figs. 5–11

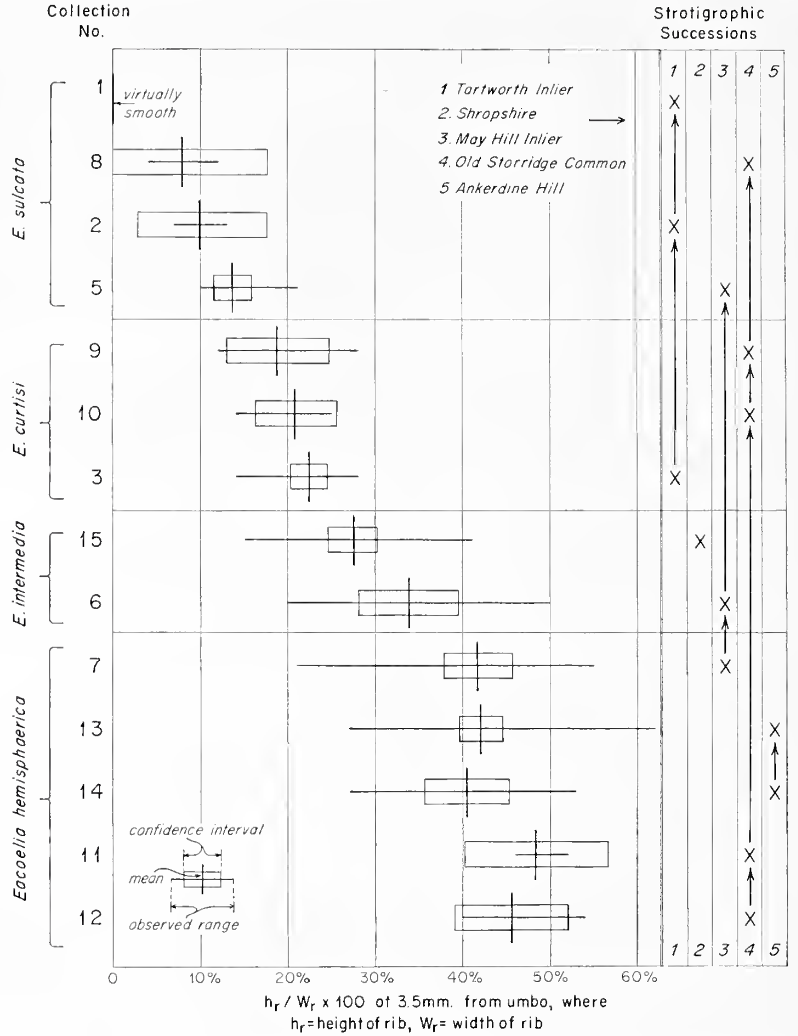
Atrypa hemisphaerica J. de C. Sowerby, *in* Murchison 1839, p. 637, pl. 20, fig. 7.
Atrypa? *hemisphaerica* J. de C. Sowerby; Davidson 1866, p. 136, pl. 13, fig. 23.
Coelospira hemisphaerica sefinensis Williams 1951, p. 113, pl. 5, figs. 19, 20.
Eocoelia quebecensis Amos and Boucot 1963, p. 447, pl. 62, figs. 1–10.

Definition. Included in this species are all populations of *Eocoelia* which consist entirely of individuals possessing umbonal cavities lateral to the dental lamellae in the pedicle valve.

Discussion. The species is strongly ribbed; the index of rib strength, mean $h_r/w_r \times 100$ (where h_r = height of rib and w_r = width of rib), for the populations identified with this species is about 40% (text-fig. 5, table 6). The individuals commonly have from 13 to 16 ribs, but may have as few as 11 or as many as 18 ribs. It should be mentioned that *E. hemisphaerica sefinensis* Williams, here synonymized with *E. hemisphaerica*, was originally said to have 12 ribs but larger collections now available clearly demonstrate a modal rib number of 14, the same as *E. hemisphaerica*; in the present work, rib counts were made only on external moulds of complete brachial valves, and failure by Williams to adhere to these standards would account for his low values.

A particularly distinctive feature of populations of *E. hemisphaerica* is the presence in many individuals of the 'lip' and 'deflection'. The lip usually occurs in about 30% of the specimens; the occurrence of the deflection is more variable and may be observed in as many as 87·5% of the individuals or as few as 15%, depending on the population (Table 7). A lip and a deflection may occur on the same specimen and occasionally two deflections are present on a single specimen. Both the lip and deflection are probably indications of maturity in *Eocoelia*; the lip would have been the final portion of the shell to grow, and the deflection usually occurs at a late growth stage of the animal, at about 85% of the shell length as measured from the umbo (text-fig. 2).

Holotype. The specimen preserved in the Geological Survey Museum (Geol. Soc. Coll. GSd 4829) is thought to be the holotype, although the artist's drawing in *The Silurian System* (pl. 20, fig. 7) by no means confirms this. The type locality of the specimen is Ankerdine Hill, seven miles west of Worcester. The species is very abundant in this small inlier of Upper Llandovery rocks, but *E. curtisi* also occurs on the west side of the hill between the Knightwick Sanatorium and the River Teme.



TEXT-FIG. 5. The range of variation in rib strength. The collections have been arranged in chronological order by palaeontological and stratigraphical evidence. The latter is summarized at the right of the figure. For localities see Appendix.

Occurrence. In the southern part of the Welsh Borderland, *E. hemisphaerica* occurs in the Cowleigh Park Beds of Ankerdine Hill and the Old Storridge Common area, both to the north of the Malvern Hills, and in the Huntley Hill Beds of the May Hill Inlier. In Shropshire the species occurs in the *Pentamerus* beds at Ticklerton, near Wenlock Edge, and at Hillend, near the Longmynd. There is a small inlier of Upper Llandovery sandstone immediately south of Presteigne, Radnorshire, where the species occurs in abundance.

At Llandovery *E. hemisphaerica* occurs in the Sefin shales, where it has been identified as *E. hemisphaerica sefinensis* Williams (1951, p. 113); the species also occurs just to the south of this area in the bottom ten feet of the Upper Llandovery beds of the Sawdde River section.

TABLE 6. *Statistics of the rib proportions* $h_r/w_r \times 100$, *where* h_r *is the height of a rib at 3·5 mm. from the umbo and* w_r *is the width of the rib at 3·5 mm. from the umbo*

Species of Eocoelia	*Collection no.*	*N*	*Lower confidence limit*	*Mean*	*Upper confidence limit*	*Standard deviation*	*Observed range*
E. sulcata	8	3	0·00	7·77	17·55	3·94	4–12
	2	3	2·01	9·87	17·73	3·16	7–13
	3	10	11·53	13·71	15·89	3·05	10–21
E. curtisi	9	6	12·98	18·84	24·70	5·58	12–28
	10	6	16·23	20·85	25·47	4·40	14–25
	3	15	20·23	22·37	24·51	3·87	14–28
E. intermedia	15	20	24·59	27·35	30·11	5·90	15–41
	6	13	28·14	33·82	39·50	9·40	20–50
E. hemisphaerica	7	25	37·74	41·72	45·70	9·65	21–55
	11	3	40·19	48·40	56·61	3·30	46–52
	13	39	39·39	41·97	44·55	7·94	27–62
	14	12	35·69	40·48	45·27	7·55	27–53
	12	5	39·11	45·56	52·01	5·20	40–54

TABLE 7. *Occurrence of the Lip and Deflection*

Species of Eocoelia	*Collection no.*	*N*	*Lip present (%)*	*N*	*Deflection present (%)*
E. sulcata	2	10	0	7	0
	5	21	0	24	0
E. curtisi	9	22	0	21	0
	10	21	0	19	0
	3	55	1·8	57	0
E. intermedia	15	61	3·3	56	39·3
	6	44	11·4	46	2·2
E. hemisphaerica	7	42	28·8	40	87·5
	11	60	30·0	71	52·1
	13	139	30·9	145	77·9
	14	38	36·8	47	14·9
	12	11	27·3	24	16·7

The species is known from the Pointe-aux-Trembles Formation of the Lake Temiscouata–Lake Touladi region of eastern Quebec where it has previously been identified as *E. quebecensis* Amos and Boucot (1963, p. 448). At Arisaig, Nova Scotia, *E. hemisphaerica* occurs in the lowest shell beds of the Ross Brook Formation at a point on the shore about 1000 ft. north-east of the mouth of Arisaig Brook.

The *Atrypina*(?) *paraguayensis* of Harrington (1950, p. 62) from beds of probable Lower Llandovery age (Wolfart 1961, p. 53) cannot at present be distinguished from *E. hemisphaerica*.

Stratigraphic range. At the type area of Llandovery, *E. hemisphaerica* occurs in the Sefin shales, an impersistent stratigraphic unit, which overlies beds of typical C_1 lithology and which was grouped with the C_1 beds by Williams (1951, p. 130). The Sefin shales contain graptolites of the zone of *Monograptus sedgwicki* (Jones 1949, p. 62) which are of early Upper Llandovery age.

The Paraguay specimens occur in beds which have been correlated with the Lower Llandovery on the basis of graptolite and trilobite evidence (Wolfart 1961, p. 53); they are the earliest known of the genus *Eocoelia.* No other Lower or Middle Llandovery occurrences are known.

The upper limit of *E. hemisphaerica* must be prior to the C_4 beds of Llandovery which contain *E. intermedia.*

Eocoelia intermedia (Hall)

Plate 83, figs. 9–12; Plate 84, figs. 1–2

Leptocoelia intermedia Hall 1860, p. 147, fig. 5.

Definition. This species includes all populations that contain individuals both with and without umbonal chambers lateral to the dental lamellae of the pedicle valve; the umbonal chambers when present are typically reduced in size by comparison with the earlier species, *E. hemisphaerica.*

Discussion. The species is distinctly ribbed, with the two populations measured showing values for the mean $h_r/w_r \times 100 \simeq 30\%$. The values measured are significantly different from the larger populations of *E. hemisphaerica* measured, which are about 40%. The populations identified as *E. intermedia* show considerable variation in rib number; sample no. 6 has an unusually high mode of 16 ribs with some specimens showing as many as 20 ribs, while sample no. 15 has somewhat fewer. The ribs of *E. intermedia* show a slight tendency to fade out and disappear in the postero-lateral parts of the shell.

The lip and deflection are developed in only a few specimens.

Holotype. The type specimen of Hall's *Leptocoelia intermedia*, now preserved in the American Museum of Natural History, no. 1634, is similar to the Welsh Borderland collections, nos. 6 and 15, in rib strength and in the very reduced umbonal cavities (Pl. 84, figs. 1–2). Hall's specimen came from Arisaig, Nova Scotia, where *Eocoelia* occurs at many horizons in the Ross Brook Formation. All four species

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EXPLANATION OF PLATE 84

For localities of Figs. 5–17 see Appendix.

FIGS. 1–2. *Eocoelia intermedia* (Hall 1860, p. 144, fig. 5). Holotype, Arisaig, Nova Scotia. AMNH 16341:0, pedicle valve; 1, posterior view of internal mould; 2, internal mould.

Figs. 3–4. *E. sulcata*, Arisaig, Nova Scotia. AMNH 16341:1 pedicle valve; 3, posterior view of internal mould; 4, internal mould.

Figs. 5–11. *E. hemisphaerica*, Collection 13. 5, OUM C6849*a*, internal mould of brachial valve; note cardinal process. 6–8, OUM C6857*a*, brachial valve; 6, internal mould; 7, rubber cast of internal mould; 8, oblique view of rubber cast of internal mould. 9–11, OUM C6966*a*, pedicle valve; 9, internal mould; 10, rubber cast of internal mould; 11, oblique view of rubber cast of internal mould.

Figs. 12–17. *E. curtisi*, Collection 3. 12–14, OUM C3189*b*, brachial valve; 12, internal mould; 13, rubber cast of internal mould; 14, oblique view of rubber cast of internal mould. 15–17, Holotype, OUM C3241*a*, pedicle valve; 15, internal mould; 16, rubber cast of internal mould; 17, oblique view of rubber cast of internal mould.


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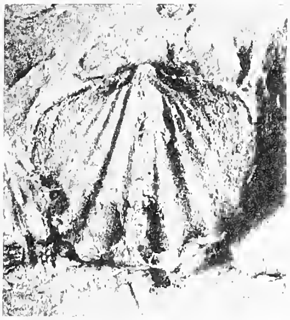
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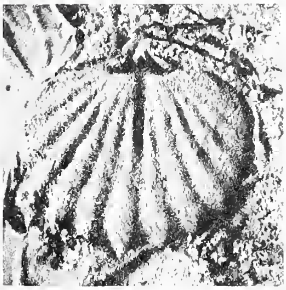
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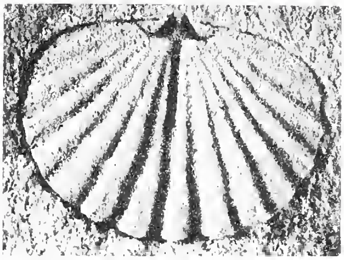
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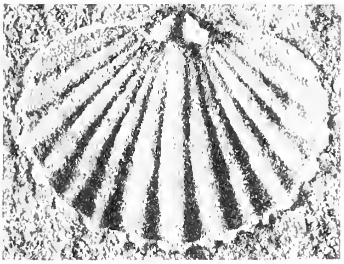
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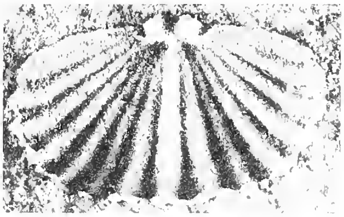
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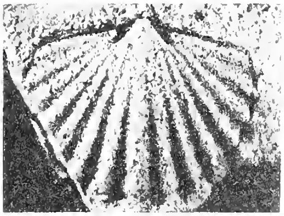
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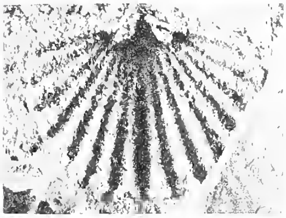
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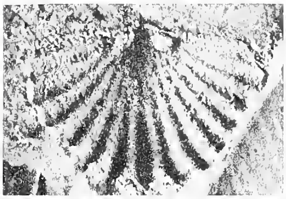
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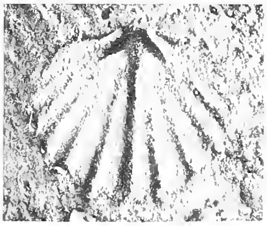
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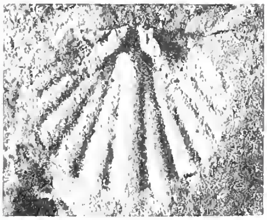
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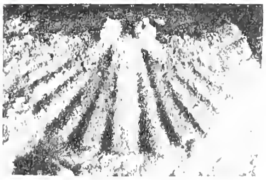
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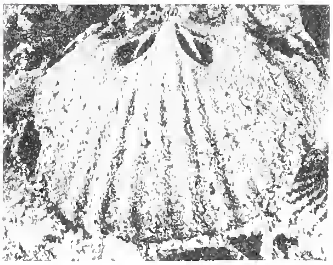
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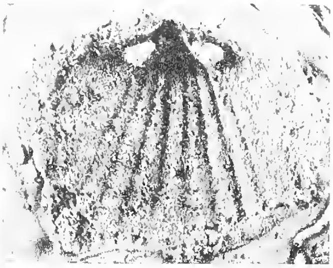
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ZIEGLER, Silurian atrypacean brachiopod *Eocoelia*

of *Eocoelia* occur in this sequence; included with Hall's type specimen in the American Museum of Natural History are some specimens with extremely weak ribs which probably came from a higher horizon than the type (Pl. 84, figs. 3–4).

Occurrence. In the Welsh Borderland *E. intermedia* occurs in the Huntley Hill Beds of May Hill, as does *E. hemisphaerica*, and in the *Pentamerus* Beds of Norbury, Shropshire. At Llandovery the species occurs in beds mapped by Jones (1925) as C_4 in an old quarry just west of the road from the village of Myddfai to the farm Gorllwyn-fawr, at the point adjacent to the farm Gorllwyn-fâch.

Stratigraphic range. As stated, at Llandovery, the species occurs in beds mapped as C_4 (Jones 1925). The upper and lower ranges cannot be determined rigorously because sufficient specimens of *Eocoelia* have not yet been found in C_3 or C_5 at Llandovery. Nor can the superposition of *E. intermedia* on *E. hemisphaerica* be rigorously demonstrated; however, mapping evidence at May Hill and Llandovery suggests this relationship.

Eocoelia curtisi sp. nov.

Plate 83, figs. 7–8; Plate 84, figs. 12–17

Atrypa? *hemisphaerica* J. de C. Sowerby; Davidson 1866, p. 136, pl. 13, figs. 24*a*, *b*, *c*.

Definition. This species is defined to include populations which show no sign of umbonal chambers or dental lamellae in the pedicle valve, but which do have distinct ribs.

Discussion. The teeth of this species are broadly based on the floor of the pedicle valve instead of being supported by dental lamellae as is the case with *E. hemisphaerica* and some specimens of *E. intermedia*. Fossettes (grooves on the median sides of the teeth) are more deeply incised in *E. curtisi* than in earlier species. The fossettes are a type of socket into which fit the laterally directed hinge plates of the brachial valve.

The ribs of *E. curtisi* are weaker than in earlier species, the value of mean $h_r/w_r \times 100$ being about 20% for the populations measured. The differences with earlier populations are statistically significant in some cases. Rib number varies about a mode of 12; this decrease with respect to earlier populations is due both to a wider spacing of ribs and to the progressive disappearance of ribs in the postero-lateral regions of the shell.

The lip and deflection are virtually absent in *E. curtisi*.

Holotype. Oxford University Museum specimen no. C3241 from collection 2, Charfield Green, Tortworth Inlier (Pl. 84, figs. 15, 16, 17).

Occurrence. The species is particularly abundant in the Damery Beds of the Tortworth Inlier and may be collected at Charfield Green and Damery Quarry, localities that were frequented by the early workers. At May Hill a few specimens, probably *E. curtisi*, have been found in the Yartleton Beds. *E. curtisi* occurs in the basal Wyche Beds both at Gullet Quarry, Malvern Hills district, and at the Gunwich Mill site, Old Storridge Common. A specimen, probably of this type, has been discovered in C_5 beds at Llandovery, 500 yards north of the farm Llwyn-Meredith in a stream section. In Ireland *E. curtisi* is abundant in the lowest beds of the Annelid Grit, north-west Co. Galway.

In North America the species has been identified from Arisaig, Nova Scotia, where it occurs at the mouth of Arisaig Brook.

Stratigraphic range. E. curtisi probably does not range higher or lower than the C_5 beds of Llandovery. *E. intermedia* occurs in C_4 at Llandovery, and in the southern part of the Welsh Borderland *E. sulcata* occurs in the top part of the Llandovery sequences, that is, in beds that are probably equivalent to the unfossiliferous C_6 shales of the type area.

Eocoelia sulcata (Prouty 1923)

Plate 83, figs. 1–6; Plate 84, figs. 3–4

Coelospira sulcata Prouty, *in* Prouty and Swartz 1923, p. 466, pl. 27, figs. 6–8.
Eocoelia sulcata (Prouty), Boucot *et al.* (in press).

Definition. Populations identified with this species have vestigial ribs, that is, ribs that are present only in the young growth stages and are not apparent at the anterior commissure of the average-sized specimen.

Discussion. The index of rib strength (mean $h_r/w_r \times 100$) is very low, the values being about 10%, as compared with those of *E. curtisi*, which are about 20%.

E. sulcata is similar to *E. curtisi* as far as the structures of the beak and of the pedicle valve are concerned; that is, umbonal chambers and dental lamellae are absent.

Holotype. Prouty's specimens from the Rochester Formation and the upper part of the Rose Hill Formation of Maryland are the types of this species. It may eventually prove necessary to designate new types as Prouty's specimens cannot be located at present (G. A. Cooper, personal communication).

Occurrence. At Tortworth *E. sulcata* occurs in the Tortworth Beds, that is, the top of the Llandovery section, and in beds mapped as Wenlock (Curtis 1955, p. 4). The species occurs in the upper part of the Yartleton Beds of May Hill and in the upper part of the Wyche Beds near Old Storridge Common. In Norway, the species is abundant in Stage 8*a-b* at Gjettum Station, Baerum, Oslo-Asker District. Apart from the type localities in Maryland, the species also occurs in North America in the Long Reach Formation of New Brunswick (Boucot *et al.*, in press).

Stratigraphic Range. The superposition of beds containing *E. sulcata* on *E. curtisi* may be demonstrated at Tortworth and Old Storridge Common. Since *E. curtisi* is of C_5 age, *E. sulcata* probably originated about C_6. *Eocoelia* may have become extinct about the middle of the Wenlock as there is no record of it in the upper Wenlock or Ludlow. Amos and Boucot would derive the Devonian brachiopod *Leptocoelia* from *Eocoelia* (1963, p. 443), but the later species of *Eocoelia* show trends in the loss of ribs that make this connexion unlikely. *Leptocoelia* may have been derived from one of the early species of *Eocoelia*, which are similar in several respects, but there is no direct stratigraphic evidence for this.

PALAEOECOLOGY

Eocoelia is a widespread element in Upper Llandovery and low Wenlock faunas, but it is only really abundant at certain localities. At these localities *Eocoelia* dominates the assemblage to such an extent that the expression *Eocoelia* Community is appropriate (Ziegler 1965). The *Eocoelia* Community occurs in the Cowleigh Park Beds of Ankerdine Hill and Old Storridge Common where it is of C_1–C_2 age, in the Huntley Hill Beds of

May Hill where it is of C_1–C_3 age, and in the Damery Beds of Tortworth where it is of C_5 age. Each of these stratigraphic units is a basal unit deposited by the transgressing Silurian sea and in each of these areas the *Eocoelia* Community is succeeded by a community dominated by *Pentameroides sp.* At Presteigne the *Eocoelia* Community is well developed in beds of C_1–C_2 age and is succeeded by a Community dominated by *Pentamerus sp.* The *Eocoelia* Community occurs in both the Conglomerate Series of Marloes Bay, Pembrokeshire, and the Annelid Grit of Co. Galway, Ireland; in each of these places it is associated with basal beds deposited by a transgressing sea.

Owing to its association with transgressive seas, and often with relatively coarse clastic rocks, the *Eocoelia* Community is thought to represent a coastal environment. It was not the only coastal community, however, as the basal Cowleigh Park Beds of the Malvern District contain a very restricted fauna dominated by *Lingula pseudoparallela* Stubblefield, '*Camarotoechia*' *decemplicata* (J. de C. Sowerby), some bivalves and gastropods, and little else.

INTERPRETATIONS OF THE TRENDS AND VARIATIONS

The most easily understood trend in *Eocoelia* is the gradual strengthening of the articulatory mechanism. Individuals with deeper fossettes, stronger hinge plates, and larger, more broadly based teeth would have had a selective advantage, particularly in the relatively rough coastal environment inferred for this brachiopod. Trends toward increased articulation have been noticed in other brachiopods; for instance, several groups of stropheodontids independently display increases in the number of denticles along their hinge lines with time (Williams 1953*b*).

The reason behind the rather striking decline in rib strength is less obvious. The ribs may have originally helped in the protection of the animal by their interlocking effect. If this were so, then the development of the articulatory mechanism might well have made the ribs redundant.

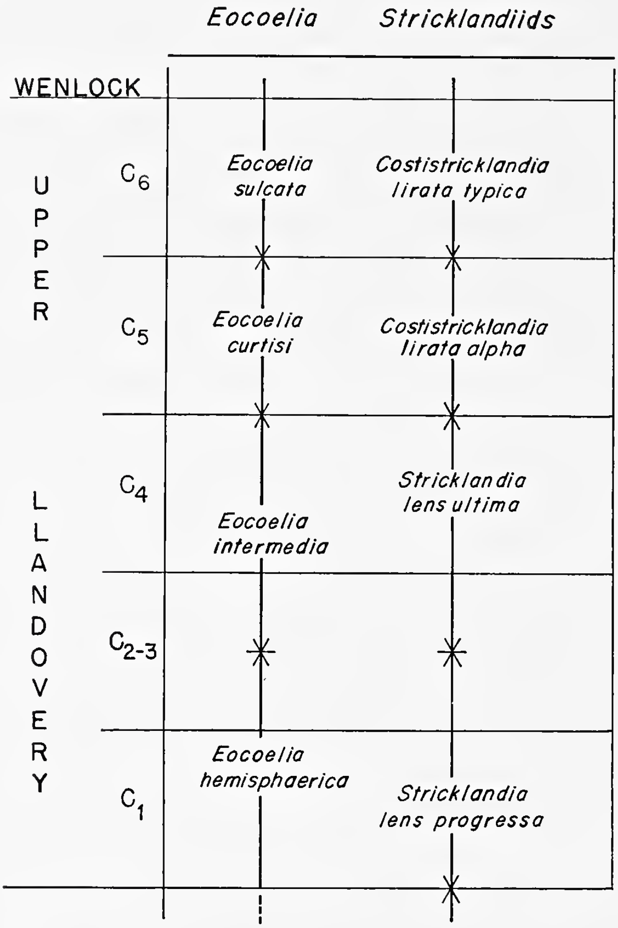
Other features of *Eocoelia* disappear during the time of the development of the articulatory mechanism; both lip and deflection are unknown in the later species. The formations of these structures, seen particularly well in populations of *E. hemisphaerica*, involved changes in the direction of growth at the anterior commissure with consequent demands for rapid reorientation of the teeth in the sockets. With time, the deepening of the fossettes to produce more of an interlocking articulation may have made this reorientation difficult and eventually impossible.

There is considerable variation between collections in both the mean size and relative numbers of *Eocoelia*. Moreover, the two factors seem to be related in a positive way, that is, when *Eocoelia* occurs in large numbers, as in the *Eocoelia* Community, the individuals tend to be large; but when it occurs sporadically the individuals are always small. The fact that size and numbers are related suggests that they were originally controlled by the general favourability of the environment for *Eocoelia*.

Finally, the reasons behind the variation in the spacing of the ribs are not at present understood. It cannot yet be established whether or not variation exists between populations at one horizon. At best, it can be said that the rib spacing appears to vary in a random way in a given stratigraphic section.

UPPER LLANDOVERY CORRELATION

The detailed correlation of strata should be based on organisms whose evolution is well understood. The mere linking of various species does not definitely establish an evolving lineage. It must be shown that all gradations from one species to the next exist; this is manifestly the case with *Eocoelia*, where the sampling is such that the problem is more in dividing up a completely intergrading set of populations than in linking together distinct species. An important check on an evolutionary trend is to detect its occurrence in widely separated areas; all the species of *Eocoelia* are known from North America and Britain and their sequence can be established on both sides of the Atlantic. Finally, evolutionary trends in unrelated brachiopods may be used as a check on each other; trends in the *Stricklandia–Costistricklandia* lineage (St. Joseph 1935, p. 421; Williams 1951, p. 98; Boucot and Ehlers 1963, p. 49) are useful in this respect.



TEXT-FIG. 6. Tentative correlation of the evolving lineages.

The correlation of the various evolving lineages with the lithologic zones mapped by

Jones (1925, 1949) at Llandovery may be established from occurrences of the species both in the type area and in surrounding areas (text-fig. 6). At Llandovery *Eocoelia hemisphaerica* and *Stricklandia lens progressa* Williams occur in beds mapped as C_1. The C_2–C_3 beds are largely unfossiliferous and only one brachial valve of *Eocoelia*, not enough for specific identification, has been found. In C_4 beds *Eocoelia intermedia* and *Stricklandia lens ultima* Williams occur together. Both lineages are represented, though somewhat unsatisfactorily, in C_5 beds; one pedicle valve of *Eocoelia*, probably *E. curtisi*, has been found, and stricklandiids occur, but are insufficiently complete to tell whether weak ribs are present. However, in an adjacent area to the south, the Sawdde River section near Llangadock, beds mapped as C_4–C_5 (Williams 1953*a*) contain abundant *Eocoelia curtisi* and *Costistricklandia lirata alpha* (St. Joseph). The C_6 beds of Llandovery are unfossiliferous and are thought to be equivalent to beds in the Welsh Borderland, such as at May Hill or Old Storridge Common, that contain *Eocoelia sulcata* and *Costistricklandia lirata typica* (St. Joseph); these beds occur just below the base of the Woolhope Limestone, the basal horizon of the Wenlock.

APPENDIX

Description of Localities

Collection no.	*Field no.*	*Grid reference*	*Exposure*	*Location*	*Horizon*	*Species of* Eocoelia
TORTWORTH INLIER						
1	T–W–B	ST/ 6947 9376	hill-side exposure	Little Daniel's Wood, 750 yds. N. 78° W. of Old Court farm, Tortworth	Wenlock Series	*E. sulcata*
2	T–D–A	ST/ 6962 9390	loose blocks in stream bed	About 150 yds. N. 60° E. of SW. corner of Daniel's Wood near Tortworth	Base of Tortworth Beds	*E. sulcata*
3	T–M–A	ST/ 7268 9212	stream section	270 yds. N. 10° W. of Hillhouse farm, Charfield	Lower Damery Beds	*E. curtisi*
MAY HILL INLIER						
4	M–S–C	SO/ 6936 2271	stream section	380 yds. N. 71° W. of Hay Farm on N. side of May Hill	Upper Yartleton Beds	*E. sulcata*
5	M–S–B	SO/ 6932 2270	stream section	430 yds. N. 81° W. of Hay Farm on N. side of May Hill	Upper Yartleton Beds	*E. sulcata*
6	M–H–A	SO/ 7047 1811	track-side exposure	Just W. of old quarry on E. side of Nottswood Hill, 760 yds. S. 62° W. of Hinders	Huntley Hill Beds	*E. intermedia*
7	M–N–A	SO/ 7014 2104	loose blocks from old quarries	Newent Wood, 400 yds. N. 45° W. of Folly Farm on SE. side of May Hill	Huntley Hill Beds	*E. hemisphaerica*
OLD STORRIDGE COMMON						
8	H–M–C	SO/ 7405 5167	stream section	W. bank of Leigh Brook, 210 yds. N. 41° E. of Mousehole Bridge (SW. of Alfrick Pound)	Upper Wyche Beds	*E. sulcata*
9	H–L–C	SO/ 7464 5108	sunk track exposure	Coneygore Coppice, 690 yds. N 30° W. of The Beck	Wyche Beds	*E. curtisi*

Collection no.	*Field no.*	*Grid reference*	*Exposure*	*Location*	*Horizon*	*Species of* Eocoelia
10	H–M–B	SO/ 7430 5152	stream section	W. bank of Leigh Brook, 440 yds. E. of Mousehole Bridge (SW. of Alfrick Pound)	Basal Wyche Beds	*E. curtisi*
11	H–F–C	SO/ 7444 5124	stream section	Small stream 950 yds. N. 36° W. of The Beck	Top of Cowleigh Park Beds	*E. hemisphaerica*
12	H–L–A	SO/ 7467 5115	track exposure	Coneygore Coppice, 740 yds. N. 25° W. of The Beck	Cowleigh Park Beds	*E. hemisphaerica*
ANKERDINE HILL						
13	A–Q–A	SO/ 7363 5630	disused quarry	Near summit of Ankerdine Hill 335 yds. N. 45° E. of church at Knightsford Bridge	Cowleigh Park Beds	*E. hemisphaerica*
14	A–H–A	SO/ 7376 5696	track exposure	Hay Wood, 200 yds. N. 45° E. of Knightwick Sanatorium on NW. side of Ankerdine Hill	Cowleigh Park Beds	*E. hemisphaerica*
NORBURY, SHROPSHIRE						
15	S–N–A	SO/ 3586 9286	disused quarry	N. of the Linley to Norbury road, 280 yds. ESE. of Linley Cottage	*Pentamerus* Beds	*E. intermedia*

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SPONGOPHYLLIDAE FROM THE DEVONIAN GARRA FORMATION, NEW SOUTH WALES

by D. L. STRUSZ

ABSTRACT. The structure of rugosans belonging to the family Spongophyllidae Edwards and Haime 1873 (here taken to include the Family Ptenophyllidae Wedekind 1923) is discussed in detail. Representatives of the Family occurring in the Emsian (or possibly early Eifelian) Garra Formation are revised or described. The Australian species ascribed to *Acanthophyllum* are reviewed, *Pseudochonophyllum* Soshkina is fully revised, and its type (and only) species, *P. pseudohelianthoides* (Sherzer) is shown to occur only in Czechoslovakia and eastern Australia. *Grypophyllum aggregatum* Hill is placed in *Lyrielasma* Hill. *Australophyllum* Stumm is discussed and its species are reviewed. Several of the eastern Australian Devonian faunas, previously thought to range from Coblenzian to late Eifelian, are considered to be probably Emsian.

New species described are: *Acanthophyllum* (*Acanthophyllum*) *aeneae*, *A.* (*Neostringophyllum*) *implicatum*, *A.* (*N.*) *turni*, *A.* (*Grypophyllum*) *jenkinsi*, *Lyrielasma*? *micrum*, *Australophyllum bilaterale*.

IN this paper are described those species of corals, occurring in the Emsian? Garra Formation of New South Wales, which comprise the acanthophyllid and spongophyllid groups. For reasons outlined below, these are for the present at least combined into the Family Spongophyllidae.

The Garra Formation has been described in a previous paper on the disphyllids and phacellophyllids (Strusz 1965*b*), and in a purely stratigraphic Note (Strusz 1965*a*). Further references, both geological and palaeontological, may be found therein. An additional reference of some interest in the correlation of this formation is Philip and Pedder (1964).

Abbreviations. The following abbreviations (fully explained in Strusz 1965*b*, p. 522) are used herein:

Dc	Corallite diameter
Dt	Tabularium diameter
R	Corallite radius
Ts	Tabularial spacing (astraeoid, etc., coralla)
n	Number of 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.
UCT F	University College of Townsville Palaeontological Collection; Townsville, Qld.
UQF	University of Queensland Palaeontological Collection; Brisbane, Qld.

[Palaeontology, Vol. 9, Part 4, 1966, pp. 544–98, pls. 85–96.]

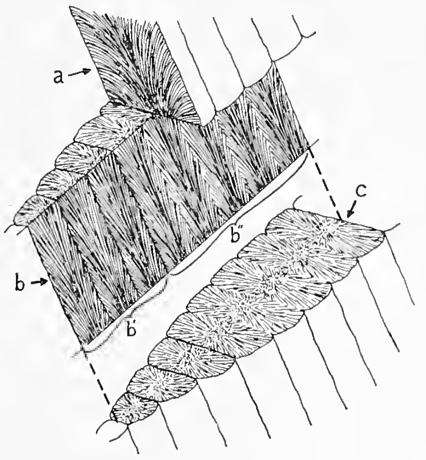
SYSTEMATIC PALAEONTOLOGY

Family SPONGOPHYLLIDAE Dybowski 1873, emend. Pedder 1964

Remarks. Following Pedder (1964, p. 436), and a tentative suggestion by Birenheide (in litt.), I place the Family Ptenophyllidae Wedekind 1923 in synonymy with this family. The thus enlarged family has the following characters:

Septa. The septal structure is rather similar to that of the Disphyllidae. The septa consist of fine trabeculae, in most cases arranged in single radial series, although in some genera there may be more than one series in outer parts of the septa. The trabeculae are arranged either broadly parallel, and inclined upwards and inwards, or in half-fans within the dissepimentarium, and usually again in the tabularium. This arrangement has been well described by Birenheide (1961).

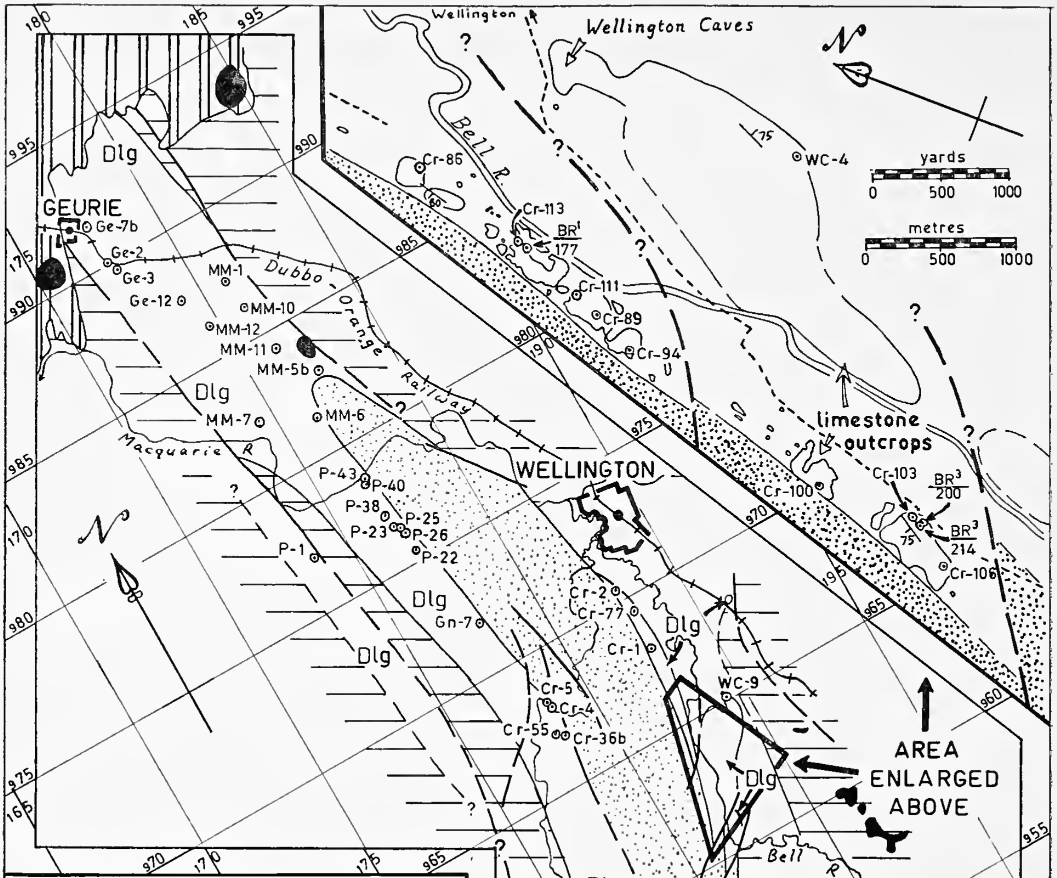
The trabeculae are monacanthine; in cross-section they are round to square in attenuate portions of a septum, becoming oval to rectangular (the long axis perpendicular to the plane of the septum) in dilated portions. Within a trabecula the fibres diverge from the axis, strongly in a tangential direction (i.e. longitudinal, and perpendicular to the plane of the septum), but only weakly in a radial direction (text-fig. 1). In transverse section a septum gives the appearance of a median dark line, from which the fibres diverge at a large angle, apparently without clear trabecular organization. As shown by Birenheide (1961, p. 85) the median dark line represents that region in which the fibres are perpendicular to the section. In tangential longitudinal section the fibres are seen to diverge strongly from the mid-line of the septum. Only in radial longitudinal section may the trabecular arrangement be seen, and even then often not very clearly. In such sections there is also seen a parallel banding perpendicular to the direction of the trabeculae. This is apparently formed partly by periodic variation in either optical orientation or composition, and partly by periodic insertion of additional trabeculae as the trabecular fan expands.



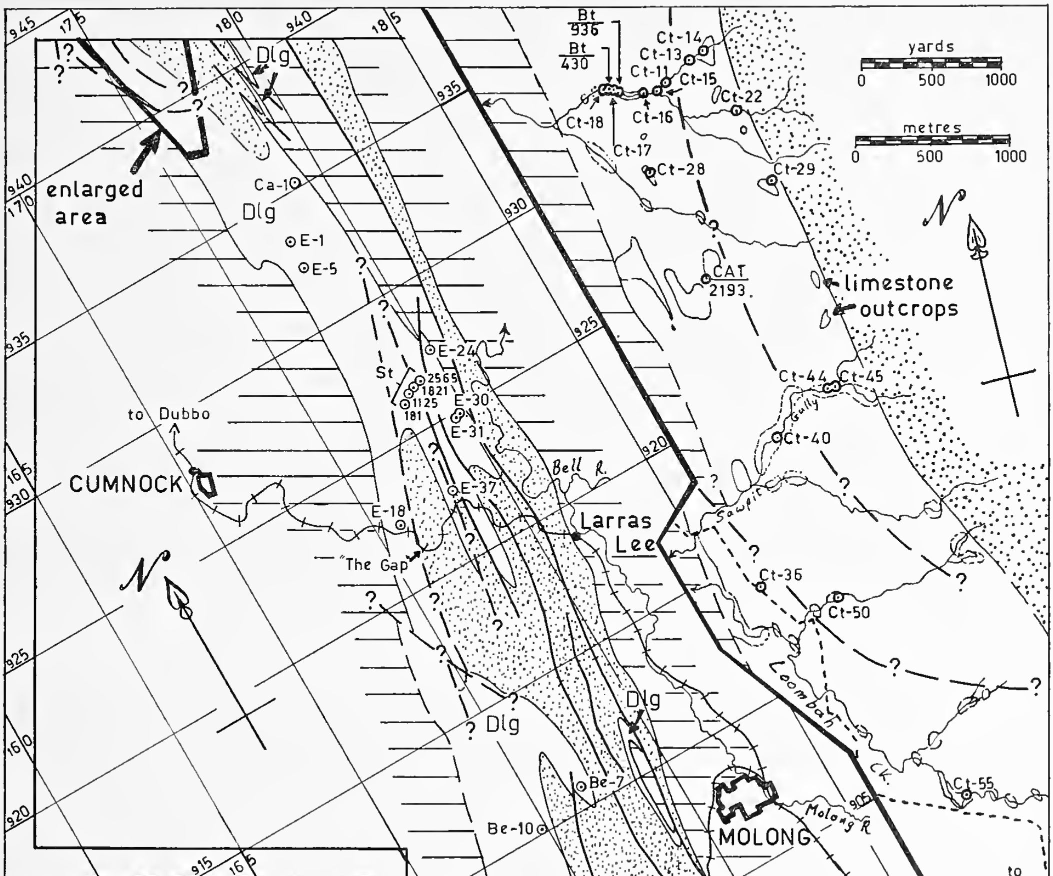
TEXT-FIG. 1. Generalized septal microstructure of the Family Spongophyllidae, approximately × 50, reconstructed mainly from thin sections of Eifel species of *Acanthophyllum* in the collection of the University of Queensland. *a*, tangential longitudinal section along the axis of one trabecula; *b*, radial longitudinal section along the median plane of the septum; *b′*, boundaries between trabeculae emphasized; *b″*, appearance in thin section; *c*, transverse section, with trabecular boundaries as for *b′*, *b″*.

In cases where parts of the septa consist of more than a single series of trabeculae, the median dark line is normally absent. The individual trabeculae are round in section, and do not greatly diverge from the direction of the septal plane. Moreover, there is generally no regular arrangement into radial series in such cases. This condition is known peripherally in *Dohmophyllum*, and over much of the dissepimentarium in *Pseudochonophyllum*.

There are no carinae (ridges on the side of a septum, formed by the lateral extension of one, or a series of successive, trabeculae at all stages of growth, and so growing in the same direction as the trabeculae). Septal modifications may be of several forms:



TEXT-FIG. 2*a*. Map showing location of the Garra Formation in New South Wales, and generalized geological map showing positions of fossil localities mentioned in the text.



TEXT-FIG. 2*b*. Southern extension of locality and geological map, text-fig. 2*a*.

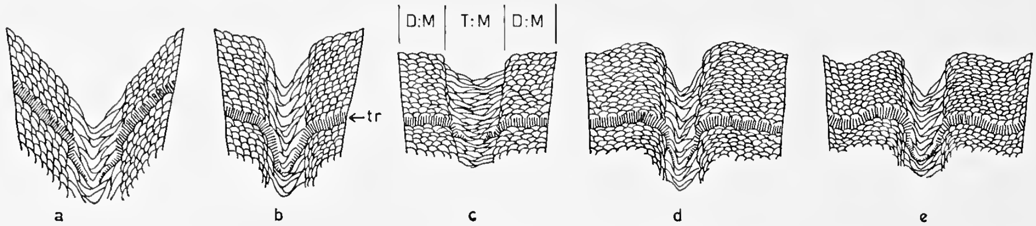
(*a*) Lateral denticles. These may be formed by individual fibres continuing a little beyond the face of the septum, or by the temporary lateral divergence of part of a trabecula from its upward direction of growth.

(*b*) Septal flanges. These are parallel to the growing edge of septum, and are formed by the lateral divergence in unison of all the trabeculae in a septum. In *Acanthophyllum*, for example, they slope downwards towards the axis. Their greatest development is frequently within the tabularium.

(*c*) Axial processes. These are usually difficult to interpret because of their complexity, but appear to be formed either by the irregular extension of trabeculae beyond the axial edge of the septum, or by irregularities in the course of the flanges in the axial region. The latter would appear to be the most common.

(*d*) Naotic plates. These are much as in *Craterophyllum*; they occur in *Pseudochonophyllum*, some *Dohmophyllum*, and occasionally in other genera.

(*e*) Finally, in some instances the septa peripherally break up into parallel strands, each consisting of a single series of trabeculae. These strands are usually anastomosing, and in some cases may be modified and extended flanges.



TEXT-FIG. 3. Diagrammatic representation of calical forms in the Spongophyllidae, shown in longitudinal section, with German terms as used by Birenheide (1961, 1962) and the equivalent terms used herein. *a*, 'Trichterkelch': inversely conical calice (characteristic of *Acanthophyllum* (*Neostringophyllum*), *A.* (*Grypophyllum*)); *b*, 'Krempenkelch': bell-shaped calice (characteristic of *A.* (*Acanthophyllum*)); *c*, 'Flachkelch': saucer-shaped calice; *d*, 'Wulstkelch': everted calice; *e*, 'sattelrandiger Wulstkelch': everted calice with flared rim. D:M—dissepimentarium; T:M—tabularium. Note the correlation between arrangement of horizontal elements, attitude of trabeculae, and shape of calice.

Tabulae. The tabulae may be flat to gently concave, and mostly complete, as in *Spongophyllum*, or gently to deeply concave with a median depression, in some cases strongly infundibuliform, as in *Acanthophyllum* and *Xystriphyllum*. In the second case, the tabulae are generally predominantly incomplete to vesicular.

Dissepiments. Characteristically the dissepimentarium is wide, and consists of numerous small, globose to elongate dissepiments. Lonsdaleoid dissepiments are common. In *Spongophyllum* the dissepimentarium is comparatively narrow, but the presence of well-developed lonsdaleoid dissepiments is characteristic, and serves to link the genus with the group around *Acanthophyllum* with wide dissepimentaria.

Genus ACANTHOPHYLLUM Dybowski 1873

1873 *Acanthophyllum* Dybowski, p. 339 (*fide* Lang, Smith, and Thomas 1940, p. 13).
1961 *Acanthophyllum* Dybowski 1873; Birenheide, p. 80; contains an extensive synonymy to 1958.
1949 *Pseudochonophyllum* Soshkina, p. 119 (*non* Soshkina 1937).
1962 *Acanthophyllum* Dybowski 1873; Philip, p. 184 (*partim*).
1964 *Grypophyllum* Wedekind 1922; Pedder, p. 439 (*partim*).

Type species. Cyathophyllum heterophyllum Edwards and Haime 1851, p. 367, pl. X, fig. 1; subsequent designation Schlüter, 1889, p. 296 (for description see Birenheide 1961, pp. 81, 89).

Diagnosis. Solitary, predominantly subcylindrical corals with more or less frequent growth swellings. Calice inversely conical or bell-shaped. Septa trabecular, thin or dilated, generally of only one radial series of trabeculae; lamellar thickening may occur in some or all growth stages; flanges, lateral denticulae, and axial processes common. Septa radial, or directed to a generally short median plane, frequently marked by elongation of the cardinal septum. Tabulae incomplete to vesicular, forming concave floors with a median depression. Lonsdaleoid dissepiments may be well developed.

Remarks. I follow Birenheide (1961) in subdividing the genus into three subgenera, distinguished on calical shape, degree of septal dilatation, and to a lesser extent degree of development of lonsdaleoid dissepiments. All three appear to be present in the Garra Formation. *Acanthophyllum mansfieldense* of Philip (1962) is a species of *A.* (*Neostringophyllum*), and is therefore the earliest representative of that subgenus yet known. Similarly, the earliest *A.* (*Acanthophyllum*) would seem to be that described by Philip (1962) from the Gedinnian or Siegenian of Victoria. The Garra record of *A.* (*Grypophyllum*) would seem to be the earliest yet known for that subgenus.

The Russian records of this group are a little difficult to interpret. Most of the specimens placed by Soshkina (1949, p. 119; 1952, p. 98) in *Pseudochonophyllum* are *Acanthophyllum*. Bulvanker (1958) described several species under the names *Acanthophyllum*, *Neostringophyllum*, *Grypophyllum*, and *Stenophyllum*, but also included species better placed in other genera of this family. Similarly, species of *Acanthophyllum* are placed by Soshkina and Dobrolyubova (in Orlov 1962) in *Ptenophyllum*, *Acanthophyllum*, *Stenophyllum*, *Neostringophyllum*, and *Grypophyllum*.

Subgenus ACANTHOPHYLLUM Dybowski 1873

Type species. See above.

Diagnosis. Subgenus of *Acanthophyllum* with bell-shaped calice. With thin peripheral stereozone, few lonsdaleoid dissepiments. Septa generally weakly to strongly fusiform, frequently further thickened during ontogeny by lamellar sclerenchyme. Trabeculae arranged in half-fans in dissepimentarium.

Remarks. According to Birenheide (1961, p. 128), *A.* (*Acanthophyllum*) characterizes the Eifelian of the Eifel. In Australia species are known as early as the Gedinnian or Siegenian, and if recent interpretations are correct (Philip 1960; Philip and Pedder 1964), are not certainly known above the lower Eifelian. Of the five species so far assigned to *Acanthophyllum* s.l., four are herein considered to be *A.* (*Acanthophyllum*). These fall into two groups, one of large corallites and the other of small ones. The small species are *A.* (*A.*) *aequiseptatum* Hill 1940, and *A.* (*A.*) *asper* Hill 1940, both from the Murrumbidgee limestones (see pl. 85, figs. 1, 2). Both have Dc = *circa* 2 cm., n = *circa* 60. The holotypes differ in the manner of dilatation of their septa (strong, axially thickened, and convoluted, major more than minor, in *A.* (*A.*) *asper*; moderate, fusiform, uniform, in *A.* (*A.*) *aequiseptatum*), and in Dt (*circa* $\frac{1}{2}$Dc in *A.* (*A.*) *asper*, *circa* $\frac{1}{4}$Dc in *A.* (*A.*) *aequiseptatum*). However, I have collected several corallites from Clear Hill, type locality of *A.* (*A.*) *aequiseptatum*, which suggest that these characters are rather variable, and that in fact the two species may be synonymous. This will require further study outside the scope of this paper.

The large Australian species are *A.* (*A.*) *clermontense* (Etheridge fil. 1911) from Clermont, Queensland, and *A* (*A.*) *mansfieldense* (Dun 1898) from Mansfield, Victoria. The former is solitary to weakly fasciculate, the latter trochoid. Both have Dc over 2·5 cm., the former reaching 6 cm. In both, Dt = *circa* $\frac{1}{4}$Dc. In *A.* (*A.*) *clermontense*, n = 80 (max.), in *A.* (*A.*) *mansfieldense* n = 50. Their most important distinction is in their septal dilatation: in the former the septa are fusiform, and axially dilated and contorted; in the latter the dilatation is in the form of concentric series of wedges increasing in size peripherally, while the septa are radial, and not greatly dilated or contorted axially.

The new species described below belongs with this second group. It is easily distinguished from the previous species by the greater width of its oval tabularium, by the strongly bilateral arrangement of its septa, and by its deeply infundibuliform tabulae.

Acanthophyllum (*Acanthophyllum*) *aeneae* sp. nov.

Plate 85, figs. 5*a*, *b*

Derivation of name. Aeneas, a Graeco-Roman mythological hero.

Holotype. SU 11291 (Pl. 85, figs. 5*a*, *b*); loc. Be–10.

Diagnosis. Large *A.* (*Acanthophyllum*) with wide, oval tabularium of deeply infundibuliform incomplete tabulae; septa unequal, directed towards long axis of tabularium, moderately dilated; minor septa long, very unequal.

Description. Solitary, trochoid, or ceratoid. The external characteristics are unknown, as all free corallites collected were worn. The epitheca is apparently thin and lined with a narrow fibrous stereozone. As deduced from longitudinal sections, the calice is the bell-shaped one characteristic of the subgenus (see text-fig. 3), with a fairly wide sloping rim and a wide, funnel-shaped axial pit. The greatest known diameter is 3·6 cm.+ (estimated *circa* 4·5 cm.), but most corallites are about 2 cm. across.

Dimensions. In mm. of representative specimens.

No.	*loc.*	*Dc*	*Dt*	*Dt/Dc*	*n*
SU 11291*	Be–10	est. 45	15×22	*ca.* 0·3–0·5	*ca.* 74
SU 11296	,,	18·5+	7×7·5	?	*ca.* 60
SU 14121	Ct–6	est. 38	6·5	*ca.* 0·2	*ca.* 60

*Holotype; measured Dc = 36 mm.

Adult corallites have some 60–70 septa. The major septa are long and unequal, extending to the axis where they are arranged about a long median plane. This plane is further delineated by an elongate septum (cardinal?) at one end, which is flanked by long minor septa. Opposite may be a rather short major septum. The septa are fusiform and moderately to strongly dilated; the dilated septa at most are equal to the interseptal loculi. The septa are rough-sided, but not markedly flanged in the dissepimentarium; thick flanges are prominent in the tabularium, where they are gently axially inclined. In the zone of maximum septal dilatation there may be intermittent reinforcement by lamellar sclerenchyme, which spreads over the surfaces of adjacent dissepiments (here strongly geniculate towards the periphery), so that an incomplete zigzag stereozone may form. In large corallites there may be two or three concentric stereozones so formed. The dilatation is somewhat variable within even the same transverse section; however, the major and minor septa are generally equally dilated. The minor septa vary in length, generally ending at the inner margin of the dissepimentarium, but at times somewhat withdrawn or extending a little way into the tabularium.

The septal structure is of fine trabeculae, approximately parallel, and diverging from the median plane of the septum. They are arranged in a broad half-fan within the dissepimentarium, the maximum inclination at the margin of the tabularium being about 50° from the vertical. The arrangement within the tabularium is less clear, but seems to consist of a much less divergent half-fan, the trabeculae being nearly vertical near the dissepimentarium, becoming moderately axially inclined (about 20° from the vertical?) near the axis. The flanges are trabecular and are perpendicular to the direction of growth of the trabeculae. Even in longitudinal section they can be readily distinguished from the lamellar sclerenchyme reinforcing the septal dilatation.

The epitheca has been worn from all available specimens, so the relative width of the tabularium is uncertain. It does appear to be rather wide (see table of dimensions). In all specimens the tabularium is markedly oval, the long axis being in the presumed counter-cardinal plane. The tabular floors are funnel-shaped, with sides inclined axially at about 30–40° from the horizontal; the margins are upturned, at times sharply, while there is a strong axial depression about $\frac{1}{4}$Dt across, and as deep. The tabulae are close, elongate, varying from nearly complete to incomplete (particularly marginally and within the axial depression).

The dissepimentarium consists of numerous small rather globose to elongate vesicles, which increase in inclination but decrease in size towards the axis. There is a definite region towards the tabularium where the rate of increase in inclination is temporarily increased. This change in slope is, however, not quite as abrupt as in the German species of *Acanthophyllum* s.s. In transverse section the dissepiments are strongly geniculate, the apices directed peripherally, over the greater part of the dissepimentarium. Lonsdaleoid dissepiments do not appear to be developed, but it is possible that complete specimens may show a narrow peripheral series.

Comparison. A. (*A.*) *aeneae* differs from the two other large Australian species—*A.* (*A.*) *mansfieldense* (Dun 1898) and *A.* (*A.*) *clermontense* (Etheridge fil. 1911)—in its wide tabularium and in the extreme bilaterality of the septa and tabularium. *A.* (*A.*) *clermontense* has similar septal dilatation, except that the major are thicker, but the tabular floors are not as deeply infundibuliform; the species may be weakly colonial. *A.* (*A.*) *mansfieldense* has fewer septa which are dilated in a distinctive manner—concentric series of wedges—and somewhat withdrawn from the axis; the calix is considerably shallower.

The closest German species is the type *A.* (*A.*) *heterophyllum* (Edwards and Haime 1851); this has rather more septa which are generally markedly convolute axially, and not nearly so strongly bilaterally arranged; moreover, the minor septa are thinner than the major. The tabulae are smaller, rather more globose, and not so steeply inclined. Similarly, the dissepiments are more globose, and are more elongate axially, whereas in *A.* (*A.*) *aeneae* they are more elongate peripherally. The manner of reinforcement of the septal dilatation by sclerenchyme differs somewhat from the German species.

Known localities. Be–10, Ct–6, Ct–53.

Acanthophyllum (*Acanthophyllum*) *clermontense* (Etheridge fil. 1911)

1911 *Cyathophyllum*(?) *clermontensis* Etheridge, p. 5, pl. B, figs. 1, 2, pl. D, fig. 3. Douglas Ck., Clermont, Queensland; 'Upper Couvinian'.
1939*b* *Acanthophyllum clermontense* Etheridge; Hill, p. 57, pl. IV, figs. 1, 2.
non 1962 *Acanthophyllum clermontense* (Etheridge); Philip, p. 185, pl. 27, figs. 1, 2. Tyers R., Victoria; Gedinnian.

Diagnosis. Large, solitary or weakly fasciculate *A.* (*Acanthophyllum*) with narrow tabularium; septa moderately dilated, fusiform, frequently with second zone of fusiform dilatation just outside tabularium, generally axially contorted; tabulae incomplete, forming bowl-shaped floors with wide axial deepening.

Remarks. This of all the Australian species most resembles the German species as described by Birenheide (1961); from them it differs particularly in being weakly fasciculate, but also in its narrow tabularium (Dt/Dc = *circa* $\frac{1}{4}$). The specimen described and figured by Philip (1962) from Victoria has distinctly domed tabular floors and apparently an inversely conical calice; it is probably a species of *Dohmophyllum* Wedekind 1923 (see Birenheide 1963), although somewhat older than described species of the genus.

A. (*A.*) sp. cf. *clermontense* (Etheridge fil. 1911)

Plate 85, figs. 3, 4, 6, Plate 86, fig. 1; text-fig. 4.

Material. Several specimens (9 sectioned) from locs. Cr–100, P–43.

Description. Most of the specimens appear to be solitary, ceratoid to cylindrical, but one at least (SU 13230, loc. Cr–100) is clearly fasciculate, consisting of a small radiating corallum of 3 or 4 corallites, increase being peripheral. The epitheca is thin, marked by narrow septal grooves. Repeated sharp rejuvenescence rims often occur. The calice has a wide, sharp-rimmed, gently sloping border, and a rather shallow, bowl-shaped axial pit. The septa form prominent ridges on the floor of the calice. The largest known corallite is about 3 cm. in diameter, but for most corallites Dc = 15–20 mm.

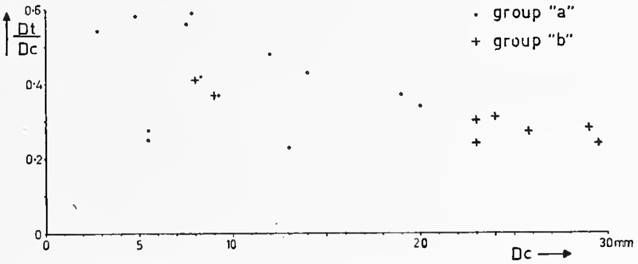
In adults n = 50–58. The major septa are long, extending unequally to the axis. Their axial structure and arrangement is variable: in some they are thin, with thin flanges, and are irregularly curved as in *A.* (*A.*) *clermontense*; in others, the arrangement is similar, but the septa are rather thickened, and heavily flanged. This leads on to those specimens in which the septa are thick and strongly flanged axially, and are bilaterally directed to a short median plane, rather than rotated as in typical *A.* (*A.*) *clermontense*.

Dimensions. In mm. of representative specimens.

No.	*loc.*	*Dc*	*Dt*	*Dt/Dc*	*n*
Group *a*: septa not greatly dilated or flanged:					
SU 13227	Cr–100	est. 22	5·5	*ca.* 0·25	54
SU 13230*	,,	4·8	2·8	0·58	38
,,	,,	est. 20	6·7	*ca.* 0·34	58
Group *b*: septa strongly dilated and flanged:					
SU 17237	P–43	est. 24	7·5	*ca.* 0·31	54
SU 17258	,,	est. 23	7·0	*ca.* 0·30	52
SU 17261	,,	est. 29·5	7·0	*ca.* 0·24	52?

* colonial.

Similarly, the septal dilatation is highly variable, even in the one transverse section. Generally the minor septa are as thick as the major and terminate at the margin of the tabularium. In some specimens the septa are fusiform in transverse section, and only moderately dilated, with broad wedge-shaped bases. Other specimens show this type, and as well strongly dilated septa tapering inwards from the thick bases, with perhaps a second zone of thickening corresponding to the zone of fusiform dilatation of the thinner septa. The other extreme (group *b* in the above table) is of extremely dilated septa, in contact over the outer half to two-thirds of the dissepimentarium, and then tapering inwards, perhaps with a narrow zone of slight fusiform dilatation just outside the tabularium. Occasionally in these specimens some of the septa are peripherally attenuate, but rapidly dilate inwards, being in contact a short distance in from the epitheca. The septa in some sections bear fine lateral denticulae, and in most cases are flanged; the inclination of the flanges increases inwards to the margin of the tabularium and then decreases to nearly horizontal. The flanges are generally weak but may become strong in the tabularium.



TEXT-FIG. 4. *A.* (*Acanthophyllum*) sp. cf. *clermontense*. Scatter diagram for Dt/Dc:Dc.

The septa consist of thin trabeculae arranged in broad half-fans in the dissepimentarium: near the periphery they are directed upwards and inwards at a small angle from the vertical. This angle increases steadily inwards until near the tabularium, where there is a sudden fairly marked increase to about 30–40°; within the tabularium they are directed more nearly vertically as the axis is approached.

In juveniles the tabularium is wide, Dt = *circa* 0·5Dc; however, it increases in width more slowly than the corallite, so that in adults it is narrow (*circa* 0·3–0·4Dc)—see text-fig. 4. The tabulae are generally incomplete, axially inclined, and only moderately convex. The tabular floors are bowl-shaped, with upturned margins, and a wide, shallow axial depression.

The dissepimentarium in adults is wide, consisting of numerous series of small dissepiments. In the outer zone these are gently to moderately axially inclined and rather globose. In a narrow zone around the tabularium they are steeply axially inclined and tend to be elongate. Lonsdaleoid dissepiments are almost entirely absent; in only one or two sections have I seen a few small ones.

Remarks. These specimens differ from the Clermont ones in their smaller size, and in their far more variable septal structure, dilatation, and axial arrangement. Were it not for the gradation shown by some specimens I would be inclined to place those with axially dilated and flanged septa directed to a short axial plane (group *b* in the table of dimensions) into a distinct species. Until the extent of variation in the Clermont species is known fully, and until considerably more Garra material is available, it is possible only to compare them.

Known localities. Cr–100 (9 or 10 specimens), P–43 (5 or 6 specimens), WC–9. Possibly also Cr–77.

Subgenus NEOSTRINGOPHYLLUM Wedekind 1922

Type species. By monotypy, *N. ultimum* Wedekind 1922, p. 16, figs. 17, 18. Type locality: Düsseltal, Bergisches Land; upper Givetian.

Diagnosis. Subgenus of *Acanthophyllum* with inversely conical calice. Epitheca thick; septa predominantly strongly dilated, composed of trabeculae directed upwards and inwards, approximately parallel. Lonsdaleoid dissepiments absent or poorly developed. Tabulae mostly incomplete, vesicular.

Remarks. None of the named Australian species can be certainly placed herein. However, several specimens, from a number of basins, previously referred to *Acanthophyllum aequiseptatum* Hill 1940, are actually representatives of *A.* (*N.*) *implicatum* sp. nov. If this subgeneric assignment is accurate—and there are no marked morphological differences from the German species as figured by Wedekind (1922), Walther (1928), and Birenheide (1961)—then this is a very early appearance of the subgenus, for in Germany and in England (Webby 1964, p. 12) it is characteristic of the Givetian. The Australian occurrences are all Lower or basal Middle Devonian. Homomorphy is possible, but for the present I consider it best to use the one subgeneric name, as in both cases the species are probably derived from *A.* (*Acanthophyllum*), and so are closely related.

Acanthophyllum (*Neostringophyllum*) *implicatum* sp. nov.

Plate 86, figs. 2–8; text-figs. 5, 6

1940*b* *Acanthophyllum* sp. Hill, p. 253, pl. 9, fig. 6. Wee Jasper, N.S.W.; Emsian or Eifelian.

1940*c* *Acanthophyllum* spp. Hill, p. 152, pl. 2, fig. 2; ?p. 153, pl. 2, figs. 3*a*–*c*. Silverwood, S. Qld.; 'lower Couvinian' (Emsian?).

1940 *Acanthophyllum* sp. Hill and Jones, p. 179, pl. 2, figs. 1, 2. Molong District, N.S.W.; Emsian?

1942*b* *Acanthophyllum* sp. Hill, p. 14, pl. 1, figs. 2*a*, *b*. Mt. Etna, Qld.; Emsian?

?1942*b* *Acanthophyllum* sp. or *Lyrielasma* sp. Hill, p. 14, unfigured. Mt. Etna, Qld.

?1942*d* *Acanthophyllum* cf. *mansfieldense* (Dun); Hill, pp. 182, 183, pl. 5, fig. 1. Wellington, N.S.W.; Emsian?

1942*d* *Acanthophyllum aequiseptatum* Hill; Hill, p. 183, pl. 6, figs. 1*a*, *b* (*non* Hill 1940*b*, p. 251). Wellington, N.S.W.

1950 *Acanthophyllum* sp. Hill, p. 139, pl. 5, fig. 2. Buchan, Vic.; Emsian? (or early Eifelian?).

1962 *Acanthophyllum aequiseptatum* Hill; Philip, p. 184, pl. 26, figs. 2, 3. Tyers R., Vic.; Gedinnian (or Siegenian?).

Derivation of name. Latin *implicatus* = entangled, confused; referring to the septal meshwork at the base of the calice.

Holotype. SU 17219 (Pl. 86, figs. 2*a*, *b*). Type locality: P–40.

Diagnosis. Small *A.* (*Neostringophyllum*) with deep, inversely conical calice whose base is filled with an extensive meshwork of septal ends and flanges; septa moderately to extremely dilated, flaring to wedge-shaped peripherally, tapering inwards, without secondary lamellar deposits; tabularium rather wide, consisting of moderately to deeply concave incomplete tabulae, generally with a small axial deepening.

Description. Solitary; corallites may form loose colonies of adherent individuals, frequently invested by a stromatoporoid. Corallites attach themselves by lateral expansions of the dissepimentarium (Pl. 86, figs. 2, 8). They are ceratoid to cylindrical, with irregular although not pronounced growth swellings and contractions; occasional rejuvenescence rims occur. The calice is deeply inversely conical, with a sharp rim, steep sides, and a concave base. The septa extend as low ridges down the sides, but at the base form a deep meshwork of lamellae and flanges, whose upper surface is gently concave, and up to 10 mm. above the topmost tabula (Pl. 86, figs. 4, 7). For normal adults, Dc = 10–20 mm.; the maximum known is 22·5 mm.

Dimensions. In mm.

No.	*loc.*	*Dc*	*Dt*	*Dt/Dc*	*n*
SU 17219	P–43	2·5	1·4	0·56	30
,,	,,	9·6	*ca.* 0·5	*ca.* 0·52	48
,,	,,	12·4	6·0	0·48	56
,,	,,	*ca.* 13·5	6·0	*ca.* 0·44	56
,,	,,	14·0	*ca.* 0·6	*ca.* 0·43	50

Measured from random sections of corallites in type specimen.

There are up to 66 septa, the usual number lying between 48 and 62. Generally they are equally dilated and straight in the dissepimentarium, to which the minor septa are confined; within the tabularium the major septa may be straight, but are more usually curved. They are frequently arranged in four ill-defined groups, apparently symmetrical about the counter-cardinal plane. This plane is frequently marked by elongation of the cardinal septum, which is often then flanked by elongate minor septa. Septal dilatation is quite variable in extent, at times even within the one corallite. It is generally moderate to strong, tapering inwards; the septal bases are generally flared or wedge-shaped, forming a stereozone which is usually about 0·5–1 mm. across, but may rarely be up to 3 mm. wide. In a few cases the septal bases do not contact at all, when there is between them a fibrous stereozone about 0·3 mm. thick. In some sections the septal dilatation is slightly fusiform or lanceolate. As the septal dilatation decreases inwards, so there is a steady increase in the degree of lateral flanging; these flanges are trabecular outgrowths, parallel to the calical surface, and perpendicular to the direction of the trabeculae. They are steeply axially inclined in the dissepimentarium, the inclination decreasing in the tabularium, such that they are best seen in slightly oblique longitudinal sections. The combination of rotated or convoluted septal ends and flanges frequently presents a highly complex picture in transverse sections of the tabularium.

The septa are composed of thin trabeculae directed upwards and inwards at about 30° to the horizontal in the dissepimentarium. This inclination changes rapidly as the septa enter the tabularium, so that they are nearly vertical. Variation in the length of the component fibres produces fine lateral denticulae on the septal sides in many specimens.

The tabularium in adults is about 0·4–0·5 Dc. It consists of slightly convex incomplete tabulae, generally increasing a little in size axially; these are arranged in gently to deeply concave tabular floors, with upturned margins, and generally with a narrow median depression of variable depth.

The dissepimentarium consists of up to 9 series of small, globose to rather elongate, highly inclined dissepiments. The inclination may be uniform, or may increase gradually towards the axis; there is, however, never the marked change in inclination from moderate to almost vertical near the tabularium which characterizes species of *A.* (*Acanthophyllum*). Only in relatively few cases is the increase in inclination sufficient for the dissepiments at the inner margin of the dissepimentarium to be vertical. Lonsdaleoid dissepiments are not developed.

Variation. This species shows considerable variation, particularly in the degree and manner of septal dilatation—features which unfortunately do not lend themselves to statistical analysis. In some specimens the septa are uniformly thin, and change little in thickness inwards, beyond the characteristic peripheral wedge-like or flaring dilatation. At the other extreme are those corallites in which the septa are in contact peripherally for up to 3 mm., then taper inwards, but remain thick even in the tabularium. As well, dilatation varies from the usual inwards taper to moderately lanceolate (maximum dilatation in outer third of septum, decreasing to either side) or fusiform (maximum dilatation at mid-length), again always with a peripheral expansion.

Further variation occurs in the degree of inclination of the dissepiments. This varies from about 30° to about 45° from the vertical. The concavity of the tabular floors also varies within wide limits.

Measurements of Dc, Dt, and n were made for 77 individuals. As this was done from thin sections, the majority of which were consciously made of adult corallites, simple frequency plots are of slight value. Graphs were plotted for Dt:Dc (text-fig. 5*a*) and for n:Dc (text-fig. 6). The former is the most significant: there is relatively little scatter, and straight-line axes show a definite change in slope at Dc = 10 mm. This is taken to represent the boundary between juvenile and adult corallites. For the juveniles, $Dt = 0{\cdot}5Dc$; for adults, $Dt = 0{\cdot}33Dc + 1{\cdot}67$ approximately. There is greater scatter in the plot of n : Dc, but here also there seems to be a distinct break in slope at Dc = *circa* 10 mm.

A plot of Dt/Dc:Dc shows a fair degree of scatter (text-fig. 5*b*). Dt/Dc changes gradually from about 0·5–0·6 for juveniles to about 0·4–0·5 for most adults; very large corallites may have a tabularium as narrow as 0·33 Dc.

EXPLANATION OF PLATE 85

All figures ×2.

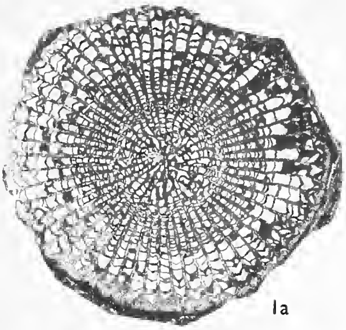
Fig. 1. *A.* (*Acanthophyllum*) *aequiseptatum* Hill 1940. 1*a*, *b*, transverse and longitudinal sections, holotype AM F 9577, Bluff Limestone, Clear Hill, Taemas, N.S.W. Photographs by courtesy of the Australian Museum, Sydney.

Fig. 2. *A.* (*A.*) *asper* Hill 1940. 2*a*, *b* transverse and longitudinal sections, holotype UQ F 4270, Wee Jasper, near Taemas, N.S.W. Photographs supplied by Mr. J. Jell, University of Queensland.

Figs. 3, 4. *A.* (*A.*) sp. cf. *clermontense* (Etheridge fil. 1911), group *a* (see pp. 552–3). 3*a*, *b*, transverse and longitudinal sections, SU 13227, loc. Cr–100. 4*a*, longitudinal section of a small colony, 4*b*, transverse section of the corallite on the right in 4*a*; SU 13230, loc. Cr–100.

Fig. 5. *A.* (*A.*) *aeneae* sp. nov. 5*a*, *b*, transverse and longitudinal sections, holotype SU 11291, loc. Be–10.

Fig. 6. *A.* (*A.*) sp. cf. *clermontense*, group *b* (see pp. 552–3). 6*a*, *b*, transverse and longitudinal sections, SU 17237, loc. P–43.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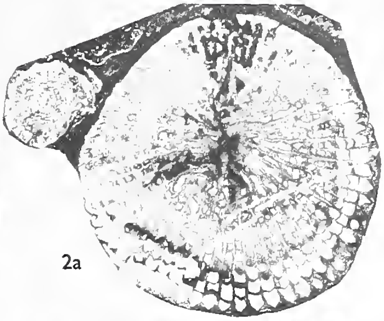
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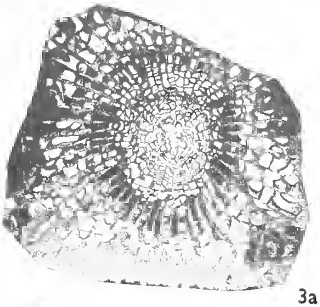
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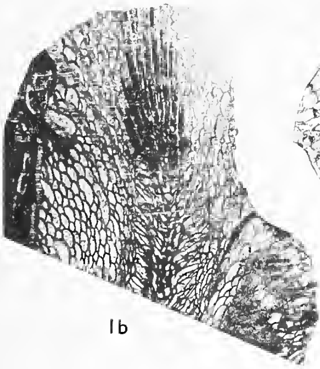
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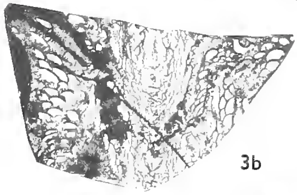
2b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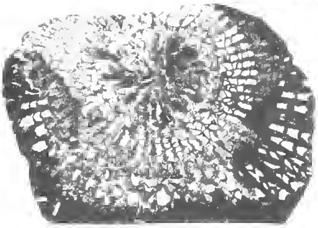
4a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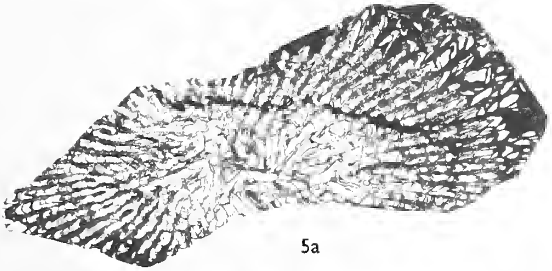
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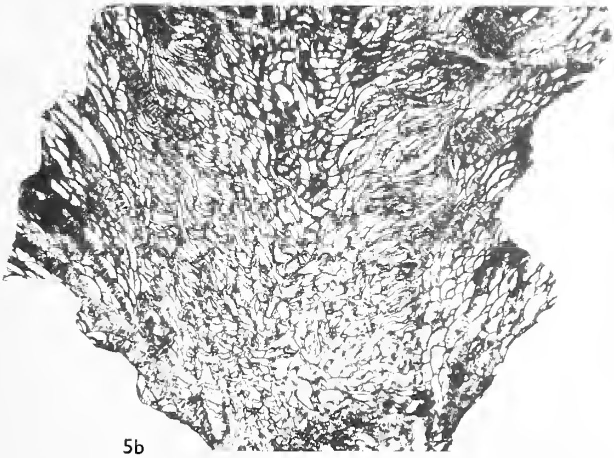
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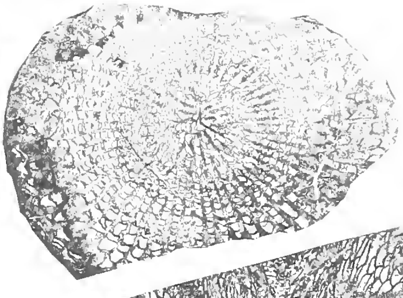
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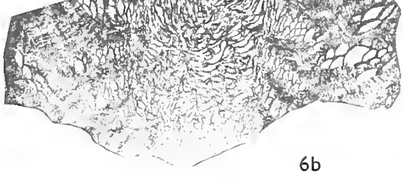
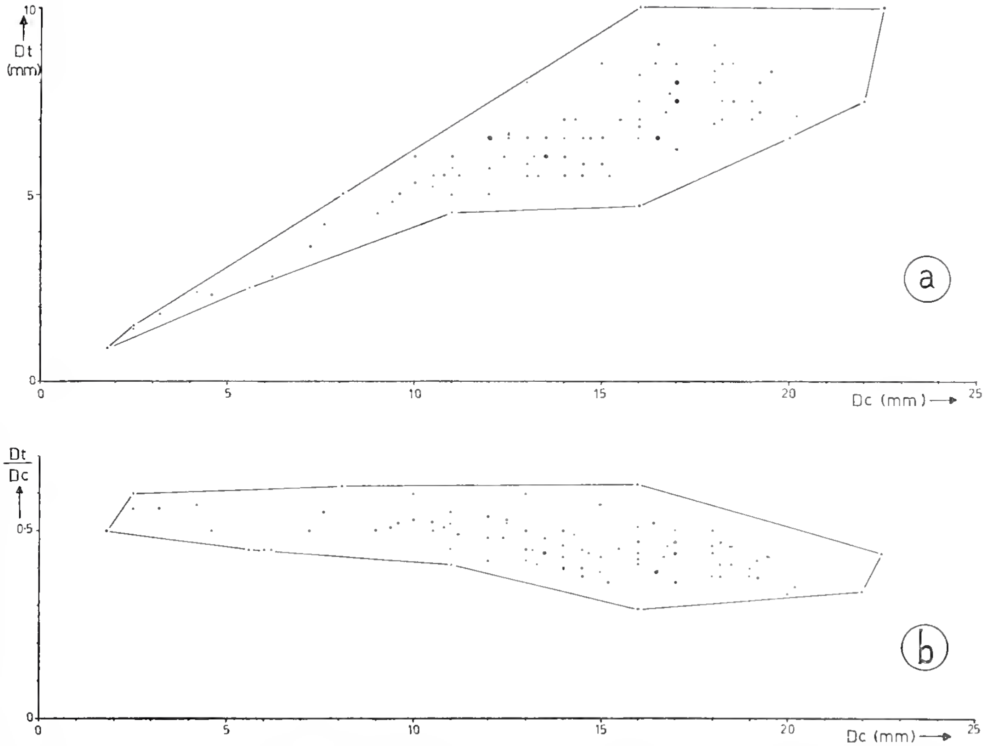
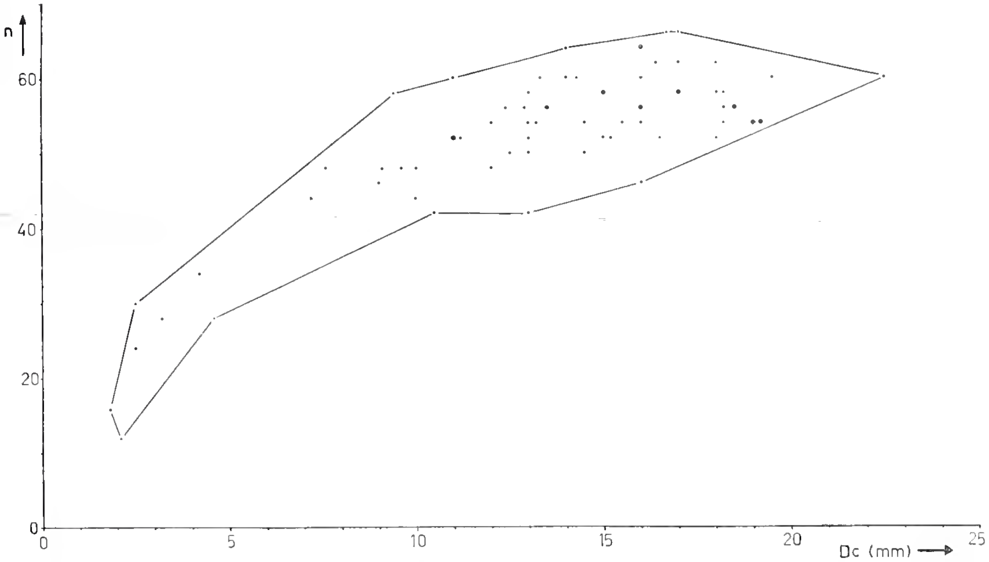

6b

STRUSZ, Devonian Spongophyllidae from New South Wales



TEXT-FIG. 5. *A.* (*Neostringophyllum*) *implicatum* sp. nov. Scatter diagrams and limiting polygons showing variation of (*a*) Dt:Dc, and (*b*) Dt/Dc:Dc.



TEXT-FIG. 6. *A.* (*Neostringophyllum*) *implicatum* sp. nov. Scatter diagram and limiting polygon for n:Dc.

Remarks. The strongest objection to placing this species in *A.* (*Neostringophyllum*) is that in the Eifelian succession the earliest known species, *A.* (*N.*) *concavum* (Walther 1928), appears at the Eifelian–Givetian boundary (see Birenheide 1961, p. 128). However, there appears to be no significant morphological difference between the German and Australian species; I feel it is unwise at this juncture to erect an endemic Australian genus solely on the basis of apparent age.

Range. This species is now known from a number of localities in eastern Australia. It is likely that most of these are Coblenzian in age. Hill (1940*b*) suggested an age about the boundary of the Lower and Middle Devonian for the Bluff Limestone fauna of the Taemas region. Philip and Pedder (1964) have forcefully suggested a Siegenian or perhaps early Emsian age for this succession. Similarly, they consider the Buchan sequence to be mainly Siegenian, as against Hill's (1950) late Emsian or early Couvinian. The two limestones have very similar faunas, including *A.* (*A.*) *aequiseptatum* and *A.* (*N.*) *implicatum*.

The Silverwood fauna, Hill (1940*c*) compared most closely within Australia with that of the Nemingha Limestone of Tamworth: the latter she (1942*c*) considered to be probably late Lower Devonian, while the former she placed in the lower Couvinian. I consider them both to be Coblenzian; *A.* (*N*) *implicatum* occurs at Silverwood, but is not yet known from Tamworth. It is also known from the Mt. Etna Limestone of Queensland, which is quite close to the Garra faunally, and which Hill (1942*b*) considered to be (at least in part) Coblenzian in age.

The oldest fauna containing *A.* (*N.*) *implicatum* is apparently the Tyers R. fauna of Victoria, which Philip (1960, 1962) considers to be Gedinnian or possibly early Siegenian.

A. (*N.*) *implicatum* would therefore seem to be characteristic of the Lower Devonian faunas of eastern Australia.

Known Garra localities. A. (*N.*) *implicatum* is widespread in the Garra Formation, second perhaps only to the digonophyllids. It has been collected from the following localities: Br–3, Br–10, Ca–1, Cr–1, Cr–2, Cr–5, Cr–86, Cr–89, Cr–94, Cr–100 (very common), Cr–103, Cr–106?, Cr–111, Ct–16?, Ct–55?, E–5, E–37?, Ge–3 (very common), Ge–7b (common), Ge–12?, Gn–7?, MM–1, MM–5b, MM–6, MM–7, MM–11, P–22 (rather common), P–23, P–25, P–26, P–38 (rather common), P–40 (type locality), P–43 (abundant), WC–4, WC–5; BR^1/177, BR^1/965?

EXPLANATION OF PLATE 86

Fig. 1. *A.* (*Acanthophyllum*) sp. cf. *clermontense* (Etheridge 1911), group *b* (see pp. 552–3). Longitudinal section through calice, SU 17258, loc. P–43; ×2.

Figs. 2–8. *A.* (*Neostringophyllum*) *implicatum* sp. nov.

2*a*, *b*, transverse to longitudinal sections of a group of corallites invested by a stromatoporoid; holotype SU 17219, loc. P–40; ×2. 3, oblique transverse section, SU 15296, loc. E–5; ×2. 4*a*, transverse section, 4*b*, longitudinal section showing septal mesh in calice; SU 7297, loc. Ge–3; ×2. Figured Hill 1942*d*. 5*a*, *b*, transverse and longitudinal sections, SU 18222, loc. P–43; ×2.

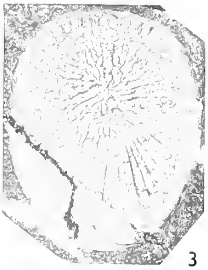
6*a*, *b*, transverse and longitudinal sections of a specimen with septa thickened in the tabularium, and with nearly flat tabular floors; SU 12177, loc. Ca–1; ×2.

7*a*, transverse section low in calice, showing septal mesh, 7*b*, longitudinal section; UCT F 1983, loc. P–43; ×2.

8, longitudinal section of a juvenile corallite adherent to the surface of a stromatoporoid colony; SU 13222, loc. Cr–100; ×4.


1


2a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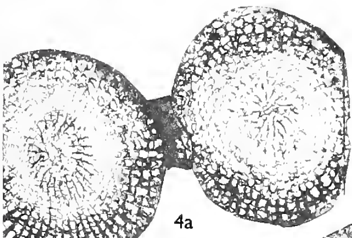
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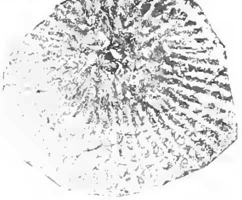
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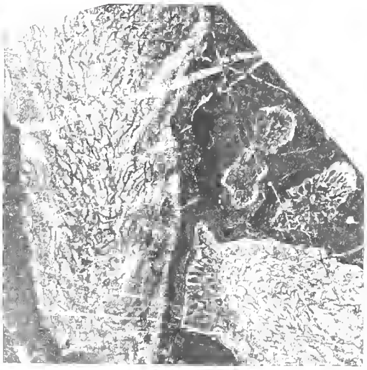
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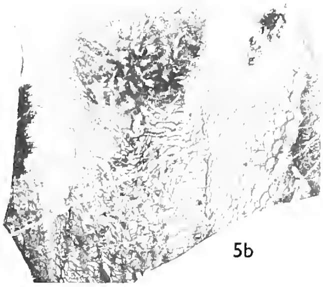
4b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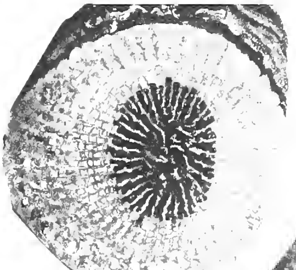
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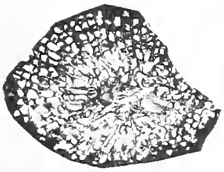

6a


8


6b


7b

STRUSZ, Devonian Spongophyllidae from New South Wales

Acanthophyllum (*Neostringophyllum*) *turni* sp. nov.

Plate 87, figs. 1, 2; text-fig. 7

Derivation of name. Turnus, commander of the Latins resisting Aeneas' settlement in Italy.
Holotype. SU 14247 (pl. 87, figs. 1*a*, *b*). Type locality: Ct–44.

Diagnosis. Small *A.* (*Neostringophyllum*) of irregular growth shape, with frequent sharp rejuvenescence rims; septa dilated to contact at periphery, and intermittently as inverse cones of septal tissue and sclerenchyme; the degree of dilatation increases distally. Tabularium fairly narrow, of concave incomplete tabulae, often axially deepened. Dissepiments steeply inclined, elongate.

Description. The solitary corallite is generally curved, ceratoid to trochoid, with marked growth irregularities; it is commonly oval to irregular in cross-section. Rejuvenescence is generally frequent and strong, forming sharp rims which are often close, so that the contracted intervening spaces are deep but almost slit-like (see text-fig. 7). The calice is deep, inversely conical, with a sharp rim and a narrow concave apex; the septa form only low ridges on its sides and floor. The epitheca, apart from transverse growth irregularities, is marked by narrow septal grooves.

Adult corallites are about 15–20 mm. in diameter.

Dimensions. In mm. of representative corallites.

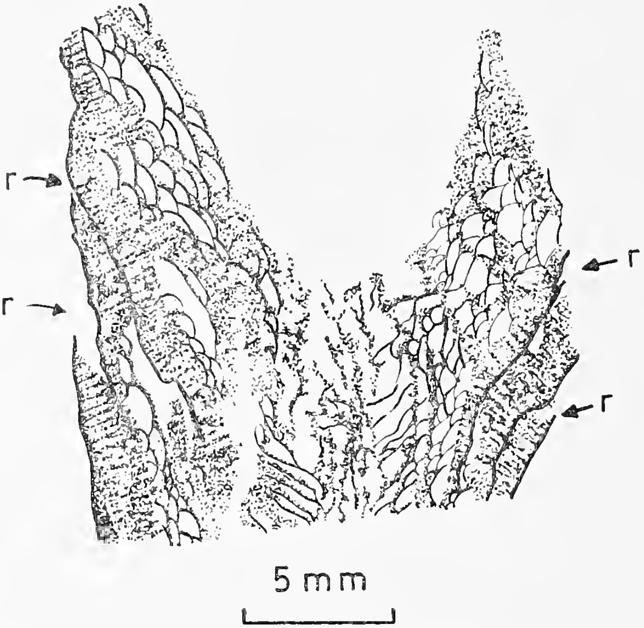
No.	*Dc*	*Dt*	*Dt/Dc*	*n*
SU 14247*	8·6	4·8	0·56	38
,,	est. 15	7·0	0·47	50
SU 14248	16·4	5·9	0·36	66
SU 14250	15·5	6·5	0·42	52

*Holotype; all specimens from loc. Ct–44. Mean values of Dc are given for oval corallites.

In adult corallites there are usually 50–64 septa. These extend inwards from the epitheca (0·03 mm. thick), unbroken by lonsdaleoid dissepiments; the major septa generally almost reach the axis, where they are usually directed to a prominent counter-cardinal plane. There may be slight to moderate rotation of the septal ends. The counter and cardinal septa are elongate, but do not meet. The shortest major septa flank these, and the septal length gradually increases away from these, being again greatest transverse to the counter-cardinal plane. The minor septa tend to be irregular in length, although on the whole they extend inwards for about R/2. Those flanking the counter (or cardinal?) septum may be somewhat lengthened. The septa are dilated to contact in a peripheral stereozone about 1–1·5 mm. wide, whose inner surface is reinforced by lamellar sclerenchyme. In this narrow region of reinforcement the septa themselves attenuate rapidly inwards, so that inside the stereozone they are thin or only weakly dilated, in the latter case being irregular to fusiform. In most corallites inversely conical sheets of sclerenchyme extend inwards from the stereozone, coating septa and dissepiments. These appear to correspond in position to prominent and very close rejuvenescence rims, seemingly representing tissue deposited on the surface of the calice immediately before constriction, and to the peripheral stereozone lining the epitheca of the immediately subsequent expansion (see text-fig. 7).

The septa are generally somewhat wavy and bear moderately developed flanges, which increase in frequency in the tabularium. Axial processes are weakly developed or absent, as are lateral denticulae.

The septal microstructure is that typical for the subgenus: approximately parallel fine monacanthine trabeculae directed upwards and inwards at 20–30° from the horizontal within the dissepimentarium, the inclination becoming much steeper in the tabularium.



TEXT-FIG. 7. *A.* (*Neostringophyllum*) *turni* sp. nov. Longitudinal section of holotype SU 14247, ×4, showing sharp rejuvenescence (r) above deep, slit-like re-entrants, and the associated inverse cones of septal dilatation. Drawn from photograph.

EXPLANATION OF PLATE 87

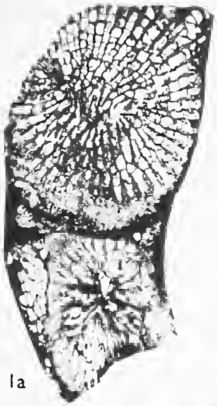
All figures ×2.

FIGS. 1, 2. *A.* (*Neostringophyllum*) *turni* sp. nov. 1*a*, transverse and oblique sections, 1*b*, longitudinal section showing rejuvenescence (cf. text-fig. 7); holotype SU 14247, loc. Ct–44. 2*a*, *b*, transverse and longitudinal sections, SU 14248, loc. Ct–44.

Figs. 3, 4. *A.* (*Grypophyllum*) *jenkinsi* sp. nov. 3*a*, transverse section at base of calice, 3*b*, transverse celluloid peel near proximal end, 3*c*, longitudinal section showing unflanged septa; holotype SU 16247, loc. Ge–2. 4*a*, transverse section showing septal thickening in tabularium, 4*b*, longitudinal section; UCT F 1947, loc. Ge–2.

Fig. 5. *Lyrielasma* sp. cf. *subcaespitosum* (Chapman 1925). Transverse section, SU 19238, loc. St/2565.

FIGS. 6–8. *Pseudochonophyllum pseudohelianthoides* (Sherzer 1892). 6*a*, *b*, off-centre longitudinal, and transverse sections, holotype, Rominger Collection, Museum of Paleontology, University of Michigan; Koněprusy, Bohemia. Photographs supplied by Prof. E. C. Stumm. 7, transverse section showing well-developed naotic plates (lower right), SU 13241, loc. Cr–100. 8*a*, *b*, longitudinal and transverse sections, UQ F 3412, Silverwood, Qld.; *Acanthophyllum* sp. cf. *mansfieldense* of Hill 1940*c*, pl. II, figs. 1*a*, *b*. Photographs by courtesy of Prof. D. Hill.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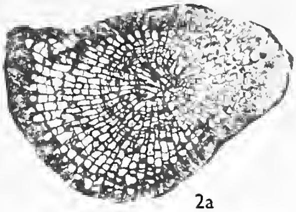
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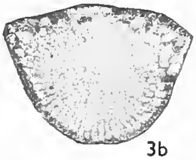
3a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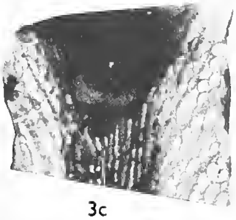
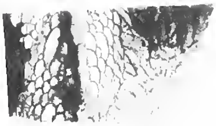
2b


3c


1b


5


4a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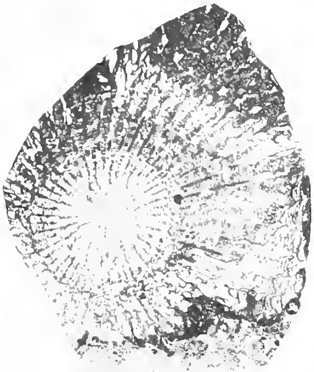
6a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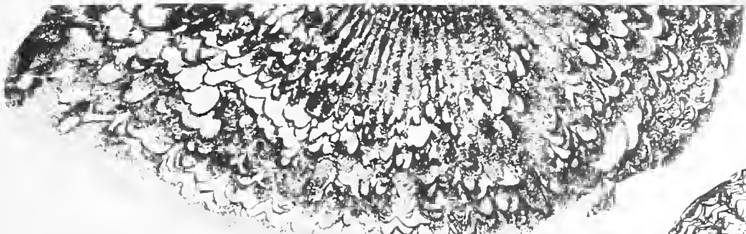
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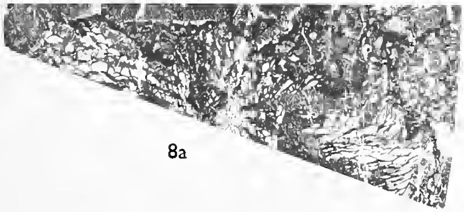
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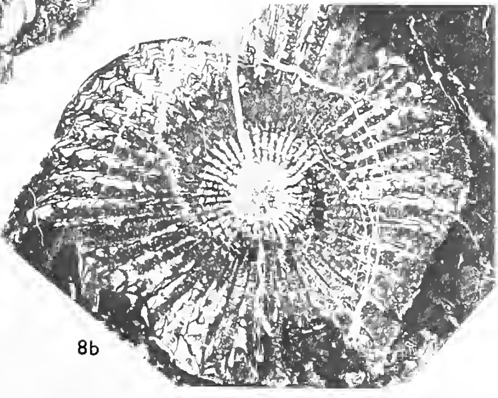

8b

STRUSZ, Devonian Spongophyllidae from New South Wales

The tabularium decreases from about ½Dc in juveniles to about 0·4Dc in adults. The tabular floors are moderately to strongly concave, with upturned margins and an axial deepening which is apparently a little eccentric. The tabulae are incomplete, elongate, and only slightly domed. They are thin, or lightly to moderately coated with sclerenchyme in the conical zones of dilatation.

The dissepimentarium consists of up to ten series of small, fairly globose to elongate, highly inclined dissepiments. These are generally uniform in size and inclination, but may become vertical at the margin of the tabularium; this is generally not vertically persistent in a single corallite.

Variation. Data are too few for rigorous treatment; plots (not figured) were made for Dt : Dc, Dt/Dc : Dc, and n : Dc. The first two appeared to be straight-line plots, the first suggesting Dt = 0·4Dc+0·4. The plot for n : Dc was apparently curved, the rate of insertion of septa decreasing steadily with age of the corallite.

Comparison. On the basis of available material, this species is inseparable in size, number of septa, and relative width of tabularium from *A.* (*N.*) *implicatum* sp. nov., and from *A.* (*Grypophyllum*) *jenkinsi* sp. nov. (described below). Examination of the data plots suggests that further material may show that Dt/Dc is slightly less than for *A.* (*N.*) *implicatum*, from which it is distinguished by its prominent rejuvenescence, its septal dilatation, and its lack of an intricate septal meshwork axially. *A.* (*G.*) *jenkinsi* lacks the wide stereozone and sharp rejuvenescence; moreover, it may have some lonsdaleoid dissepiments distally. Both of these species lack the periodic conical dilatation characteristic of *A.* (*N.*) *turni*. In this feature it differs also from all of the European species.

Remarks. This species is placed in *A.* (*Neostringophyllum*) because of its peripherally strongly thickened septa and its complete lack of lonsdaleoid dissepiments.

Known localities. Ct–44, Ct–45.

Subgenus GRYPOPHYLLUM Wedekind 1922

Type species. G. denckmanni Wedekind 1922, p. 13, figs. 13, 14. Type locality: Bergisch–Gladbach, Bergisches Land; Büchel Beds, Givetian.

Diagnosis. Subgenus of *Acanthophyllum* with inversely conical calice, usually with fairly rounded margin. Septa predominantly thin, composed of fine trabeculae directed upwards and inwards, roughly parallel. Lonsdaleoid dissepiments, particularly interrupting minor septa only, common; dissepiments inclined uniformly inwards. Tabulae incomplete, vesicular.

Remarks. Hill (1940*b*, p. 267) interpreted *Grypophyllum* as fasciculate, and has described several species from Australia on this basis. Of these, '*G.*' *aggregatum* Hill 1940 and '*G.*' *lophophylloides* Hill 1942*a* I tentatively place in *Lyrielasma* Hill 1939. The other species from north Queensland assigned by Hill (1942*a*) to *Grypophyllum* have tabulae which suggest that they may not even be spongophyllids.

Pedder (1964, p. 439) followed Hill in interpreting the genus as fasciculate, and described a Canadian species which seems to be allied to '*G.*' *aggregatum* Hill 1940, both of which differ from typical *Lyrielasma* in their rather thin peripheral stereozone. For the present, however, I would leave them in that genus.

Acanthophyllum (*Grypophyllum*) *jenkinsi* sp. nov.

Plate 87, figs. 3, 4

Derivation of name. For Dr. T. B. H. Jenkins, of the University of Sydney.

Holotype. SU 16247 (pl. 87, figs. 3 *a–c*). Type locality: Ge–2.

Diagnosis. A. (*Grypophyllum*) up to 25 mm. across, with thin epitheca; minor septa well developed; cardinal and counter septa elongate; septal processes absent; lonsdaleoid dissepiments occur only in adult stage.

Description. Solitary, cylindrical or ceratoid, with some growth irregularities. The epitheca has distinct interseptal ridges and faint growth lines. The calice is inversely conical, rather deep, with a concave base. Septa form low ridges down its sides, and somewhat higher ridges across its base. The greatest known Dc = 23 mm.; it is usually about 15–20 mm.

Dimensions. In mm.

No.	*Loc.*	*Dc*	*Dt*	*Dt/Dc*	*n*
SU 16247*	Ge–2	8·5	4·0	0·47	48
,,	,,	10·9	4·3	0·40	50
,,	,,	16·0	5·0	0·31	56
,,	,,	16·5	5·2	0·32	56
UCT F 1947	,,	13·9	8·0	0·58	52

*Holotype: serial sections over a length of 40 mm.

In adults, n = 50–60. The septa are long, fusiform, and only slightly dilated. Their peripheral ends, however, expand rapidly as broad, blunt wedges, to form a dentate stereozone. The septal bases are slightly concave externally (in transverse section), so giving rise to the interseptal ridges of the epitheca. The septa are smooth, or bear fine lateral denticulae; they are gently waved on a small scale, appearing straight at first glance. Weak, discontinuous flanges occur near and in the tabularium. There are no axial processes. In juveniles the septa are complete, but in adults some peripheral discontinuities generally develop. The minor septa end just inside the tabularium. The major septa extend unequally to a fairly short median plane, which is marked by elongate counter and cardinal septa. The counter (?) septum is flanked by elongate minor septa.

The septa consist of fine almost parallel trabeculae directed upwards and inwards at about 20° from the horizontal. Their arrangement within the tabularium is unknown.

The tabularium is rather narrow—about 0·3Dc in adults, somewhat greater in juveniles. The tabular floors are concave and often moderately deepened axially. The tabulae are incomplete, elongate, and weakly convex.

The dissepimentarium consists of up to 9 series of globose to rather elongate dissepiments, steeply axially inclined. They are fairly uniform in size and increase in inclination only slightly towards the tabularium. Lonsdaleoid dissepiments, only rarely interrupting the major as well as the minor septa, are poorly developed in adult stages.

Comparison. A. (*G.*) *jenkinsi* sp. nov. does not closely resemble any previously described Australian species. *A.* (*N.*) *implicatum* sp. nov. is at first glance rather similar, and their data plots coincide, but it may be distinguished by the different septal dilatation (tapering axially, and rather greater), and the complete lack of lonsdaleoid dissepiments; also it has a generally thicker epitheca and stereozone, and a wider tabularium. Finally, the septal mesh at the base of its calice is highly distinctive of *A.* (*N.*) *implicatum*.

A. (*G.*) *jenkinsi* is rather close to *A.* (*G.*) *denckmanni* (Wedekind 1922) sensu Engel and Schouppé (1958) in size, number of septa, septal dilatation and arrangement, and structure and relative width of tabularium. However, the German species has more frequent lonsdaleoid dissepiments, so that in transverse section the minor septa are usually highly discontinuous; also it has a rather thicker and less dentate peripheral septal stereozone. In all other described European species the minor septa are much shorter and the tabularium wider.

Known localities. Ge–2 (type); Be–7, Cr–36b, ?Ct–36.

Genus PSEUDOCHONOPHYLLUM Soshkina 1937

1937 *Pseudochonophyllum* Soshkina, pp. 59–60, 96 (*partim*?); remaining synonymy as for species.

Type species. Chonophyllum pseudohelianthoides Sherzer 1892, p. 275, pl. 8, fig. 6; designated Soshkina 1937, p. 59. Type locality: Koněprusy, Bohemia; Lower Devonian.

Diagnosis. Trochoid to cylindrical rugosan with an everted calice. Septa trabecular, the trabeculae arranged in half-fans in the wide dissepimentarium. Septa strongly dilated in dissepimentarium, generally to contact, and peripherally partly replaced by more or less well-developed naotic plates. Septa flanged in narrow tabularium. Tabularium of incomplete tabulae arranged in concave floors, frequently depressed axially.

Discussion. Počta (in Barrande 1902, pp. 123–4), describing topotypic material, considered Sherzer's species to have characteristics sufficiently removed from those of *Chonophyllum* Edwards and Haime 1850 for it to be a distinct genus, but went no further. Soshkina (1937) erected the new genus *Pseudochonophyllum* with Sherzer's species as type; in the English summary (p. 96) she referred to Sherzer's original description as being a sufficient diagnosis. In the Russian text (pp. 59–60) she gives the following (my translation):

> Coral solitary, now and then giving off buds. External form subcylindrical, frequently turbinate or mushroom-shaped. Calice small, goblet-shaped, with very wide top and weak basal boss. Septal apparatus constructed of stout lamellar septa of 2 orders. These are peripherally strongly thickened with stereoplasm, and towards the axis become very thin and sometimes curved; subsequently some of them again are a little thickened at the immediate centre. Each vertical lamellar septum consists of curved roof-like platelets, superimposed one on another. Interseptal apparatus in the peripheral zone consists of numerous lamellae in the form of small vesicles. In the central zone are developed numerous very thin, strongly vesicular incomplete and confused tabulae.
>
> Distinguished from the genus *Chonophyllum* by its pleomorphic structure and the development of 2 orders of septa. At the same time, they are similar in: 1) external form, 2) form of calice, 3) roof-shaped axial boss of complicated incomplete tabulae.

Since this paper, Soshkina has several times referred Russian species to the type species which in fact differ markedly from it, and are closer to *Acanthophyllum*. This has been recently recognized by Bulvanker (1958, p. 95), who considers Soshkina's species to be *Acanthophyllum*, but apparently without explicitly committing herself on the Bohemian type species. She does, however, place *Pseudochonophyllum* in the synonymy of *Acanthophyllum*. She also points out the further confusion arising from Soshkina (1952, p. 98) naming as type species *P. pseudohelianthoides* Soshkina *non* Sherzer. Spasskiy (1960, p. 43) places Soshkina's species in synonymy with *Acanthophyllum heterophyllum* (Edwards and Haime 1851), but Birenheide (1963, pp. 407, 409) considers it to be a species of *Dohmophyllum* Wedekind 1923. I agree with this, and also with Birenheide's specific exclusion of Sherzer's species.

Professor E. C. Stumm has kindly sent me photographs of sections he has recently had made of the holotype of *P. pseudohelianthoides*. From this, and from the descriptions and figures given by Sherzer (1892) and Počta (in Barrande 1902) of material from the type locality, I consider *Pseudochonophyllum* to be closely related to *Acanthophyllum* and *Dohmophyllum*. It differs from the former essentially in having a reflexed calice, in having septa composed of more than one radial series of trabeculae, and in the naotic modification of the peripheral parts of the septa. *Dohmophyllum* has flat to domed tabular floors, and septa whose greatest dilatation is near the tabularium; however, the multitrabecular structure of the peripheral parts of the septa in *Dohmophyllum* (Birenheide, 1963, p. 372: text-fig. 3) is identical with the structure of the dilated portions of the septa in *Pseudochonophyllum*. The dissepimentarium and the arrangement of the septa in *Pseudochonophyllum* are typically acanthophylloid.

Of the Russian material, only that figured by Soshkina (1937, pl. 18, figs. 1–4) from the Coblenzian of the Urals probably belongs to the genus.

Pseudochonophyllum pseudohelianthoides (Sherzer 1892)

Plate 87, figs. 6–8, Plate 88, figs. 1–3

1892 *Chonophyllum pseudohelianthoides* Sherzer, p. 275, pl. 8, fig. 6. Koněprusy, Bohemia; Lower Devonian.
1902 *Chonophyllum pseudohelianthoides* Sherzer; Počta, p. 123, pls. 47, 48, 109 (figs. 3–6), 113 (figs. 21, 22), *in* Barrande. Same locality.
?1937 *Pseudochonophyllum pseudohelianthoides* Scherzer (*sic*); Soshkina, p. 60, pl. 18, figs. 1–4. Urals; Coblenzian.
1940*c* *Acanthophyllum* sp. cf. *mansfieldense* (Dun); Hill, p. 152, pl. 2, figs. 1*a*, *b*. Silverwood, Qld.; Couvinian?
non 1949 *Pseudochonophyllum pseudohelianthoides* (Scherzer); Soshkina, p. 119, pl. 27, figs. 1, 2, pl. 28, figs. 2–5, pl. 29, figs. 2–5. Urals; D_1^2–D_2^1.
non 1950 *Chonophyllum pseudohelianthoides* Sherzer; Termier and Termier, p. 99, pl. 39, figs. 23, 24. Morocco, N. Africa; Emsian.
non 1952 *Pseudochonophyllum pseudohelianthoides* Soshkina non Sherzer; Soshkina, p. 98, pl. 38. Urals and Armenia; Coblenzian and Eifelian. (The specimen figured is *Acanthophyllum*.)
non 1955 *Pseudochonophyllum pseudohelianthoides* Scherzer (*sic*); Krayevskaya, p. 218, pl. 42, figs. 4*a*, *b*, in Khalfin. W. Siberia; Coblenzian to Eifelian.
non? 1955 *Pseudochonophyllum pseudohelianthoides* Soshkina; Spasskiy, p. 314 (*fide* Bulvanker 1958, p. 95).
1962 *Pseudochonophyllum pseudohelianthoides* Sherzer; Soshkina, p. 309, in Orlov. Bohemian material only (unfigured).

Holotype. The specimen figured by Sherzer (1892, pl. 8, fig. 6) from the Lower Devonian (F2) Koněprusy Limestone of Bohemia, now in the Rominger Collection of the Museum of Palaeontology, University of Michigan. Sections have recently been made; they are figured herein (Pl. 87, figs. 6*a*, *b*).

Diagnosis. Solitary, up to 5 cm. in diameter, with strongly reflexed calice and numerous septa which may split into parallel strands peripherally; dissepiments small, gently domed, near-horizontal except in narrow zone around tabularium, where vertical.

Description. The corallite is turbinate or trochoid, becoming irregularly cylindrical, with narrow rejuvenescence rims, and growth swellings and contractions. Sherzer recorded a maximum Dc = 5 cm.; this is also known from the Wellington specimens, which generally have Dc = 3–3·5 cm. The calice is weakly to strongly everted, sometimes with a flared outer margin (the 'sattelrandiger Wulstkelch' of Birenheide 1963, p. 371, text-fig. 1). The axial pit is narrow and shallow and may have a low axial boss formed of a meshwork of septa. The septa form rounded ridges on the surface of the calice. The thin epitheca may be faintly marked by shallow interseptal grooves: unfortunately in most of the Wellington specimens it has been weathered away.

As noted also by Soshkina (1937, p. 59), and figured by Počta (pl. 47, fig. 21, in Barrande 1902), occasionally a single peripheral calical bud may occur. I have seen such small buds on 2 of the 25 or more specimens collected from the Wellington district.

Dimensions. Of representative corallites in mm.

No.	*loc.*	*Dc*	*Dt*	*Dt/Dc*	*n*
SU 13180	Cr–94	32*	4·5	0·14	62
13246	Cr–100	45*	4·5	0·10	50
13248	,,	34*	5·0	0·15	64
,,	,,	50*	6·0	0·12	68
13252	,,	47	5·5	0·12	70
14104	Cr–111	34	4·2	0·12	66

* estimated value.

In the Wellington specimens, n = 52–68; Sherzer recorded 72. The major septa extend equally towards the axis, leaving an axial space up to 2 or 3 mm., into which septal flanges and axial processes may extend; the minor septa end just inside the tabularium. In the tabularium the septa are thin, straight, radial, and bear strong flanges; there may be some slight axial dilatation. The flanges appear in longitudinal section to be arranged in a regular zigzag pattern, and extend inwards and downwards at a low angle. In the dissepimentarium the septa are equally dilated; this increases rapidly outward from the tabularium. Within 2 or 3 mm. the septa are generally wider than the loculi, and over most of the outer half of the dissepimentarium they are in contact. An unusual feature of a number of specimens in transverse section is the apparent fusion of 2 or 3 septa to become one, as they are traced inwards from the periphery (pl. 88, fig. 3). The dilatation appears to be periodically interrupted by intervals of growth during which the septa were comparatively thin; in these intervals the septa are horizontally corrugated. This is best seen on the surfaces of weathered corallites.

In the zone of extreme dilatation the septa are frequently modified. In some instances a few septa may split into two or three parallel or anastomosing strands for a greater or lesser distance, as may occur in *Dohmophyllum* (Birenheide 1963, pl. 59, fig. 56). More often, the septa are replaced by naotic plates, supported by isolated trabeculae. These plates are small, very gently domed, radially elongate, and parallel in inclination to the dissepiments. Unlike *Craterophyllum* Foerste, the plates generally do not extend from one side of the septum to the other in a regular manner; they overlap in a manner more like that of dissepiments, and may occasionally extend across two or three septa (see Sherzer 1892).

The septal trabeculae are up to 0·2 mm. thick; they diverge from a median plane in the septum, although that plane is not expressed morphologically; they are radially arranged in half-fans. A few millimetres outside the tabularium they are vertical; outside this, they are directed upwards and slightly outwards, until at the periphery they may again become vertical. Towards the tabularium they are directed axially upwards at an angle of about 30° from the vertical. The trabeculae in the tabularium are too fine to show whether a second fan develops there as in *Acanthophyllum* s.s.

The tabularium is narrow: Dt = *circa* 5 mm., and Dt = 0·12Dc approximately, being generally between 0·11 and 0·14Dc. The tabular floors are gently sagging, with slightly to strongly upturned margins; there may be a slight median depression. The tabulae are incomplete, thin, and flat to slightly convex.

The very wide dissepimentarium consists of small gently to strongly domed dissepiments. Over most of the dissepimentarium they are horizontal to slightly inclined outwardly, following the calical shape. In a narrow zone around the tabularium they are vertical and elongate. The dissepiments may be coated with thin fibrous extensions of the septal dilatation.

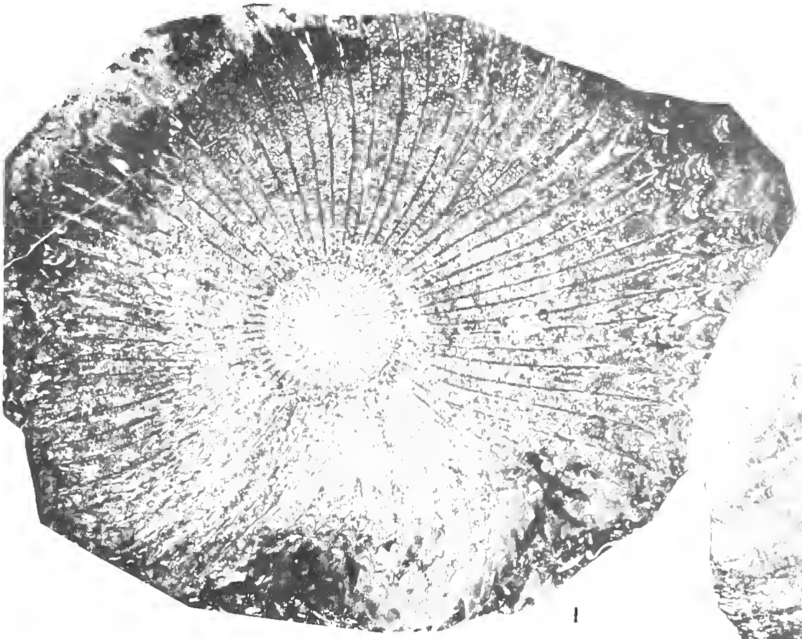
Remarks. From an examination of the photographs kindly supplied by Professor Stumm, and of the figures of Sherzer and Počta, there would seem to be very little difference between the Garra and Koněprusy material. The naotic plates in the Bohemian specimens apparently show a greater tendency to extend across two or three septa, and the dilatation of the septa does not show the periodic reduction to nearly the same extent. The only possible argument against specific identity is that, as the Russian material is excluded from the species, there is no record of it between Bohemia and Eastern Australia.

The Silverwood specimen described by Hill (1940*c*) as *Acanthophyllum* sp. cf. *mansfieldense* has all the features of the present species—extreme septal dilatation consisting of thick trabeculae, peripheral naotic modification, reflexed calice—and I consider it to be specifically identical with the present species. It is figured herein for comparison (pl. 87, fig. 8*a*, *b*).

Range. The Koneprusy Limestone is considered to be time-transgressive, extending through the whole of the Lower Devonian (see, e.g. Havlíček 1959). Hill (1940*c*) considered the Silverwood fauna to be probably Lower Couvinian, and equivalent to the Nemingha fauna of Tamworth. I consider both these, and the Garra Formation, to be more likely Emsian in age (see Strusz 1965); this would be supported by correlation with Koněprusy.

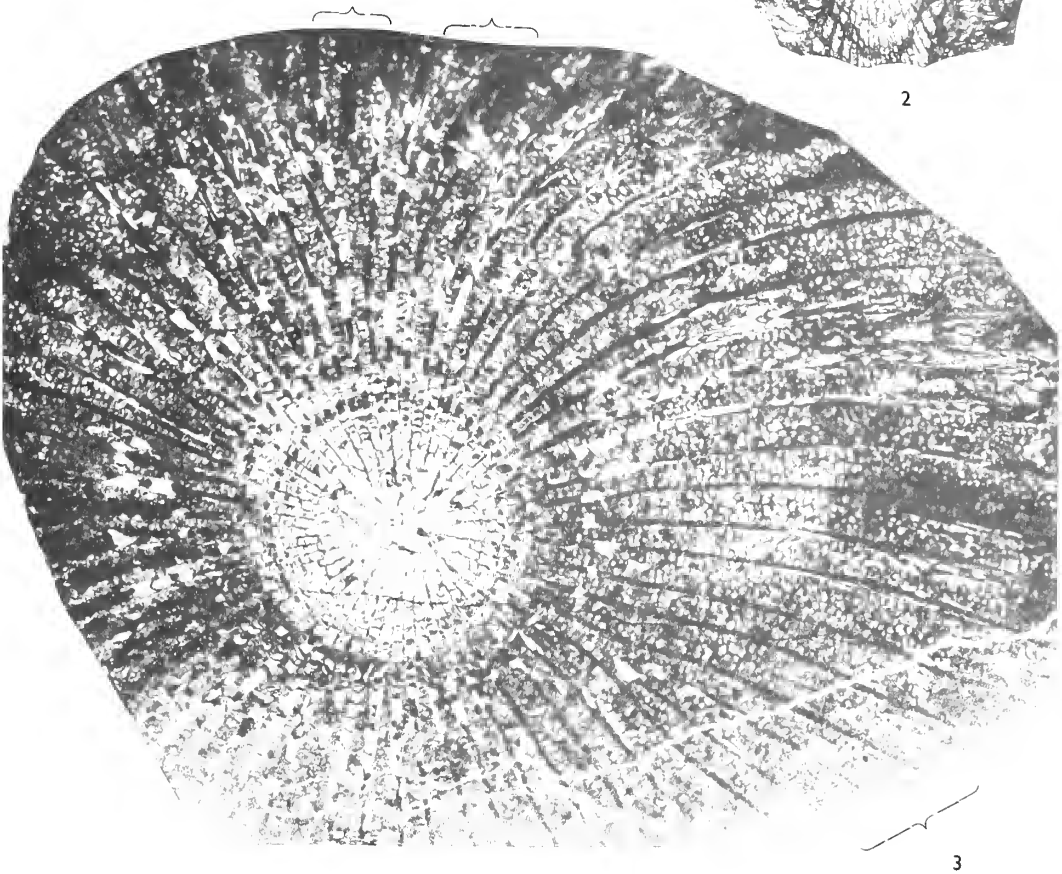
EXPLANATION OF PLATE 88

Figs. 1–3. *Pseudochonophyllum pseudohelianthoides* (Sherzer 1892). 1, transverse section showing septa at various degrees of dilatation; SU 13248, loc. Cr–100; ×2. 2, oblique longitudinal section showing acanthophylloid tabularium, and septal flanges; SU 13249, loc. Cr–100; ×2. 3, transverse section showing details of septal structure; 'fused' septa are bracketed peripherally (see p. 565); SU 13248, loc. Cr–100; ×4.



1

2



3

STRUSZ, Devonian Spongophyllidae from New South Wales

Known Garra localities. All specimens have been collected from three localities in a biostrome cropping out in the generally massive limestones on the west bank of the Bell River, opposite the Wellington Caves Reserve: Cr–94, Cr–100 (common), Cr–111.

Genus LYRIELASMA Hill 1939

1925 *Cyathophyllum* (*partim*) Chapman, p. 112.
1939*a* *Lyrielasma* Hill, p. 243.

Type species. *Cyathophyllum subcaespitosum* Chapman 1925, p. 112, pl. 13, figs. 15, 16*a*, *b*. Cave Hill Lilydale, Vic:; Siegenian?—Philip 1960, p. 151.

Diagnosis. As *Acanthophyllum*, but fasciculate to subcerioid; calice inversely conical; with wide peripheral stereozone.

Discussion. Corallites of *Lyrielasma* are narrow, cylindrical, with an inversely conical calice (the 'trichterkelch' of Wedekind—see Birenheide 1961). There is usually a relatively wide peripheral stereozone formed by the dilatation of the septal bases; this is widest in the type species, and narrowest in '*Grypophyllum*' *aggregatum* Hill 1940. In some cases this stereozone is partly broken up by lonsdaleoid dissepiments. The characters of the dissepimentarium and tabularium are much as in *Acanthophyllum* (*Grypophyllum*).

Grypophyllum aggregatum Hill 1940*b*, from the Eifelian? of the Murrumbidgee River, is a phaceloid species, and so is here removed from *Grypophyllum*, which Birenheide (1961, p. 114) has shown to be solitary, to *Lyrielasma* (see pp. 570–1).

Lyrielasma curvatum Hill 1942*a* (p. 238), from the Givetian Fanning River Limestone, differs from the type species in having flat to domed tabular floors. It is more akin to *Grypophyllum compactum* Hill 1942 (p. 255) and *G.* sp. Hill 1942 (p. 255), from the same formation, none of these species being either *Lyrielasma* or *Grypophyllum*.

Lyrielasma? *micrum* sp. nov.

Plate 89, figs. 1, 2; text-fig. 8

Derivation of name. Greek μικρος = small.

Holotype. SU 18200 (Pl. 89, fig. 1*a*, *b*). Type locality: P–43.

Diagnosis. *Lyrielasma* about 5–6 mm. in diameter with relatively wide peripheral stereozone and zigzag septa, and lacking lonsdaleoid dissepiments; calice deeply conical.

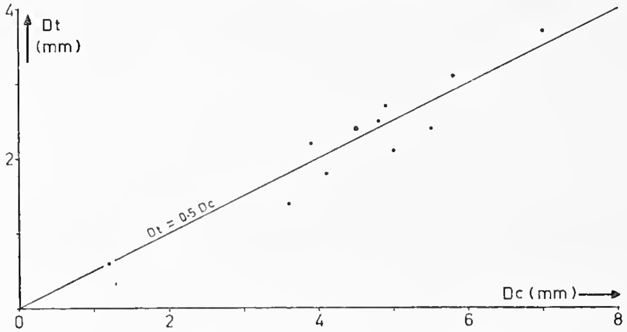
Description. The form of the corallum is unknown, as all specimens are of fragmentary cylindrical corallites; however, the holotype shows evidence of a dendroid growth form, with lateral increase. The epitheca is thin, longitudinally and transversely wrinkled, but without regular septal grooves. Narrow, sharp rejuvenescence rims occur (holotype, and SU 18195). Longitudinal sections suggest a very deep calice, inversely conical in shape, with a sharp or slightly rounded rim and a narrow concave base. Maximum Dc = 7 mm., normal adults being 4–6 mm. across.

Dimensions. In mm. of representative corallites.

No.	*loc.*	*Dc*	*Dt*	*Dt/Dc*	*n*	L_2
SU 16299	Gg–2	4·9	2·7	0·55	32	0·3 R
SU 18195	P–43	7·0	3·7	0·53	38	0·4–0·7 R
SU 18200*	,,	1·2	0·6	0·50	12	—
,,	,,	4·5	2·4	0·53	36	0·4 R
,,	,,	5·0	2·1	0·42	—	—

* Holotype

Lining the thin epitheca is a relatively wide stereozone composed of dilated septal bases, which in some instances apparently merge into lamellar sclerenchyme parallel to the epitheca. This last may, however, be an effect of recrystallization. The stereozone is 0·5–1·0 mm. wide. In adults, n = 30–40; the major septa extend unequally to the axis, where they are curved and arranged about a median plane. One major septum (K?) may be elongate, extending across the axis. The minor septa vary in length from 0·3R to 0·7R, being generally about 0·5R. Inside the stereozone the septa are equally and moderately dilated, irregularly wavy, and bear zigzag flanges which are inclined steeply down towards the axis.



TEXT-FIG. 8. *Lyrielasma? micrum* sp. nov. Scatter diagram for Dt:Dc; the estimated approximate mean, Dt = 0·5Dc, is added.

The trabeculae are very narrow and are approximately parallel throughout their length. The structure of the trabeculae is much as described by Birenheide (1961) for *Acanthophyllum.* They are directed axially upwards at a very small angle above the horizontal.

Dt = 0·5Dc approximately (see text-fig. 8), ranging between 0·39–0·56. The tabular

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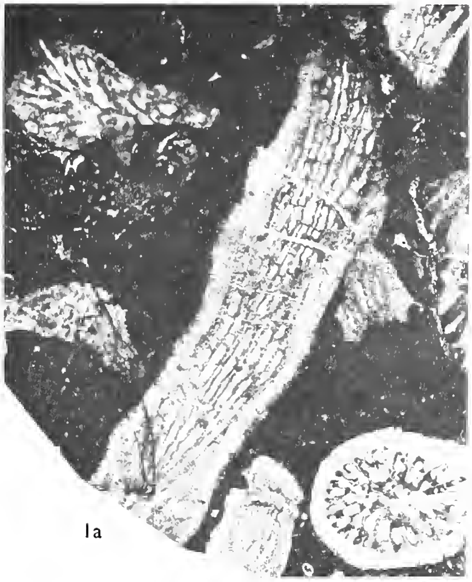
EXPLANATION OF PLATE 89

Figs. 1, 2. *Lyrielasma? micrum* sp. nov. 1*a*, *b*, transverse and longitudinal sections, holotype SU 18200, loc. P–43; ×4. 2*a*, transverse section showing wide stereozone, thick septa, 2*b*, longitudinal section; SU 18195, loc. P–43; ×4.

Figs. 3–6. *Lyrielasma aggregatum* (Hill 1940). 3*a–c*. transverse and longitudinal sections, holotype AM F 10132, Wee Jasper, near Taemas, N.S.W.; figured Hill 1940*b*; ×2. Photographs by courtesy of the Australian Museum, Sydney. 4, transverse section at base of calice, SU 19147, loc. St/1821; ×2. 5, random section through a fragmented colony, UCT F 1946, The Gap (loc. E–18?); ×2. 6*a*, *b*, transverse and longitudinal sections, SU 14257, loc. Ct–50; ×2.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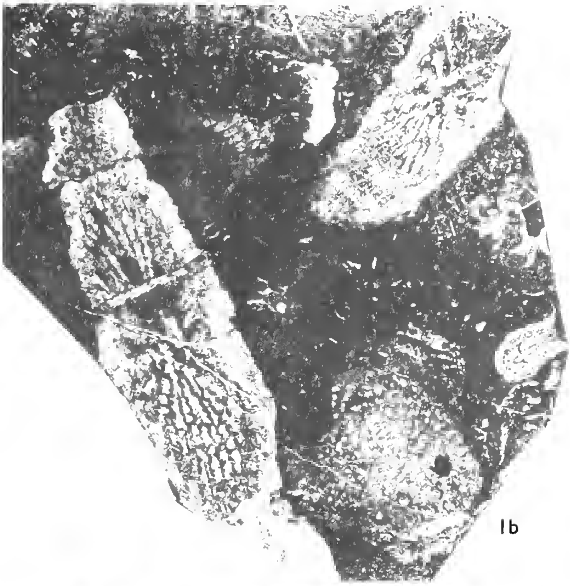
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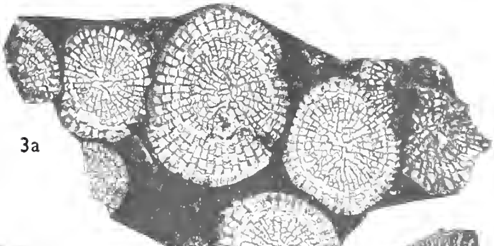
2a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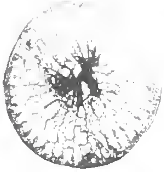
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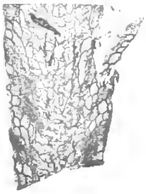
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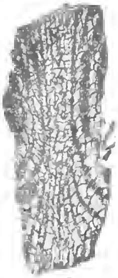
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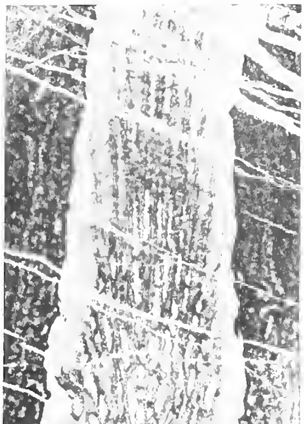
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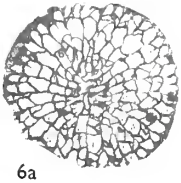
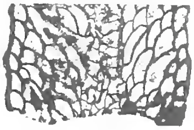
5


6a


6b

STRUSZ, Devonian Spongophyllidae from New South Wales

floors are deeply inversely conical, with a narrow concave base, but a median depression has not been seen. The tabulae are incomplete, steeply inclined, elongate, and but little inflated.

The dissepimentarium consists of 2–4 series of almost vertical fairly elongate to moderately globose dissepiments, generally uniform in size.

Comparison. L? micrum differs from all other Australian species of *Lyrielasma* in its small size and proportionately wide stereozone. The type species is closest in appearance, differing essentially in size and number of septa.

Remarks. Because of the slight doubt whether this species is colonial or not, it is for the present only tentatively assigned to *Lyrielasma.*

Known localities. Gg–2, P–43; BR¹/177.

Lyrielasma subcaespitosum (Chapman 1925)

1962 *Lyrielasma subcaespitosum* (Chapman); Philip, p. 188, pl. 28, figs. 6–7. *Cum Syn.*

Holotype. NM 1731, 14065: Cave Hill, Lilydale. Figured Hill (1939*a*), pl. XIV, figs. 1–3.

Diagnosis. Phaceloid *Lyrielasma* about 12 mm. in diameter, with long wavy to zigzag or flanged septa seldom interrupted by lonsdaleoid dissepiments.

Remarks. L. subcaespitosum praecursor Philip 1962 (p. 119) differs from *L. subcaespitosum* s.s. in being wider, with a wider stereozone, wide tabularium (Dt = ½Dc), and frequent lonsdaleoid dissepiments, interrupting both major and minor septa. The specimens described below have features in common with both subspecies.

Lyrielasma sp. cf. *subcaespitosum*

Plate 87, fig. 5

Material. SU 12245 (loc. Cr–4)?; SU 19238 (Pl. 87, fig. 5), 19241 (loc. St/2565).

Description. The material consists of fragmentary corallites; it is not known whether or not they are from fasciculate coralla. The external characters are unknown.

Dimensions. In mm.

No.	*Dc*	*Dt*	*Dt/Dc*	*n*
SU 12245	est. 10	est. 4·5	*ca.* 0·45	60?
SU 19238	est. 9	5·5	*ca.* 0·6	46

The corallites are about 10 mm. in diameter. There is a peripheral stereozone about 0·7 mm. wide, formed of the dilated ends of septa. Inside this the septa suddenly reduce in thickness, and maintain a fairly uniform moderate dilatation to the axis. Irregular flanges occur in both dissepimentarium and tabularium.

The major septa extend unequally to the axis, being directed towards a median plane which in SU 19238 is marked by one long and one short major septa. n = about 50–60. The minor septa vary considerably in length between ¼R and ½R, being mostly about R/3. Septal microstructure is not clear in the available material. Dt = *circa* 0·5 to 0·6 Dc. The tabular form is not known. The rather narrow dissepimentarium is not well known; for the most part it is masked by the peripheral stereozone and the septal dilatation.

It apparently consists of small, highly inclined dissepiments. I have seen no lonsdaleoid dissepiments.

Remarks. The available material differs from *L. subcaespitosum* s.s. in its wider tabularium, and possibly in having smaller dissepiments. From *L. subcaespitosum praecursor* Philip 1962, which also has a wide tabularium, the specimens differ in lacking all sign of lonsdaleoid dissepiments, and in having a narrower stereozone.

Lyrielasma aggregatum (Hill 1940)

Plate 89, figs. 3–6, Plate 90, fig. 1; text-figs. 9, 10

1940*b*	*Grypophyllum aggregatum* Hill, p. 268, pl. X, figs. 8*a*, *b*, pl. XI, figs. 1*a–d*. Wee Jasper, N.S.W.; Eifelian.
1942*d*	?*Grypophyllum* ?*aggregatum* Hill; Hill, pl. VI, fig. 4. Wellington, N.S.W.; 'Early Couvinian' (probably Emsian).

Holotype. AM F 10132, Wee Jasper, Goodradigbee R., N.S.W., figured Hill (1940*b*) pl. XI, figs. 1*a–d*; figured herein Plate 89, figs. 3 *a–c*.

Diagnosis. Lyrielasma with thin septa, narrow stereozone, wide tabularium, and absent or rare lonsdaleoid dissepiments.

Description of Garra material. Available material is more or less fragmentary, but UCT F 1946 shows evidence of a dendroid corallum in which increase is both sexual (planulae settling on the sides of existing corallites) and by peripheral budding. The latter apparently produces only one bud at a time and is non-parricidal. The epitheca is smooth, or marked with faint longitudinal grooves which show little relationship to the septa; it is thin. The calice is uncertain; longitudinal sections suggest a deeply inversely conical calice with a narrow rounded rim. The maximum observed Dc = 11·8 mm.; adults are normally about 5–9 mm. across.

Dimensions. In mm. of representative corallites.

No.	*loc.*	*Dc*	*Dt*	*Dt/Dc*	*n*	L_2	*stereozone*
SU 14257	Ct–50	11·8	*ca.* 0·5	*ca.* 0·42	50	0·2–0·4 R	0·5 mm.
UCT F 1946	'The Gap'	2·9	1·7	0·59	26	0·1–0·2 R	0·1
,,	,,	4·3	3·6	0·84	30	0·1–0·3 R	0·3
,,	,,	6·5	3·2	0·49	38	0·3–0·4 R	0·6
,,	,,	8·8	4·2	0·48	38	0·3–0·5 R	0·4
SU 19147	St/1821	10·1	4·5	0·45	44	0·3–0·8 R	0·4

Maximum observed n = 50; for normal adults n = 34–44, mostly 38 or 40. The major septa extend unequally towards a median plane, and generally leave a small axial space. The minor septa are considerably more variable in length, even in the same corallite, ranging between 0·1–0·8 R; they are usually 0·3–0·5 R. The septa are equally dilated; their bases are flared to form a peripheral stereozone 0·5 mm. wide at

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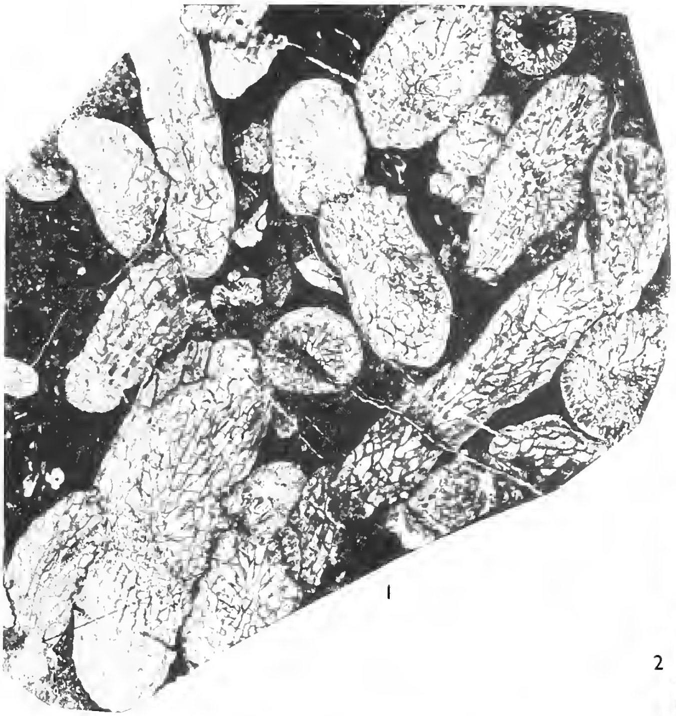
EXPLANATION OF PLATE 90

Fig. 1. *Lyrielasma aggregatum* (Hill 1940). Random section through a fragmented colony; note the peripheral buds in the longitudinal section of a large corallite, lower left; UCT F 1946, The Gap (loc. E–18?); ×2.

Figs. 2, 3. *Spongophyllum halysitoides halysitoides* Etheridge fil. 1918. 2, transverse section, SU 16224, loc. E–30; ×4. 3*a*, *b*, longitudinal sections, SU 16223, loc. E–30; ×4.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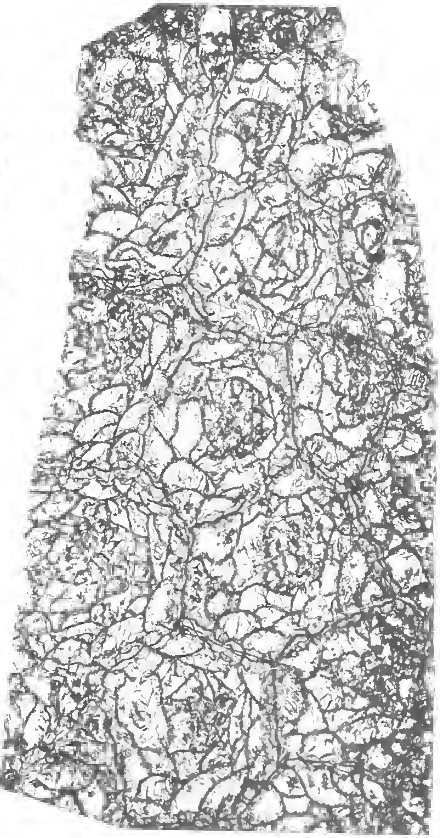

2


3a


3b

STRUSZ, Devonian Spongophyllidae from New South Wales

most. Inside this they are tapered, generally only moderately to slightly dilated, and frequently attenuate in the tabularium. They are zigzag, and occasionally bear weak flanges; their inner ends may be curved. In SU 14257 the minor septa are contratingent, and thus indicate the median plane: at one end they lean away from the major septum (C?), and they continue leaning in that sense until at the other end the one major septum (K?) has two touching minor septa. Generally, however, the minor septa are far less regular.

Dt = 0·5Dc approximately. The tabularium consists of elongate, highly inclined, slightly convex incomplete tabulae, forming moderately to strongly inverse conical tabular floors.

There are from one to four series of globose highly inclined dissepiments which tend to become vertical and rather elongate near the tabularium. Lonsdaleoid dissepiments are rare, and when present only intersect the minor septa. I have seen them in SU 5280 (collected E. M. Basnett 1940, from loc. MM–10) and in two corallites from loc. Ct–50.

Variation. Plots have been made for Dt:Dc, Dt/Dc:Dc, and n:Dc. The estimated curve of best fit for the first approximates to Dt = 0·5Dc. The points fall slightly above this line between Dc = 0 and 8·0 mm., and then slightly below it for greater Dc (text-fig. 9*a*). This is shown more accurately by the plot Dt/Dc:Dc (text-fig. 9*b*); at Dc = 3 mm., Dt/Dc is about 0·55; at Dc = 8 mm., Dt/Dc = 0·50; and at Dc = 11 mm., Dt/Dc has fallen to about 0·45.

The number of septa apparently increases rapidly at first (text-fig. 10), as at Dc = 2·9 mm. (the smallest measurement), n = 26. Beyond this, however, the relationship of n:Dc is linear, approximating to n = 20+2·5Dc.

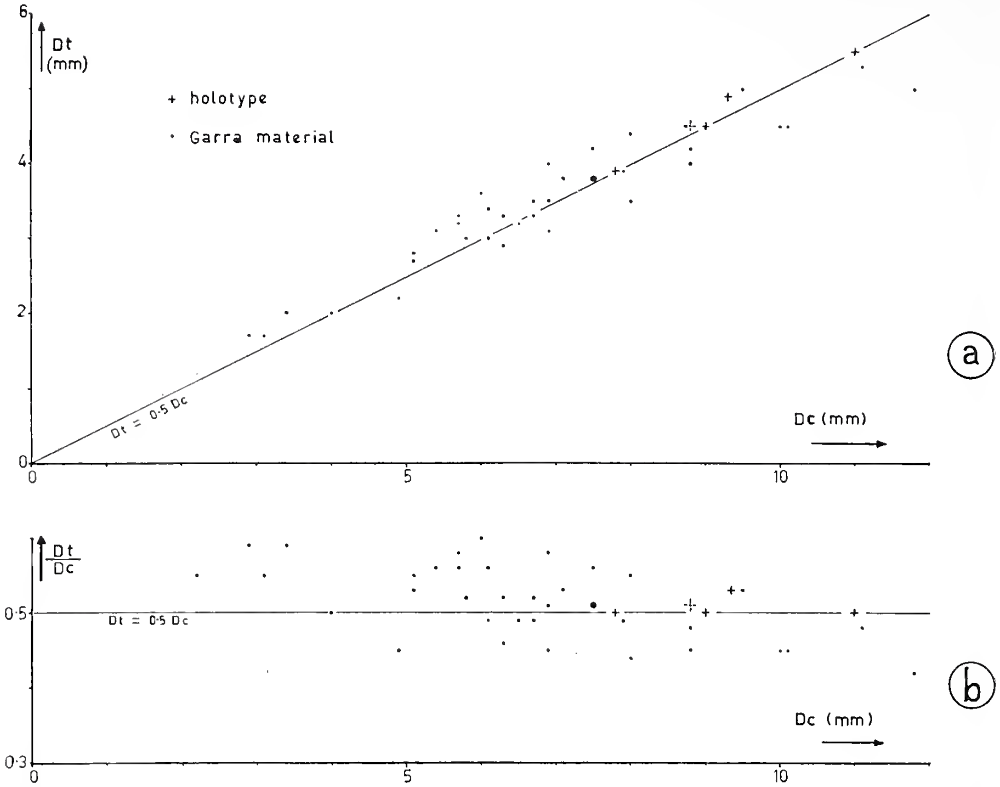
In no cases is the scatter of points excessive.

Comparison. L. aggregatum differs from *L. subcaespitosum* s.s. in a smaller average size, a narrow stereozone, and thinner septa. From *L. subcaespitosum praecursor* Philip 1962 it differs especially in the general lack of lonsdaleoid dissepiments, and also in size and width of stereozone. From *L. floriforme* Hill 1942 it differs in size, width of stereozone, and in having tapered rather than fusiform septa; *L. aggregatum* also has a wider tabularium. *L. lophophylloides* Hill 1942 is very similar; it is distinguished by having four prominent, longer and thicker major septa, and a narrower tabularium.

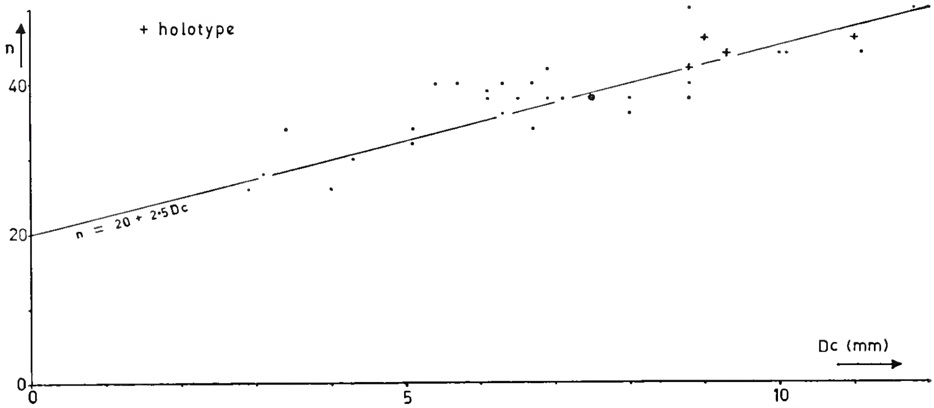
Remarks. Hill (1940*b*, p. 268) placed this species in *Grypophyllum* because at that time she considered that that genus included phaceloid species. However, she also drew attention to the similarity of the species to *Lyrielasma*. As Birenheide (1961) has shown that *Grypophyllum* is a solitary subgenus of *Acanthophyllum*, and as '*G.*' *aggregatum* differs from other species assigned to *Lyrielasma* essentially only in having a narrow stereozone, I have herein placed it in *Lyrielasma*.

Range. The species has been recorded from the Murrumbidgee limestones (Couvinian according to Hill 1940*b*, p. 249; Emsian according to Philip and Pedder 1964), and from the Garra Formation (which I consider to be probably Emsian). It has also been found at Douglas Creek, Clermont, Qld. (UQ F 36328), considered by Hill (1939*b*) to be probably upper Couvinian in age.

Known Garra localities. Ct–50, MM–10, MM–12; St/181, St/1125, St/1821; also collected by Dr. J. Conolly from 'The Gap', probably loc. E–18.



TEXT-FIG. 9. *Lyrielasma aggregatum*. Scatter diagrams for (*a*) Dt:Dc, and (*b*) Dt/Dc:Dc, with data for the holotype added (measured from published photographs); for comparison, the line Dt = 0·5Dc is added.



TEXT-FIG. 10. *Lyrielasma aggregatum*. Scatter diagram for n:Dc, with data for the holotype added; the estimated approximate mean n = 20+2·5Dc is also added.

Genus SPONGOPHYLLUM Edwards and Haime 1851

1851 *Spongophyllum* Edwards and Haime, p. 425 (*fide* Lang, Smith, and Thomas 1940, p. 121).
1962 *Spongophyllum* Edwards and Haime 1851; Birenheide, p. 69 (*partim*). Contains an extensive synonymy, to which add:
1962 *Neomphyma* Soshkina 1937; Soshkina and Dobrolyubova, p. 335, in Orlov (*partim*).

Type species. By monotypy, *S. sedgwicki* Edwards and Haime 1851, p. 425. Neotype, selected Jones (1929, p. 88), figured Birenheide (1962) pl. 9, fig. 8, pl. 10, fig. 10. Torquay, Devonshire; Middle? Devonian.

Diagnosis. Phaceloid or, more usually, cerioid, with small corallites; narrow tabularium of flat or gently concave complete tabulae; dissepimentarium of only a few series of globose lonsdaleoid dissepiments and smaller interseptal dissepiments; septa thin, poorly developed, generally based on lonsdaleoid dissepiments.

Remarks. The genus has been well revised by Jones (1929), Prantl (1952), and Birenheide (1962). Birenheide would include *Australophyllum* Stumm 1949. As proposed by Stumm, there is certainly no difference; however, the type species shows certain points which I consider sufficient to justify retention of the genus. The tabulae are concave, with a definite median depression such as typifies the acanthophylloid genera. Also the dissepimentarium is rather wide for typical *Spongophyllum*.

Spongophyllum halysitoides halysitoides Etheridge fil. 1918

Plate 90, figs. 2, 3; text-figs. 11, 12

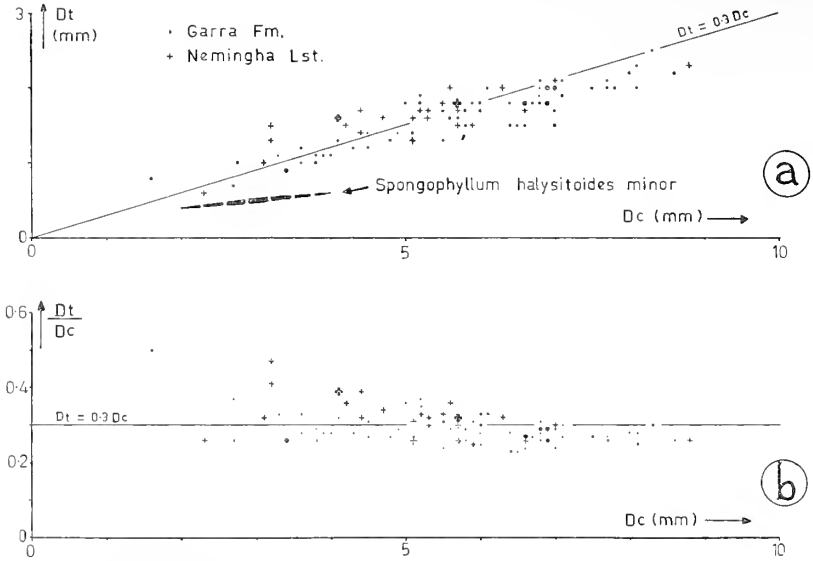
1918 *Spongophyllum halysitoides* Etheridge fil., p. 49, pl. VII. Tamworth, N.S.W.; Coblenzian.
1932 *Spongophyllum halysitoides* Etheridge fil.; Jones, p. 56 (*partim*—not text-fig. 2). Tamworth.
1942*c* *Spongophyllum halysitoides* Etheridge; Hill, p. 161, pl. II, figs. 5*a*, *b*. Tamworth.
non 1958 *Spongophyllum halisitoides* (*sic*) Etheridge; Bulvanker, p. 132, pl. LXIV, figs. 1*a*, *b*, 2. Kuznets Basin, U.S.S.R.; lower Eifelian.
?1960 *Spongophyllum halysitoides* Etheridge; Spasskiy, p. 55, pl. XXIX, figs. 3, 4. Altai, U.S.S.R.; lower Middle Devonian.

Holotype. AM F 16453 (AM 187), figured Etheridge, jr. 1918, pl. VII, figs. 1–3. Type locality: road near Beedle's Farm, Moonbi, Co. Inglis, Tamworth, N.S.W. Nemingha Limestone, Coblenzian.

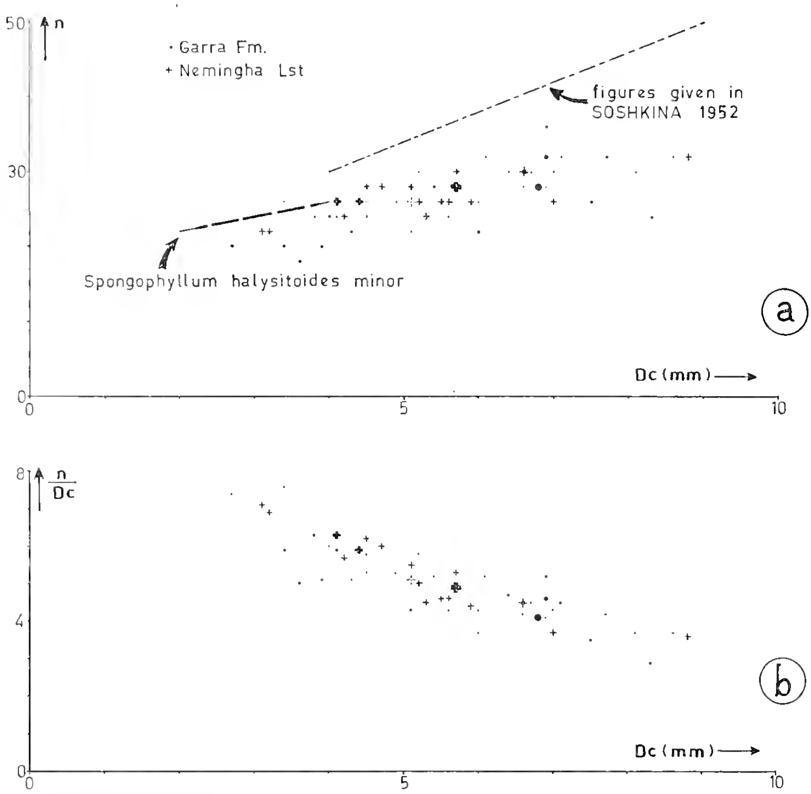
Diagnosis. Cerioid *Spongophyllum* with corallites mostly 4–6 mm. in diameter, with thick moniliform walls; septa much reduced or absent; tabularium narrow.

Remarks. The specimens from the Garra Formation agree closely with the descriptions and figures of Etheridge, jr. (1918) and Jones (1932). The only differences lie in a slightly stronger and more frequent development of septa, and in thicker walls. Some of the Garra specimens have noticeably irregular corallites.

The Garra material has been statistically compared with a specimen I have collected from the Nemingha Limestone in a quarry just north of Attunga (near Tamworth), and with SU 6241 from the same horizon at Por. 256, Ph. Burdekin, near Tamworth. The Tamworth and Garra specimens agree completely (text-figs. 11, 12). The range of variation is greater than stated by Etheridge, the maximum diameter being nearly 9 mm.; most corallites are about 3·5–7 mm. across. For both, Dt = 0·3Dc approximately, and Dt/Dc seems to decrease only slightly with increasing Dc. A plot of n/Dc:Dc suggests a slight change in rate of septal insertion with age.



TEXT-FIG. 11. *Spongophyllum halysitoides halysitoides.* Scatter diagrams for (*a*) Dt : Dc, and (*b*) Dt/Dc : Dc; data from specimens from the Garra Formation and the Nemingha Limestone (the type horizon). The estimated approximate mean line Dt = 0·3Dc is shown, and also in (*a*) the range of values for *S. halysitoides minor* (from the figures given by Hill).



TEXT-FIG. 12. *Spongophyllum halysitoides.* Scatter diagrams for (*a*) n : Dc, and (*b*) n/Dc : Dc for *S. halysitoides halysitoides* from the Garra Formation and the Nemingha Limestone. In (*a*) the range of values given by Soshkina (1952), and for *S. halysitoides minor* by Hill (1940*c*) are also shown.

'Varieties' of *S. halysitoides* have been established by both Hill (1940*c*) and Soshkina (1949), distinguished principally on corallite size. I consider that their geographic separation, taken with the morphological differences, suffice for these to be subspecies. Etheridge jr.'s original species is a distinct subspecies. *S. halysitoides minor* Hill 1940 is diminutive (Dc = 2–4 mm.), with a very narrow tabularium; from the figures given by Hill, its range of variation for Dt:Dc falls below the area of scatter for the nominate subspecies. It is known from the Coblenzian? of Silverwood, Qld., and the Urals. *S. halysitoides media* Soshkina 1949, from the Eifelian of the Urals, is close to, indeed may be synonymous with, the nominate subspecies (Dc = 5–6 mm.), but has better developed septa. The size range, and number of septa, given for the species by Soshkina (1952)—probably based on the Russian material—falls well above the scatter area for n:Dc for *S. halysitoides halysitoides* (text-fig. 12), suggesting that the Russian material may differ in this respect also. *S. halysitoides major* Soshkina 1949, also from the Eifelian of the Urals, is large (Dc = 8–9 mm.), with well-developed septa; it should perhaps be considered a separate species.

The specimen figured by Bulvanker (1958, pl. 64) from the Eifelian of the Kuznets Basin has very well-developed septa—in fact in most corallites they appear to be continuous—as well as smaller dissepiments and distinctly acanthophylloid tabulae. It is probably a species of either *Australophyllum* or *Xystriphyllum*.

Range. The species is known from the Coblenzian of Eastern Australia, and the Coblenzian and Eifelian of the U.S.S.R. The nominate subspecies is known only from the Coblenzian.

Known Garra localities. Ct–29?, E–24, E–30, E–31; Bt/430, Bt/936.

Spongophyllum rosiforme Yoh 1937

1937 *Spongophyllum rosiforme* Yoh, p. 54, pl. VI, figs. 1*a–c*. Kwangsi, China; middle Middle Devonian.

Diagnosis. Phaceloid *Spongophyllum* with corallites about 9 mm. in diameter, buttressed by lateral expansions; septa few, irregular, confined to tabularium; one peripheral series of large geniculate dissepiments, supplemented axially by intermittent small, vertical elongate dissepiments; tabularium narrow, of close, gently concave tabulae.

Spongophyllum sp. cf. *rosiforme* Yoh 1937

Plate 91, figs. 1*a*, *b*; text-fig. 13

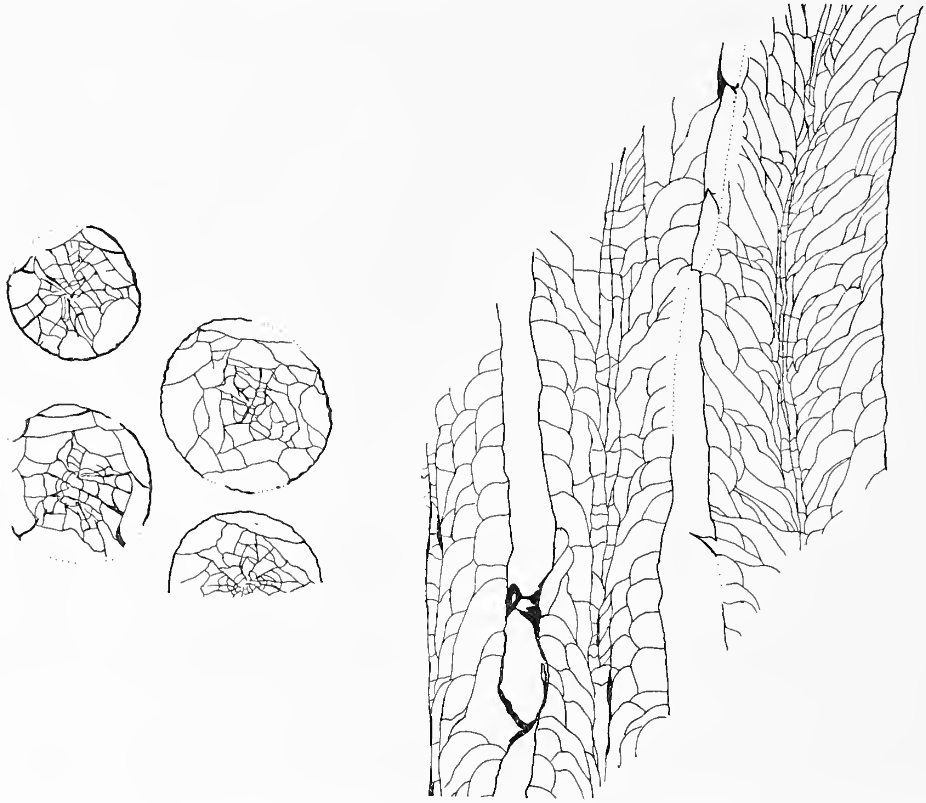
Material. SU 17167, loc. P–1.

Description. The corallum is phaceloid, composed of cylindrical corallites with frequent lateral processes. The epitheca is apparently smooth, with gentle growth swellings. The calice is deep, inversely conical to bell-shaped. Dc = 6–8 mm.

The septa, consisting of discontinuous crests on the dissepimental surfaces, are unequal and not divisible into two orders. n = 14–16 in general. Most are confined to the tabularium but exceptionally they may extend outwards as far as the epitheca. The longest septa often interfinger axially. The thin epitheca is lined by a lamellar stereozone 0·2 mm. thick, in which septal bases are not visible. Septal microstructure is unknown.

Dt = $\frac{1}{4}$Dc or less. The tabulae are close, and gently but irregularly sagging, at times with upturned edges.

The wide dissepimentarium consists of a peripheral series of large globose to geniculate lonsdaleoid dissepiments, and an incomplete inner series of very elongate, steeply inclined dissepiments, some of them lonsdaleoid, which may be supplemented by occasional small convex plates.



TEXT-FIG. 13. *Spongophyllum* sp. cf. *rosiforme*. Transverse and longitudinal sections of SU 17167, ×3; drawn from photographs.

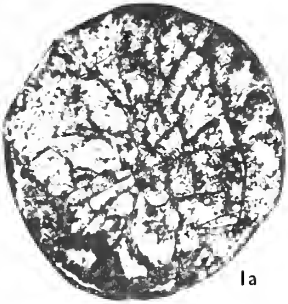
Comparison. This specimen differs from Yoh's only in a slightly smaller diameter, and 14–16 instead of 20 septa. The differences could be of subspecific value, but as the possible variation in both cases is unknown, I consider it best for the present simply to compare them.

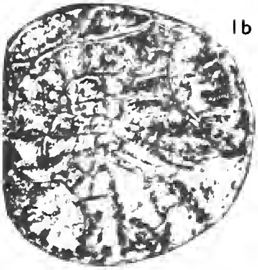
EXPLANATION OF PLATE 91

All figures ×4.

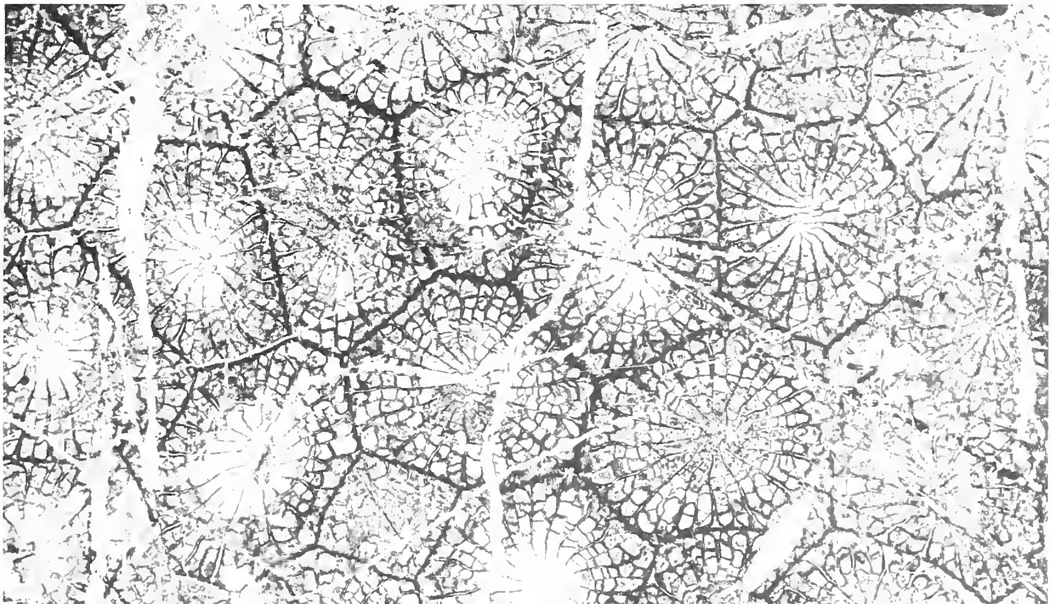
Fig. 1. *Spongophyllum* sp. cf. *rosiforme* Yoh 1937. 1*a*, *b*, transverse sections of individual corallites (cf. text-fig. 13), SU 17167, loc. P–1.

Fig. 2. *Xystriphyllum dunstani* (Etheridge fil. 1911). 2*a*, *b*, longitudinal and transverse sections, paralectotype AM F 9492–3, AM 733 A, B, Clermont, Qld. Photographs by courtesy of the Australian Museum, Sydney.


1a


1b


2a


2b

STRUSZ, Devonian Spongophyllidae from New South Wales

Genus XYSTRIPHYLLUM Hill 1939

1939*b* *Xystriphyllum* Hill, p. 62.
1940*b* *Xystriphyllum* Hill; Hill, p. 269.
1940*c* *Xystriphyllum* Hill; Hill, p. 163.
1942*c* *Xystriphyllum* Hill, 1939; Hill, p. 147.
1942*d* *Xystriphyllum*; Hill, p. 183.
1949 *Xystriphyllum* Hill; Stumm, p. 33.
1949 *Stenophyllum*; Soshkina, p. 127 (*partim*).
1950 *Xystriphyllum* Hill, 1939; Hill, p. 140.
1950 *Xystriphyllum* Hill, 1939; Wang, p. 218.
1952 *Stenophyllum* Wdkd.; Soshkina, p. 83 (*partim*).
?1955 *Pseudospongophyllum* Zhmaev; Krayevskaya, p. 213, in Khalfin (*partim*?).
1955 *Stenophyllum* Amanshauser, em. Wedekind; Krayevskaya, p. 211, in Khalfin (*partim*).
?1955 *Spongophyllum* M. Edwards et Haime; Krayevskaya, p. 214, in Khalfin (*partim*?).
1956 *Xystriphyllum* Hill; Clauss, p. 16.
1956 *Xystriphyllum* Hill, 1939; Hill, p. F304, *in* Moore.
1958 *Stenophyllum* (Amanshauser) emend. Wedekind, 1925; Bulvanker, p. 146 (*partim*).
non 1960 *Xystriphyllum* Hill; Crickmay, p. 11.
?1961 *Xystriphyllum* Hill 1939; Fontaine, p. 158 (*partim*?).
1962 *Xystriphyllum* Hill 1939; Philip, p. 188.
1962 *Xystriphyllum* Hill, 1939; Soshkina and Dobrolyubova, p. 335, *in* Orlov.

Type species. *Cyathophyllum dunstani* Etheridge fil. 1911, p. 3, pl. A, figs. 1, 2 (see below).

Diagnosis. Cerioid; septa long, wavy, thin axially, dilated peripherally; tabulae close, complete or incomplete, concave with axial depression; dissepiments globose, axially inclined, becoming steep at margin of tabularium; minor septa occasionally cut by lonsdaleoid dissepiments.

Remarks. Many of the Russian species assigned to *Stenophyllum* Wedekind (*non* Verhoeff 1897) are *Xystriphyllum*; others are *Acanthophyllum* s.l. I would place the following in *Xystriphyllum*: *Stenophyllum altum* Soshkina 1949, p. 128 (Eifelian, Urals); *S. uralicum* Soshkina 1949, p. 129 (Eifelian, Urals); *S. gorskii* Bulvanker in Krayevskaya, 1955, p. 211, in Khalfin (Coblenzian, Kuznets Basin, Central Salair; Eifelian, Kuznets Basin—Bulvanker 1958); this probably is synonymous with *X. dunstani*, which see; *S. sibiricum* Bulvanker in Krayevskaya 1955, p. 211, in Khalfin (Eifelian, Kuznets Basin); *S. devonicum* Bulvanker in Krayevskaya 1955, p. 211, in Khalfin (Eifelian, W. Siberia, Kuznets Basin, and Altai mineral field); *S. salairicum* Zhmaev in Krayevskaya 1955, p. 212, in Khalfin (Eifelian, Kuznets Basin); *S. soshkinae* Zhmaev in Krayevskaya 1955, p. 212, in Khalfin (Eifelian, Kuznets Basin); *S. taimyricum* Kravtsov 1963, p. 40 (Emsian, central Taimyr).

The following may also belong in *Xystriphyllum*: *Spongophyllum minimum* Zhmaev in Krayevskaya 1955, p. 215, in Khalfin (Lower Devonian, Salair); *Pseudospongophyllum massivum* Zhmaev in Krayevskaya 1955, p. 213, in Khalfin (Eifelian, Kuznets Basin); *Spongophyllum halysitoides* Etheridge of Bulvanker 1958, p. 132 (*non* Etheridge jr. 1918) (Lower Eifelian, Kuznets Basin).

Range. The genus is known from the Lower Devonian of America and Czechoslovakia, the upper Lower to basal Middle Devonian of Australia, the Coblenzian to Eifelian of the U.S.S.R., the Couvinian of Laos?, and the Frasnian of Menorca.

Xystriphyllum dunstani (Etheridge fil. 1911)

Plate 91, fig. 2, Plate 92; text-figs. 14–17

1911 *Cyathophyllum dunstani* Etheridge fil., p. 3, pl. A.
non 1935 ?*Cyathophyllum dunstani* Etheridge; Allan, p. 6, pl. V, figs. 4, 5. Reefton, N. Zealand; Eifelian?
1939*b* *Xystriphyllum dunstani* (Etheridge); Hill, p. 62, pl. V, figs. 5–8. Clermont, Qld.; Eifelian?
1940*c* *Xystriphyllum dunstani* (Etheridge); Hill, p. 163, pl. III, figs. 4*a*, *b*. Silverwood, Qld.; Eifelian?
1942*d* *Xystriphyllum dunstani* (Etheridge); Hill, pp. 183, 184, pl. VI, figs. 2*a*, *b*. Wellington, N.S.W.; Emsian?
?1955 *Stenophyllum gorskii* Bulvanker in Krayevskaya, p. 211, pl. XXXVII, fig. 2, in Khalfin. Kuznets Basin and Central Salair, U.S.S.R.; Coblenzian.
?1958 *Stenophyllum gorskii* Bulvanker (*partim*); Bulvanker, p. 147, pl. LXXI, figs. 1*a*, *b*, 2, pl. LXXII, figs. 1*a*, *b*. Kuznets Basin, U.S.S.R.; Eifelian.

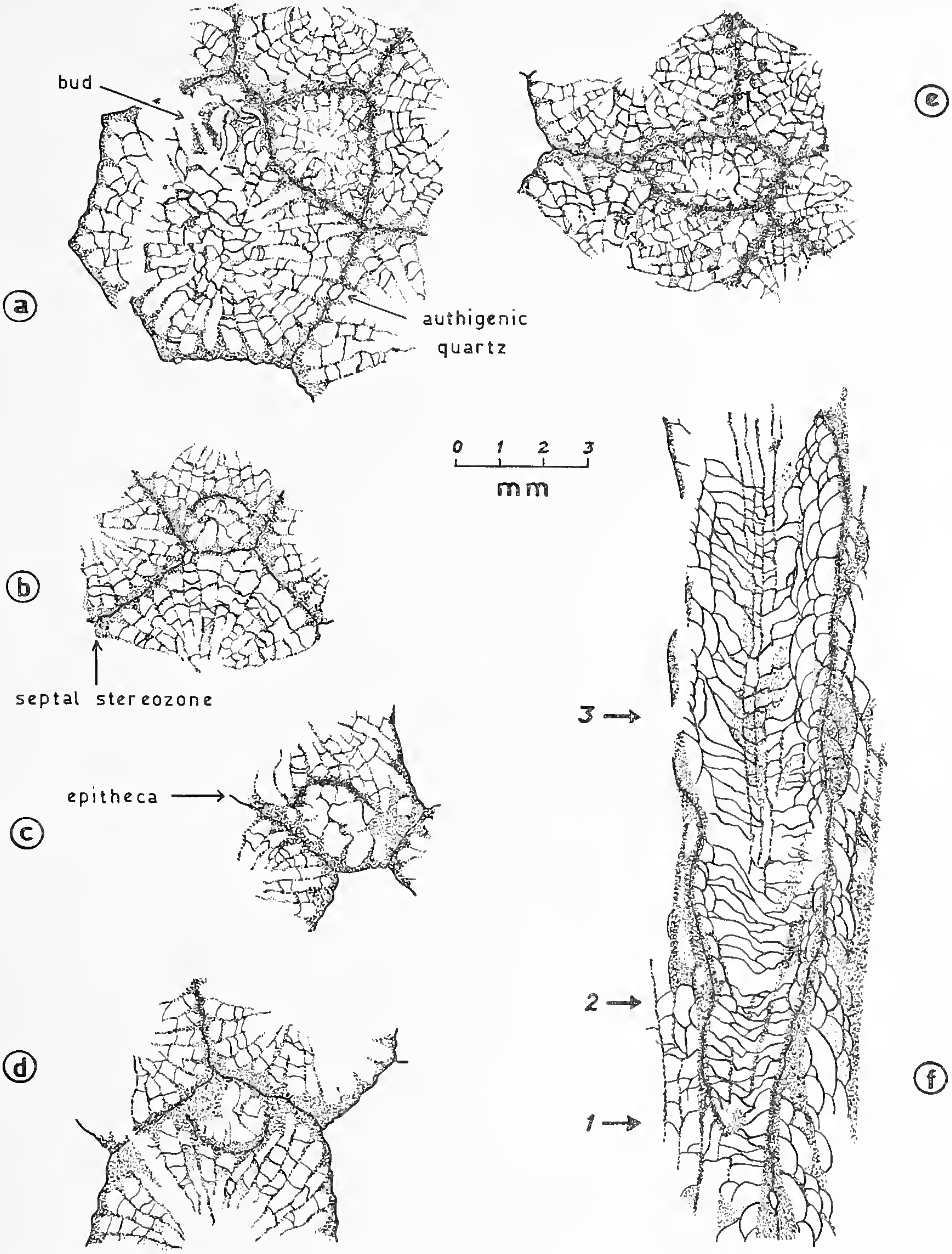
Lectotype. GSQ Cl.6; subsequent designation Hill (1939*b*) p. 62, where figured plate V, figs. 5–8. Type locality: Douglas Ck., Clermont, near Rockhampton, Qld. Eifelian? Paralectotype AM F 9492–9493 (sections AM 733), figured Etheridge jr. (1911), pl. A, figs. 1, 2; figured herein plate 93, figs. 2*a*, *b*.

Diagnosis. *Xystriphyllum* with corallites of average diameter 6–8 mm., in which the major septa interdigitate axially.

Description. I have collected a large amount of material from the Garra Formation, and have compared it with the lectotype, and with other material in the collections of the University of Queensland, the University of Sydney, and the Australian Museum. The following description is based on all of this, but principally on the extensive Garra material.

The corallum is massive and may reach a large size. Thus SU 17184 (loc. P–22) is 30 cm. high and over 30 cm. across, and is part of a non-radiating corallum. The holotheca is unknown. Calices are deep, conical to slightly bell-shaped, with steep, straight to moderately convex walls, narrow rims, and narrow concave bases. Individual corallites are 4- to 8-sided, generally with straight or slightly crenulate walls. The majority of adult corallites are 6–8 mm. in diameter (see text-fig. 15*a*). The corallite epitheca is longitudinally ribbed, but shows only sparse and very faint transverse growth marks. The wall structure comprises a thin dark median surface, representing the epitheca of adjacent corallites (the 'axial plate' of Flower 1961). On either side of this is a layer of calcite fibres growing perpendicularly outwards, forming a non-septal stereozone. Quartz euhedra are common within these wall tissues in the Garra coralla.

Up to 44 septa have been counted, but the usual maximum for a corallum is 38–40. Normal adult corallites contain 32–36 septa (see text-fig. 16). The septa, of two orders, are thin in the tabularium, becoming gradually dilated outwards, until about 0·2–0·3 mm. from the periphery, where there is a rapid wedge-wise dilatation. These prominent septal bases merge with the fibrous wall tissue to form a narrow (*circa* 0·1 mm.) composite stereozone. The septal bases of adjacent corallites may be opposite or alternate. The major septa are unequal, and approach or interdigitate at the axis; generally one extends across the axis, or two opposite major septa may unite axially. The minor septa are



TEXT-FIG. 14. *Xystriphyllum dunstani*, SU 13263, ×6. (*a*)–(*e*): transverse sections showing stages in the growth of a juvenile corallite. (*f*) longitudinal section through a single bud; (1) inception of bud, (2) appearance of first series of dissepiments, at a length of about 3 mm., (3) adult appearance attained, at a length of about 9 mm.

generally $\frac{2}{3}$–$\frac{3}{4}$ the length of the major, and extend some distance into the tabularium. The septa are commonly sinuous but never flanged.

Dt = *circa* $\frac{1}{2}$Dc. The tabulae are crowded, complete and incomplete, moderately to deeply concave or often strongly funnel-shaped. Their margins are upturned.

There are 2–4 series of globose dissepiments, rather irregular in size. They are axially inclined, the inclination being moderate peripherally, increasing inwards. Those at the inner margin of the dissepimentarium are very steeply inclined or vertical and often elongate.

Ontogeny. Budding and the development of corallites has been reconstructed from the large number of sections made, although serial sections were not used (text-fig. 14).

Budding is peripheral. The bud forms in the corner of the parental calice with an initial diameter of about 1–1·5 mm. The first skeletal element seen in transverse section is a very short segment of wall tissue within the dissepimentarium (text-fig. 14*a*). The initial septa are inserted immediately in a very irregular pattern—the typical fourfold rugosan pattern apparently does not occur. The ends of the wall segment rapidly expand to meet the walls of the parent corallites, and septal insertion continues at a rapid rate (text-fig. 14*b–d*). At a diameter of about 2 mm. the first series of dissepiments appears; the corallite at this stage is about 3 mm. long (text-fig. 14*f*). Once the young corallite is completely enclosed by wall tissue it expands by a lengthening of all its wall segments, and so quickly assumes a polygonal shape, simulating an 'inter-mural offset' (text-fig. 14*e*). The second series of dissepiments appears about 4–5 mm. above the proximal extremity.

The above sequence suggests that in most, if not all, massive rugosan corals, the so-called 'inter-mural increase' (see Hill, p. F248, in Moore 1956) is in fact peripheral calical increase.

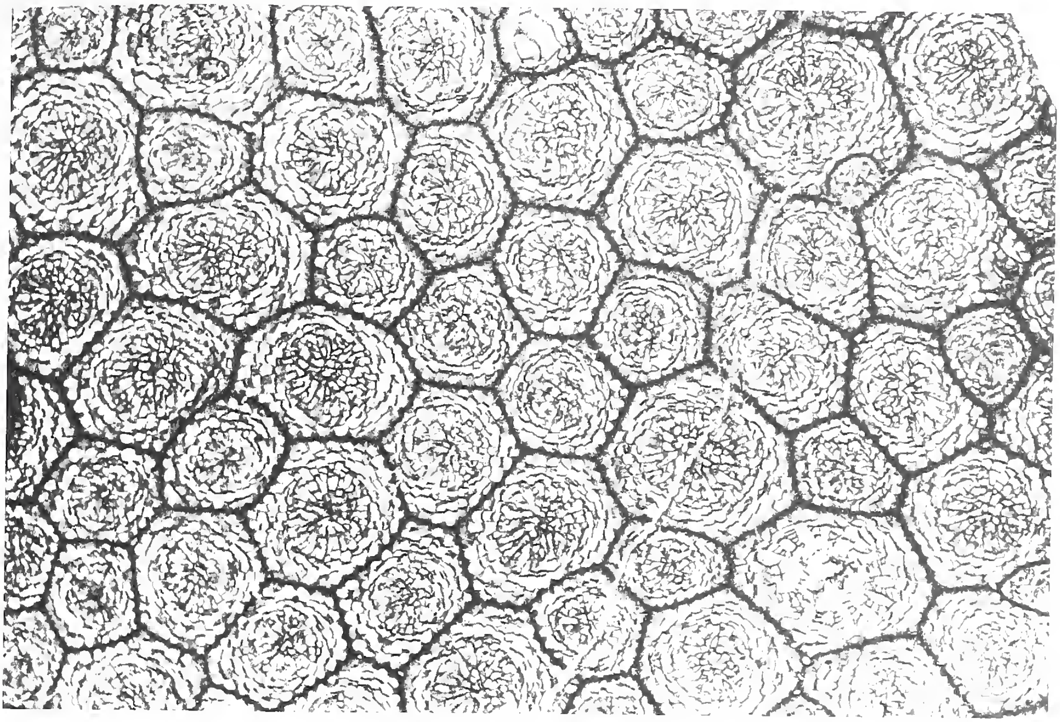
Variation (text-figs. 15–17). Dc, Dt, and n were measured for 6 coralla from the Garra Formation (up to 100 measurements of each), as well as 37 measurements of sections of 3 north Queensland coralla. It was found that frequency curves for all but Dc were of little value. Dc was plotted with a class interval of 0·7 mm.; the curves show considerable variation. Most are bimodal, with peaks at about 3–4 mm. and 5–7 mm. SU 5282 (loc. MM–12) and 13263 (loc. Cr–100) have skewed unimodal curves.

Bivariate plots of n:Dc for three coralla from loc. P–22 showed no significant differences, but that for the Queensland coralla was inconclusive (clearly about 100 measurements are needed from one corallum for great accuracy). In both this set of curves, and that for n/Dc:Dc, scatter diagrams show a marked change of slope in the region of Dc = 3·5 mm., and n = 28. This is interpreted as indicating rapid septal insertion in juvenile polyps, followed by slow insertion after the attainment of maturity, at an average diameter of 3·5 mm.

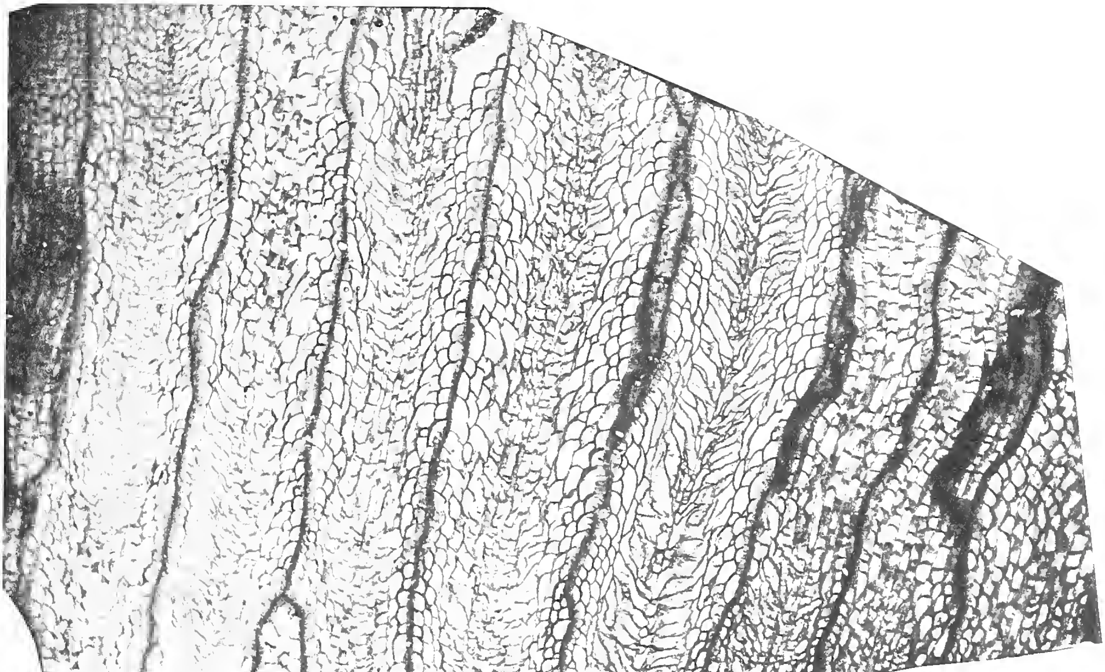
Comparison. As noted by Hill (1939*b*), *X. dunstani* is very similar to *X. mitchelli* (Etheridge fil. 1892). The latter has proportionately more septa, which show less tendency to inter-

EXPLANATION OF PLATE 92

Xystriphyllum dunstani (Etheridge fil. 1911). Transverse and longitudinal sections, SU 13263, loc. Cr–100; ×4.



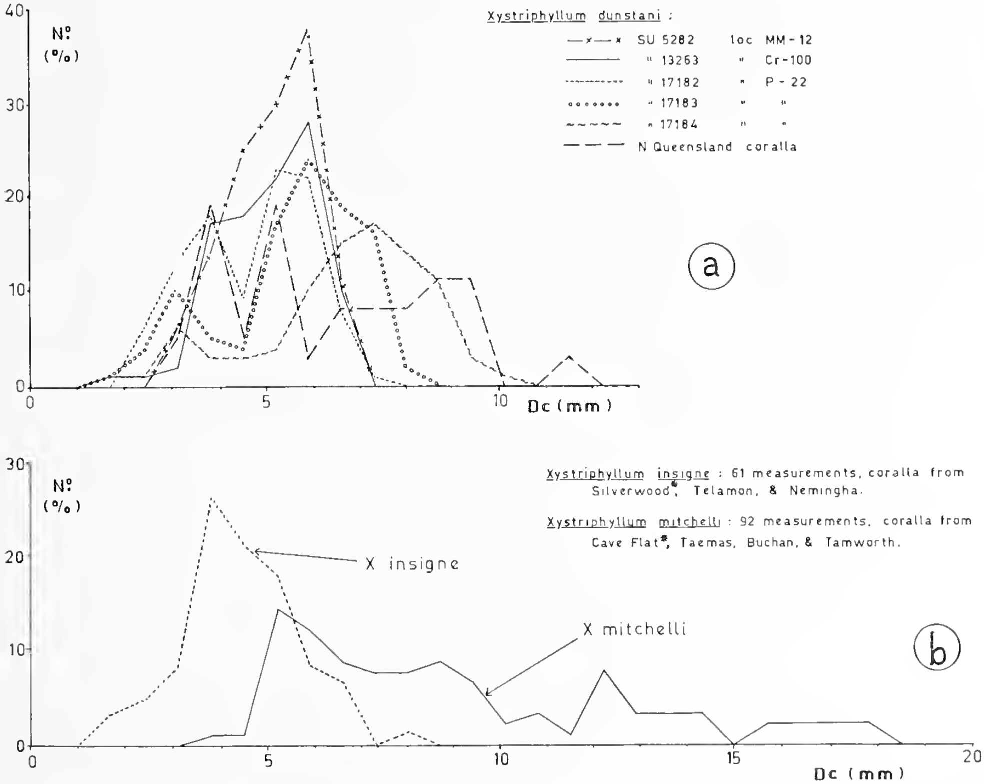
1



2

STRUSZ, Devonian Spongophyllidae from New South Wales

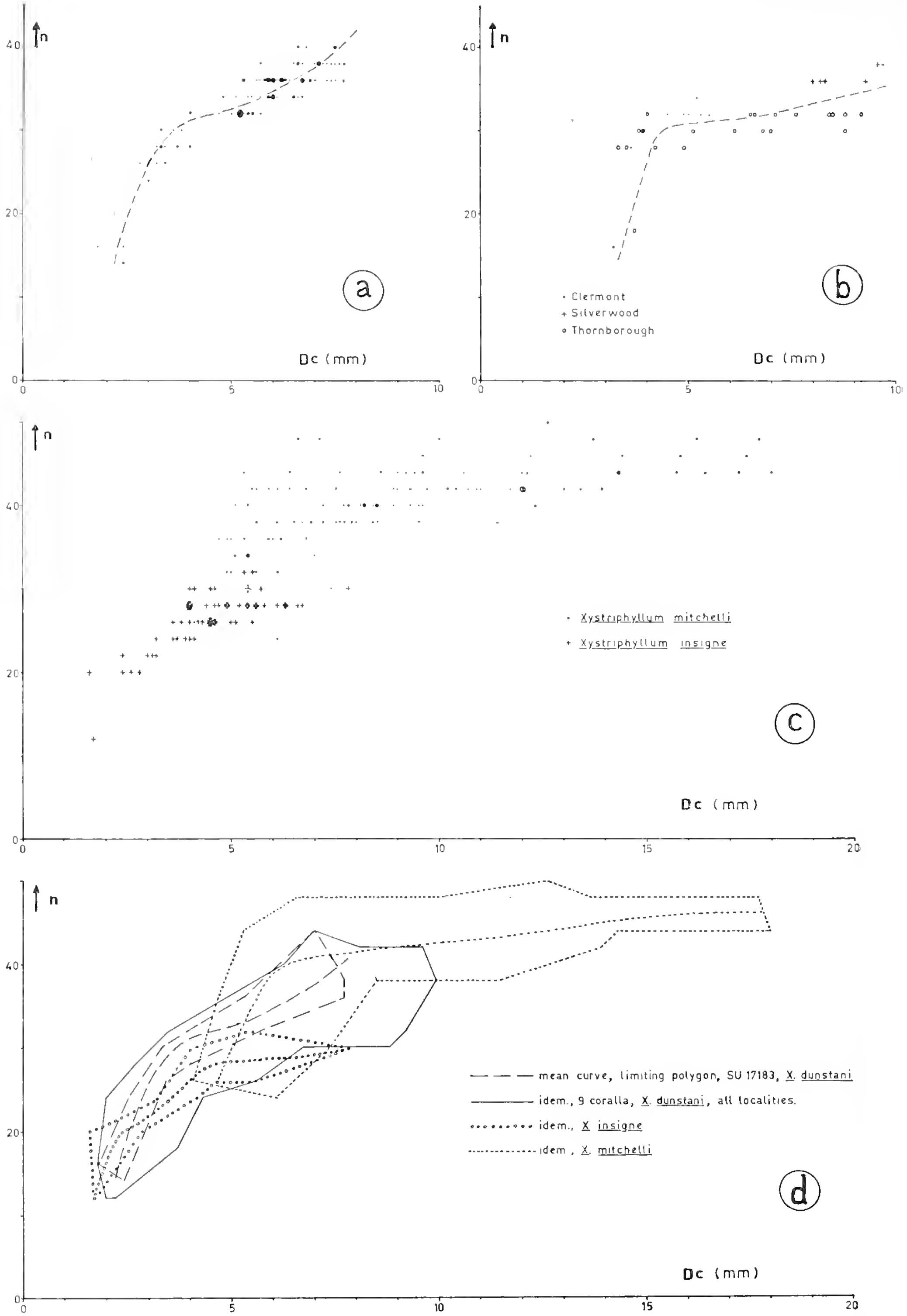
digitate axially. Also, coralla of *X. mitchelli* from the Murrumbidgee Devonian may have much larger corallites (up to Dc = 18 mm.). Plots of n:Dc and n/Dc:Dc show significant differences from those for *X. dunstani* (text-figs. 16, 17). The plot for n/Dc:Dc has the same form as that for *X. dunstani*—perhaps, therefore, a generic character—but differs in that the change of slope occurs at Dc = *circa* 6 mm. A further morphological distinction between the two species is in the nature of the peripheral septal dilatation. In *X. dunstani* this is wedgewise and distinctly triangular in transverse section. In *X. mitchelli* the dilated portions are longer and often ogival in section.



TEXT-FIG. 15. *Xystriphyllum spp.* Frequency polygons for Dc. (*a*) five Garra coralla and coralla from north Queensland localities (combined), *X. dunstani*; (*b*) coralla of *X. insigne* and *X. mitchelli*, including * type localities.

Scatter diagrams for *X. insigne* Hill 1940 are much closer to those for *X. dunstani* than are those of *X. mitchelli* (text-figs. 15–17), but the two species are readily distinguishable morphologically. *X. insigne* is smaller than *X. dunstani*, with fewer septa and proportionately thick walls.

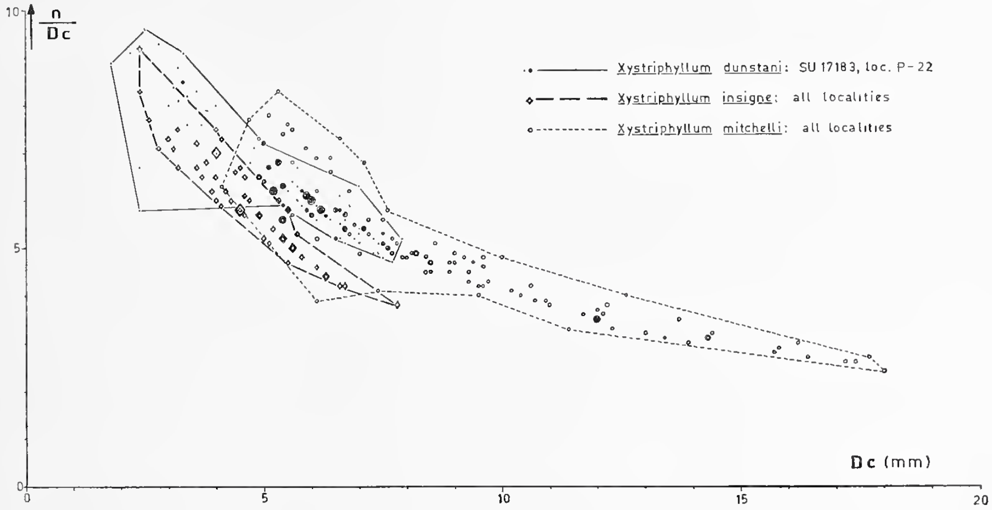
Remarks. Stenophyllum gorskii Bulvanker in Krayevskaya 1955, from the Coblenzian and Eifelian of Asian U.S.S.R., cannot be distinguished from the type sections of *X. dunstani*. Despite the considerable geographic separation, I at least tentatively place



TEXT-FIG. 16. *Xystriphyllum spp.* Variation of n:Dc. (*a*) scatter diagram for *X. dunstani*, SU 17183 (Garra Formation) with mean curve obtained from density-contouring of plot; (*b*) idem, north Queensland *X. dunstani*; (*c*) scatter diagrams, *X. insigne* and *X. mitchelli*; (*d*) comparison of mean curves and limiting polygons for the three species.

them in synonymy. This is to a certain extent supported by the presence in the same region of *Rhizophyllum enorme* Etheridge fil. 1903 (Bulvanker 1958, p. 46), another Garra species.

Range. *Xystriphyllum dunstani* is now known from a number of localities in the Lower and Middle Devonian of Eastern Australia. Hill (1943) considered the type locality—Douglas Creek, Clermont, N. Qld.—to be Couvinian, and equivalent to part of the Murrumbidgee succession. The presence of *Lyrielasma aggregatum* (see p. 570) supports this; I feel the type locality may be as old as Emsian, although the fauna is too small for accuracy.



TEXT-FIG. 17. *Xystriphyllum spp.* Scatter diagram and limiting polygons for n/Dc:Dc, *X. dunstani* (SU 17183), *X. insigne*, and *X. mitchelli*, showing the close similarity of form for the three species.

The Silverwood fauna agrees very closely with that of the Buchan–Taemas–Garra faunal association, and is also probably Emsian, as pointed out by Hill (1943). In the Garra Formation *X. dunstani* apparently is commonest in a biostrome high in the succession, and may be Emsian or basal Eifelian. Philip (1960, p. 149) reports *X. dunstani* from the limestone at Toongabbie, Victoria, an horizon which he correlates with his Gedinnian Cooper's Creek Formation. Professor Hill's collection contains specimens from the Middle? Devonian of Thornborough, N. Qld., and the Eifelian? of the Broken River, N. Qld. (locality BRS 48—see Hill and Denmead 1960, fig. 21). SU 3193 is from the Emsian or Eifelian of Wee Jasper, N.S.W.

X. dunstani would therefore seem to be characteristic of the Emsian and Eifelian of Eastern Australia, possibly occurring as early as the Gedinnian. It apparently occurs in rocks of a similar age in the Kuznets Basin and Central Salair, Asian U.S.S.R.

Known Garra localities. Cr–100 (common), Ct–11, Ct–13, Ct–15, Ct–22, MM–11, MM–12, P–22 (common), P–25; Bt/1838.

Xystriphyllum magnum Hill 1942

Plate 93, fig. 1

1942*c* *Xystriphyllum magnum* Hill, p. 147, pl. III, figs. 2*a*, *b*. Attunga, Tamworth, N.S.W.; Emsian or early Eifelian.
1942*d* *Xystriphyllum magnum* Hill; Hill, p. 183, pl. VI, fig. 3. Wellington, N.S.W.; Emsian?

Holotype. SU 7270. Type locality: pors. 88/115, ph. Burdekin, behind Sulcor Quarry, Attunga, N.S.W. Sulcor Limestone.

Diagnosis. *Xystriphyllum* with large corallites, up to 28 mm. in diameter, and about 22 long septa of each order. (After Hill 1942*c*, p. 147.)

Remarks. No further specimens have been found. The only comment that may be added to the description of Hill (1942*c*) is that the corallites in the type sections are up to 28 mm. across, although Hill gives the maximum as 20 mm. The Garra specimen has a maximum diameter of 20 mm.

Genus AUSTRALOPHYLLUM Stumm 1949

?1888 *Endophyllum*; Foerste, p. 131.
?1889 *Lonsdaleia*?; Etheridge fil., p. 22.
1899 *Spongophyllum*; Etheridge fil., p. 158.
1911 *Spongophyllum*; Etheridge fil., pp. 7–8 (*partim*).
?1925 *Spongophyllum*; Chapman, pp. 112–15 (*partim*?).
1932 *Spongophyllum*; Jones, p. 50 ff. (*partim*).
1939*b* *Spongophyllum*; Hill, pp. 60–61.
?1940*a* *Spongophyllum*; Hill, p. 408 (*partim*?).
1940 *Spongophylloides*?; Hill and Jones, p. 181.
1942*c* *Spongophyllum*; Hill, p. 161 (*partim*).
1949 *Australophyllum* Stumm, p. 34.
1956 *Australophyllum*; Hill, p. F306, in Moore.
?1960 *Xystriphyllum*; Crickmay, p. 11.
1961 *Australophyllum*; Lenz, p. 509.
?1961 *Xystriphyllum*; Fontaine, p. 158.
1962 *Spongophyllum*; Birenheide, p. 69 (*partim*).
1962 *Neomphyma*; Soshkina and Dobrolyubova, p. 335, in Orlov (*partim*).
?1962 *Australophyllum*; McLaren, p. 8, in McLaren, Norris, and McGregor.
non 1964 *Australophyllum*; McLaren, p. 13, in McLaren and Norris.

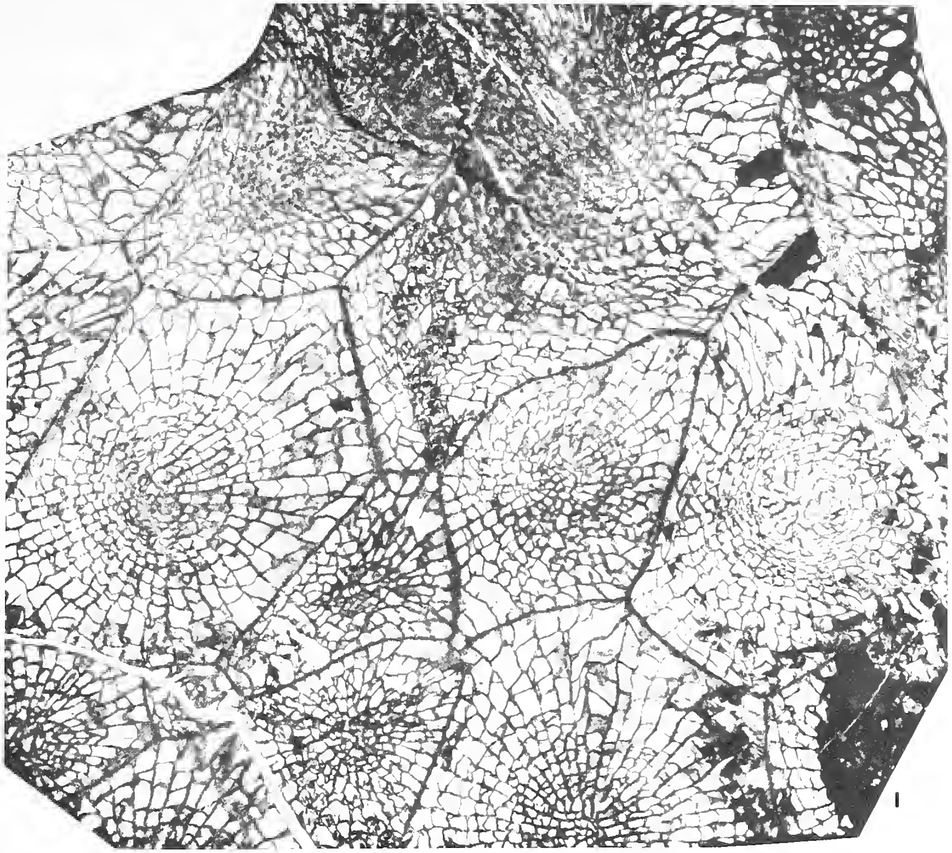
Type species. *Spongophyllum cyathophylloides* Etheridge fil. 1911, p. 7, pl. A, fig. 3, pl. C, figs. 1, 2. Subsequent designation Stumm 1949, p. 34.

Diagnosis. Cerioid, with septa as in *Acanthophyllum*; tabulae close, concave with axial depression; dissepimentarium wide, with well-developed lonsdaleoid dissepiments; inclination of dissepiments increasing axially, becoming steep at margin of tabularium.

EXPLANATION OF PLATE 93

Fig. 1. *Xystriphyllum magnum* Hill 1942. Oblique transverse section, SU 5292, loc. MM–10, figured Hill 1942*d*; ×3. Photograph supplied by Dr. T. B. H. Jenkins, University of Sydney.

Fig. 2. *Australophyllum*? *spongophylloides* (Foerste 1888). 2*a*, transverse section showing similarity to typical *Spongophyllum*, 2*b*, longitudinal section showing acanthophylloid tabulae as in *Australophyllum*; UCT F 1621, Hume Limestone, Yass, N.S.W.; ×2.



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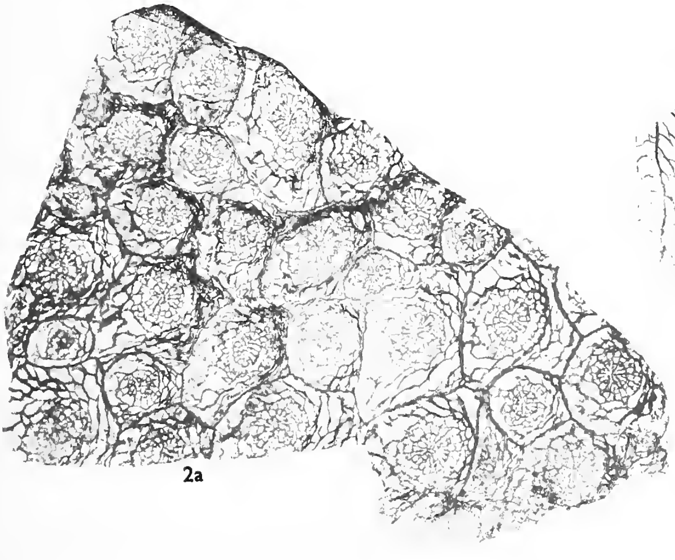
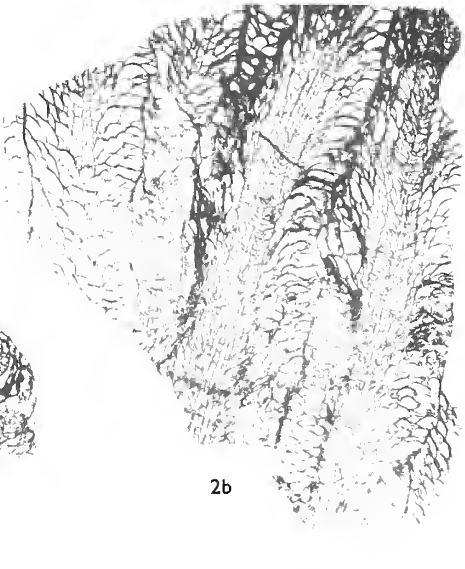


2a



2b

STRUSZ, Devonian Spongophyllidae from New South Wales

Discussion. Stumm (1949) considered the type species to be related to *Hexagonaria*, differing from 'typical *Spongophyllum*' in its wide dissepimentarium and carinate septa. This interpretation is wrong on two counts: firstly, Stumm apparently based his concept of *Spongophyllum* principally on the American species, which have very narrow dissepimentaria. These Birenheide (1962, p. 81) has since referred to the new genus *Smithiphyllum*, which Pedder (1964, p. 436) suggests may be an Endophyllid. *Australophyllum* is in fact quite close to true *Spongophyllum*, probably being derived from it. Secondly, Stumm's interpretation of the type species is inadequate. '*S.*' *cyathophylloides* does not have septal carinae, such as occur in the Disphyllidae, but the flanges and axial septal processes of the Spongophyllidae; moreover, the structure of both dissepimentarium and tabularium, and the septal microstructure, differ from those of *Hexagonaria*.

Birenheide (1962, pp. 50, 69, 72) places *Australophyllum* in synonymy with *Spongophyllum* on the grounds that septal processes (the character stressed by Stumm) occur also in true *Spongophyllum*. However, after examining the holotype and topotypes of *A. cyathophylloides*, I consider that there are sufficient differences to warrant retention of the genus. The dissepimentarium is better developed than in *S. sedgwicki* and other European *Spongophyllum*. More significantly, the tabulae are of the ptenophylloid type —concave, often incomplete, with a median depression—rather than the more regular spongophylloid type, with no median depression. As pointed out by Hill (1939*b*, p. 62), the resemblance of the septal arrangement and tabulae to those of *Xystriphyllum* is striking, the only significant difference being in the far greater development of lonsdaleoid dissepiments.

I would refer the following Australian species to *Australophyllum*: *Spongophyllum cyathophylloides* Etheridge fil. 1911—type, Clermont, N. Qld., Eifelian?; *S. giganteum* Etheridge fil. 1899 (Hill 1942*c*, p. 161), Tamworth, N.S.W., Givetian; *Spongophylloides*? *thomasae* Hill and Jones 1940, Cudal, N.S.W., Emsian? (see below).

In addition, I feel that the Silurian species *Spongophyllum spongophylloides* (Foerste 1888) from Yass (see Hill 1940*a*) is sufficiently close to the Devonian species of *Australophyllum* to be considered a probable ancestral, or near-ancestral, species. I here assign it tentatively to *Australophyllum* (see Pl. 93, figs. 2*a*, *b*).

Xystriphyllum hyperbolicum Crickmay 1960, placed in *Australophyllum* by McLaren (in McLaren, Norris, and McGregor 1962), differs in having the flat tabulae of *Spongophyllum*, although the septa and dissepimentarium are similar to those of *Australophyllum*. Its affinities are uncertain. Probably allied to it is *Australophyllum*? cf. *A.*? *thomasae* of McLaren (p. 13, in McLaren and Norris 1964), which differs from true *Australophyllum* in having axially domed, peripherally depressed tabulae. The close similarity of this form to the Australian species is superficial. The only remaining North American record is that of Lenz (1961); I cannot be sure from his figures of the generic affinities of this form.

Xystriphyllum laosense Fontaine 1961 is almost certainly *Australophyllum*, characterized by considerable variation in the development of lonsdaleoid dissepiments; however, these do not apparently become as rare as in *X. dunstani*.

Range. Wenlockian?, Emsian to Givetian of Australia; Eifelian? of Laos; Eifelian of Canada?

Australophyllum thomasae (Hill and Jones 1940)

Plate 94, figs. 1*a*, *b*; text-fig. 18

1940 *Spongophylloides*(?) *thomasae* Hill and Jones, p. 181, pl. IV, figs. 1*a*, *b*. Cudal, N.S.W., Emsian?

non 1964 *Australophyllum*? cf. *A.*? *thomasae* (Hill and Jones); McLaren, p. 13, pl. IV, figs. 3*a–c*, in McLaren and Norris. Horn Plateau, Canada, Givetian.

Holotype. SU 6188 (= NS 1296) (Pl. 94, figs. 1 *a*, *b*). Type locality: pors. 2, 3, ph. Cudal, west of Orange, N.S.W. (probably my loc. Cu–2). Garra Formation, Emsian?

Diagnosis. Large *Australophyllum* with large lonsdaleoid dissepiments in several series; tabulae deeply funnel-shaped; septa rarely developed in zone of lonsdaleoid dissepiments; intercorallite walls lack septal bases.

Description. See Hill and Jones 1940, p. 181.

Remarks. The peripheral septal crests described by Hill and Jones are confined to a narrow zone at the outer ends of the septa, and almost exclusively represent minor septa, resting on an innermost series of 'secondary' lonsdaleoid dissepiments (see Birenheide 1962, pp. 46–48). In a wide zone outside this, large geniculate lonsdaleoid dissepiments are developed, and in this zone there are no septal crests; a very few major septa extend across the zone to reach the epitheca.

The one offset visible in the transverse section of the holotype resembles in every way the peripheral calical buds described herein (pp. 71–72) for *Xystriphyllum dunstani*.

Known localities. Cu–2 (or nearby); Ct–14? (one poor specimen).

Australophyllum? sp. cf. *thomasae* (Hill and Jones 1940)

Plate 94, figs. 2–5, Plate 95, figs. 1–3; text-fig. 18

Material. 28 specimens (12 sectioned) from loc. Ct–18; one each from locs. Ct–28, CAT/2193.

Description. The corallum form is a little uncertain. The specimens are from a pink crinoidal calcarenite at the base of a bioherm; their appearance in the outcrop suggests that they grew unattached in the sand. Many of the corallites appeared to be solitary, conical, with sharp rejuvenescence. Others had flaring distal ends, giving rise to several buds which then became a small cerioid corallum. Most of the material collected from the massive limestone is fragmentary, and the few sections of colonial coralla do not conclusively show whether they are truly cerioid, closely phaceloid, or even at times astraeoid. In several cases critical parts of the sections show solution phenomena or broken skeletal tissues. The calice is broadly bell-shaped to slightly everted, with a wide,

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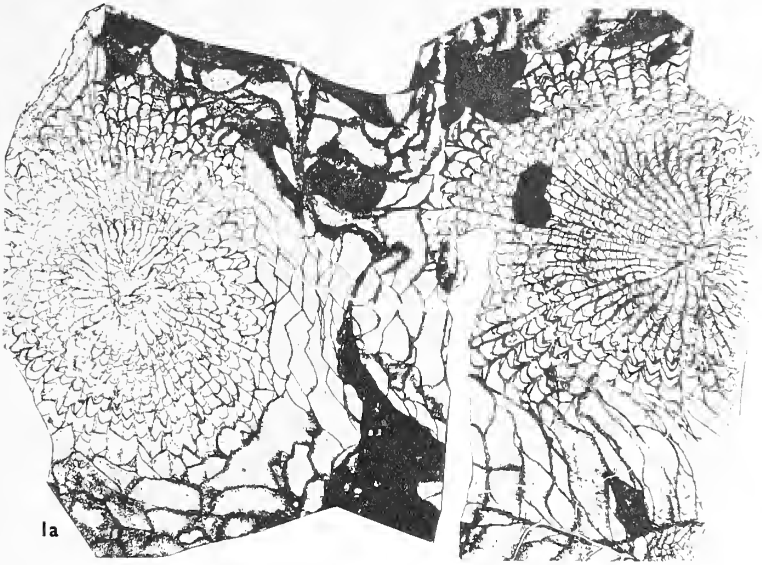
EXPLANATION OF PLATE 94

All figures ×2.

Fig. 1. *Australophyllum thomasae* (Hill and Jones 1940). 1*a*, transverse section (note peripheral bud, lower right), 1*b*, longitudinal section, holotype SU 6188, loc. Cu–2. Photographs by courtesy of Prof. D. Hill.

Figs. 2–5. *Australophyllum*? sp. cf. *thomasae*. 2, transverse section of two corallites showing cerioid? habit; SU 18114, loc. Ct–18. 3, transverse section showing strongly dilated septa; SU 14155, Ct–18. 4, longitudinal section, SU 14149, loc. Ct–18. 5, transverse section of three corallites showing phacelo-cerioid habit; SU 20125, loc. Ct–18.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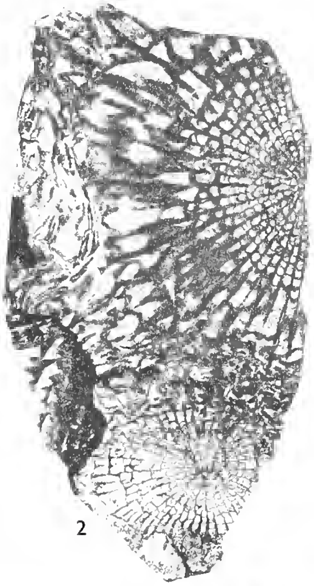
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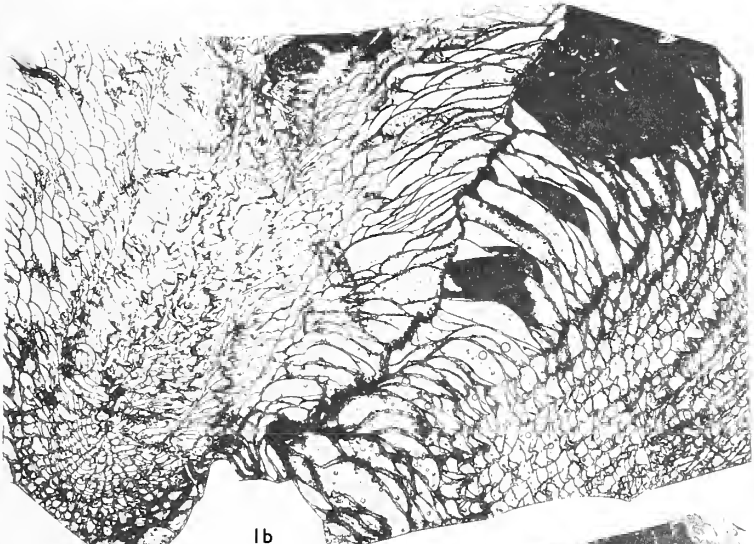
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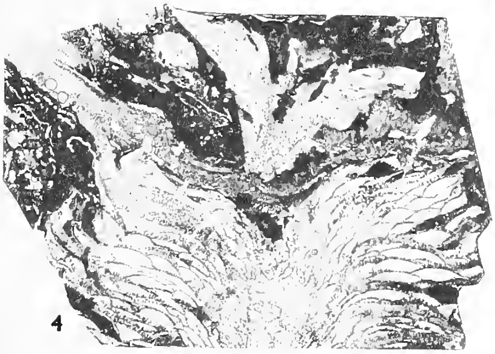
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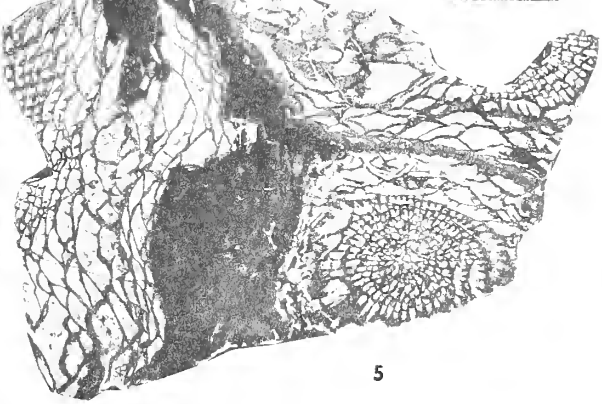
5

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flaring, sharp-edged rim, and a narrow inversely conical to funnel-shaped axial pit. Diameters up to 46 mm. have been measured, adults apparently varying from about 16 mm. to 46 mm. (or more?).

There are generally 62–72 septa. The major septa extend well into the tabularium, where they are bilaterally or quadrilaterally arranged about two opposite septa which may meet or pass each other at the axis. There may or may not be a slight axial vortex. The minor septa vary greatly in length. Most do not reach the inner margin of the dissepimentarium, but an occasional one extends well into the tabularium. In the tabularium the septa are thin and may be strongly waved. The degree of dilatation in the dissepimentarium is highly variable. In some the septa remain only slightly dilated throughout. Most corallites have strongly dilated septa, which in some cases are in contact over much of the dissepimentarium. The dilatation may increase continuously outwards or may take the form of a series of wedges on succesive dissepiments. There is a peripheral stereozone up to 1 mm. wide formed by wedge-wise dilatation of the septal bases.

The septa are generally highly discontinuous, the minor more than the major; the degree of discontinuity increases outwards, and there may be a narrow peripheral zone of lonsdaleoid dissepiments. The major septa are generally continuous near the tabularium, and always within it, as are those few elongate minor septa. In extreme cases the septa consist of short wedge-shaped crests on successive series of dissepiments. In the tabularium the septa are zigzag flanged, frequently strongly; in those corallites where the septa are relatively continuous and thin, these flanges may extend out into the dissepimentarium.

The septa consist of monacanthine trabeculae about 0·1 mm. thick. In longitudinal sections these are seen to be arranged as in *Acanthophyllum*: half-fans in the dissepimentarium, again becoming nearly vertical in the tabularium. In thin parts of the septa they are in one series, but in dilated parts all regularity of arrangement is lost. In these parts the septa consist of numerous trabeculae set in lamellar sclerenchyme, the lamellae being parallel to the attitudes of the dissepiments. The dilatation, both trabecular and lamellar, may spread laterally as thin coatings on the dissepiments.

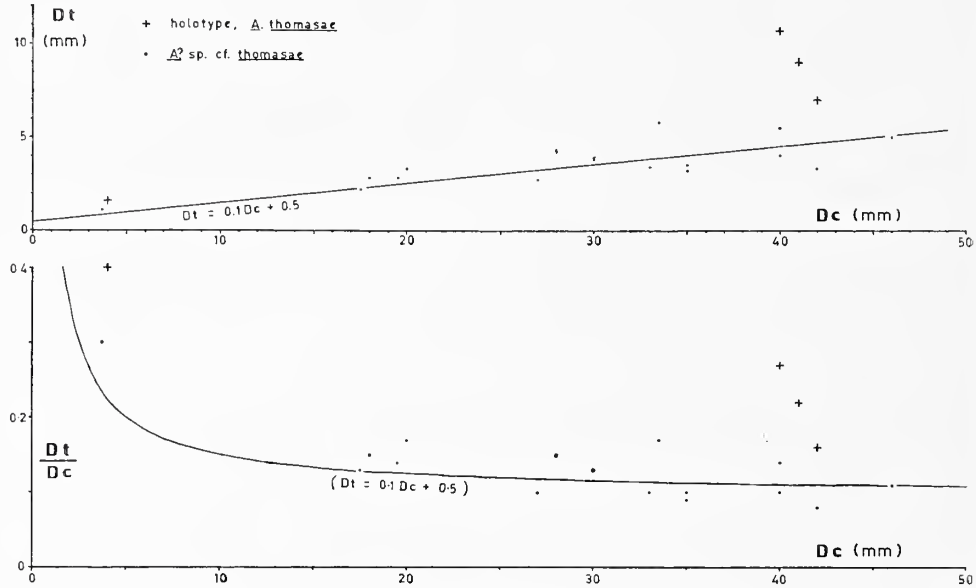
Dt is a little over 0·1 Dc, decreasing gradually with age. The tabular floors are moderately to strongly funnel-shaped, generally with upturned margins. The tabulae are mostly incomplete; they are crowded, irregularly sagging to slightly convex, and much broken up by the often wavy ends of the major septa.

The wide dissepimentarium consists of large elongate dissepiments. Peripherally, these are slightly to strongly axially inclined and usually only slightly convex. Over the outer half of the dissepimentarium they may be horizontal, even slightly peripherally inclined, or more usually gently inclined axially; in this region they are generally moderately convex. Towards the axis the dissepiments become increasingly steeply axially inclined, and increasingly smaller, until at the inner margin of the dissepimentarium they are vertical, and again fairly elongate.

Budding is apparently peripheral, calicinal.

Variation. Plots of Dt:Dc and Dt/Dc:Dc show only slight scatter, and suggest that approximately $Dt = 0{\cdot}1Dc + 0{\cdot}5$. However, the data are insufficient for accuracy and certainty. There are insufficient data for n:Dc to be of any use.

Comparison. In size and number of septa individual corallites of this form are very close to those of *A. thomasae*. However, the latter has a wider tabularium (see text-fig. 18). Other points of difference from the holotype of that species are several: the strongly differentiated wide zone of lonsdaleoid dissepiments is lacking; the septa are far more discontinuous, and the septal crests extend well outside the ends of the continuous portions, if, indeed, the septa do not consist entirely of crests in the dissepimentarium; in dilated portions, the septa consist of numerous trabeculae embedded in sclerenchyme, and not arranged in a single series; finally, the peripheral stereozone consists of wedge-shaped septal bases (that of *A. thomasae* is of undifferentiated fibrous calcite). It is likely that this form is a distinct species, but this cannot be ascertained with certainty until (*a*) topotypic material is available of *A. thomasae*, and (*b*) the corallum form is established.



TEXT-FIG. 18. *Australophyllum thomasae*, *A*? sp. cf. *thomasae*. Scatter diagrams for Dt:Dc and Dt/Dc:Dc, with estimated approximate mean curve Dt = 0·1Dc+0·5 for *A*? sp. cf. *thomasae*.

Known localities. Ct–18 (= Bt/352), Ct–28?; CAT/2193. All the same horizon, a crinoidal biostrome.

EXPLANATION OF PLATE 95

All figures ×2.

Figs. 1–3. *Australophyllum*? sp. cf. *thomasae* (Hill and Jones 1940). 1, longitudinal sections of several corallites, possibly forming a loosely dendroid corallum (note small peripheral calical bud at *b*); SU 20126, loc. Ct–18. 2, transverse section, SU 14162, loc. Ct–18. 3, transverse section of solitary corallite showing wall structure; SU 14159, loc. Ct–18.

Fig. 4. *Australophyllum bilaterale* sp. nov. Transverse section, holotype SU 15158, loc. E–1.

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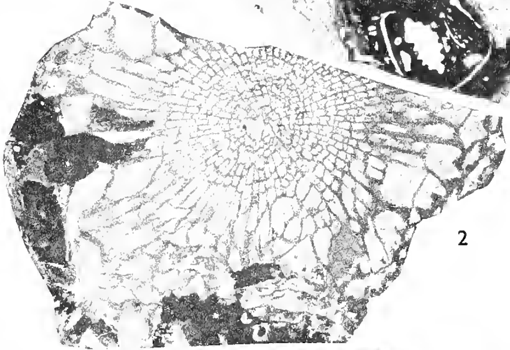
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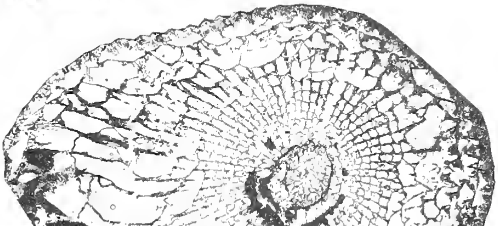
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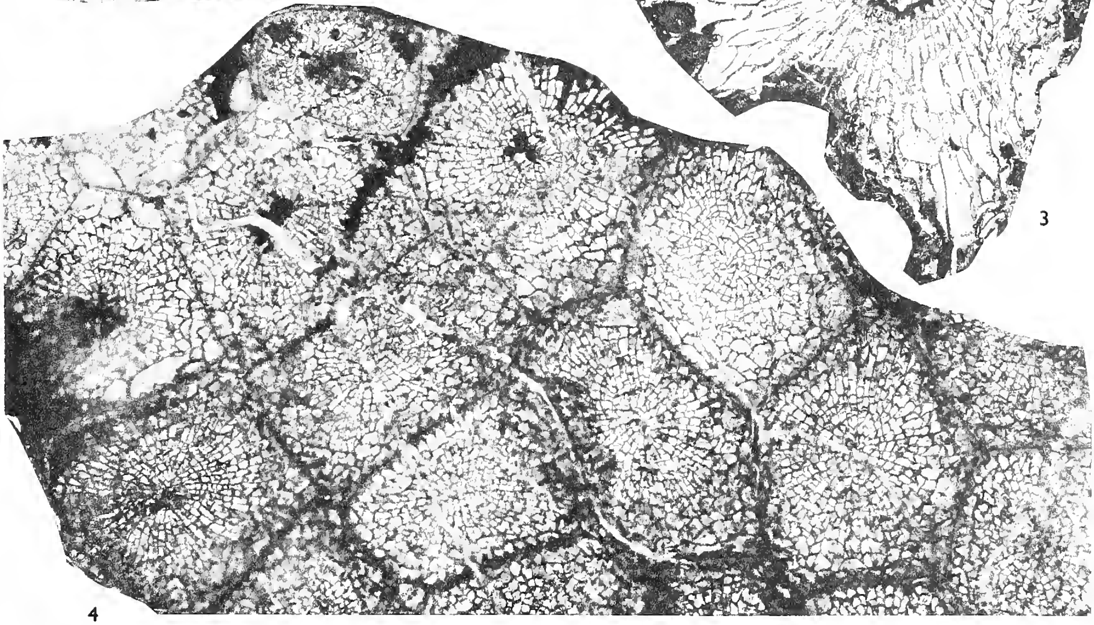
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STRUSZ, Devonian Spongophyllidae from New South Wales

Australophyllum bilaterale sp. nov.

Plate 95, fig. 4; Plate 96, fig. 1; text-figs. 19, 20

Derivation of name. Latin *bis* = twofold + *lateralis* = lateral; refers to the marked bilateral septal arrangement.

Holotype. SU 15158 (Pl. 95, fig. 4; Pl. 96, figs. 1*a*, *b*). Type locality: E–1.

Diagnosis. Large *Australophyllum* with septa typically arranged in four subequal quadrants, having bilateral symmetry; minor septa reduced to septal crests; occasional very large dissepiments appear in a wide lonsdaleoid dissepimentarium.

Description. The corallum is cerioid and large—the holotype was measured in the field as about 50 × 25 cm., and 25 cm. high. The prismatic corallites are not greatly divergent. The epitheca bears narrow septal grooves, and in longitudinal section is seen to be finely wrinkled. The calice is deeply inversely conical, with a slightly rounded rim and a concave base.

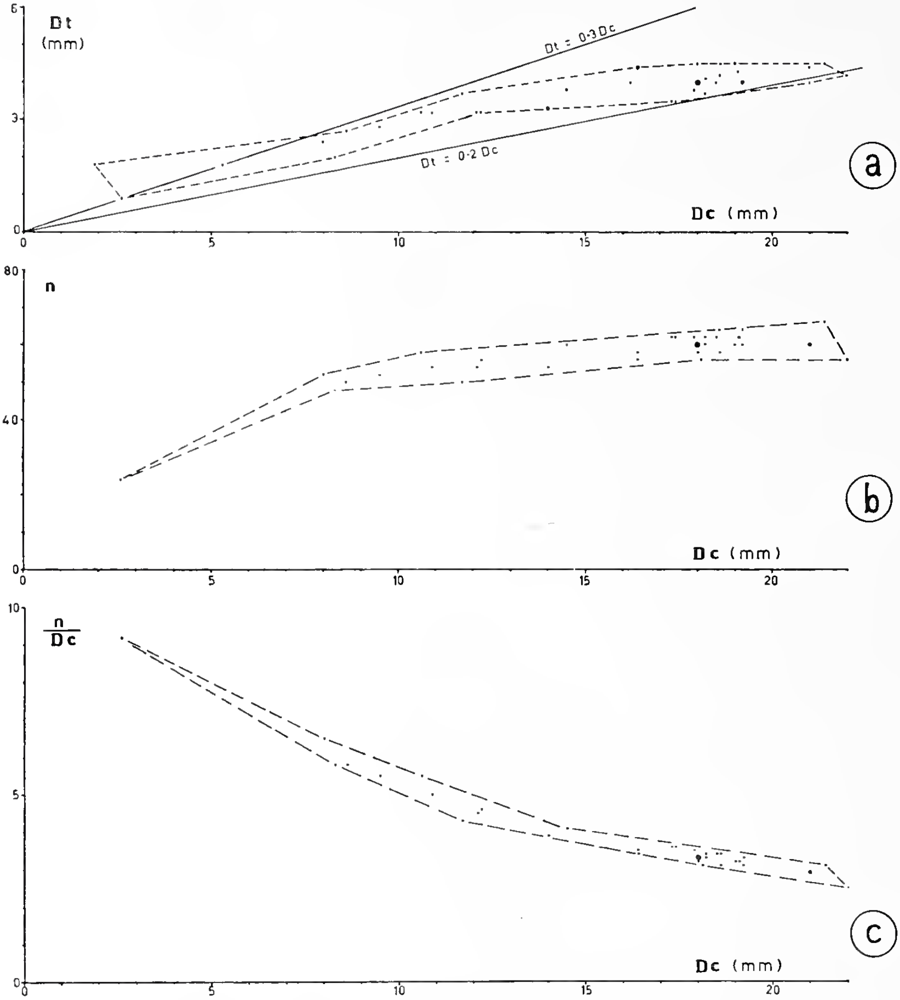
Adult corallites are generally 16–20 mm. in diameter, the maximum known being 22 mm.; they are bounded by thick, straight, or slightly curved walls. The thin epitheca is lined by a stereozone formed by strong wedge-shaped bases; these are generally opposite, giving the wall a strongly beaded appearance in transverse section. There are usually between 50 and 64 septa; these are attenuate inside the peripheral stereozone, often strongly waved or zigzag, but are unflanged. The major septa are long, continuous in the tabularium and inner dissepimentarium, but usually discontinuous peripherally. The longest four septa divide the septal apparatus into four subequal quadrants, arranged on either side of the plane containing two of the four septa (C and K?), which reach, and may combine at, the axis. The other major septa are of variable lengths, the shortest being midway between the longest; the shortest are about $\frac{3}{4}$ R. The minor septa are more variable in length, generally being about $\frac{1}{3}$–$\frac{1}{2}$ R. They are generally discontinuous, particularly towards the periphery, where the individual septal segments commonly only reach half-way to the succeeding dissepiment.

The septa are constructed of very fine trabeculae directed inwards and upwards from the periphery at a fairly constant angle.

The tabularium is relatively narrow, Dt = 0·2 to 0·3 Dc. The tabular floors are moderately concave, with upturned margins and an axial deepening. The thin tabulae are crowded, complete and incomplete, gently concave to slightly convex.

There are up to four series of peripheral lonsdaleoid dissepiments, although generally only the outermost of these interrupts the major septa. There are occasional very large lonsdaleoid dissepiments which interrupt several major septa. Inside the zone of lonsdaleoid dissepiments are several series of rather more elongate normal dissepiments, whose inclination is steep, increasing to nearly vertical at the margin of the tabularium.

Budding is probably peripheral, but has not been seen in longitudinal section. In transverse section the evidence is inconclusive (see text-fig. 20). In three sections there are small trigonal buds at the intersection of three large corallites; these are about 2 mm. in diameter, with a single series of lonsdaleoid dissepiments and a few very short septal segments on these. They lack a peripheral septal stereozone or prominent septal bases: the epitheca is lined with fibrous sclerenchyme about 0·02 mm. thick. In two other sections even smaller lenticular buds have been seen along the wall between two corallites. These also lack a septal stereozone, and only one has any trace of internal structure: one dissepiment?, and possibly very tiny peripheral septal traces. The evidence suggests peripheral budding, with the corallite rapidly becoming prismatic, but does not prove it.



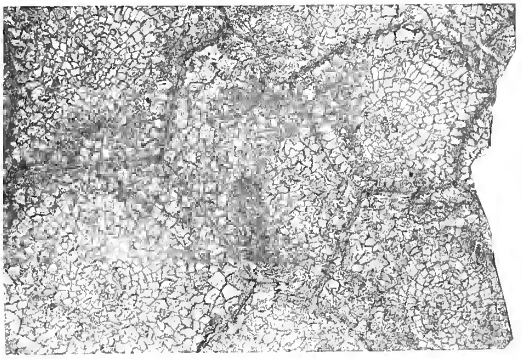
TEXT-FIG. 19. *Australophyllum bilaterale* sp. nov. Scatter diagrams and limiting polygons for (*a*) Dt:Dc —reference lines Dt = 0·3Dc, Dt = 0·2Dc, added—(*b*) n:Dc, and (*c*) n/Dc:Dc.

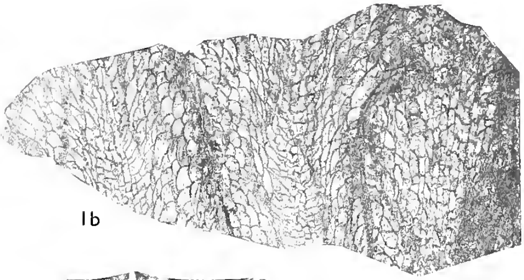
EXPLANATION OF PLATE 96

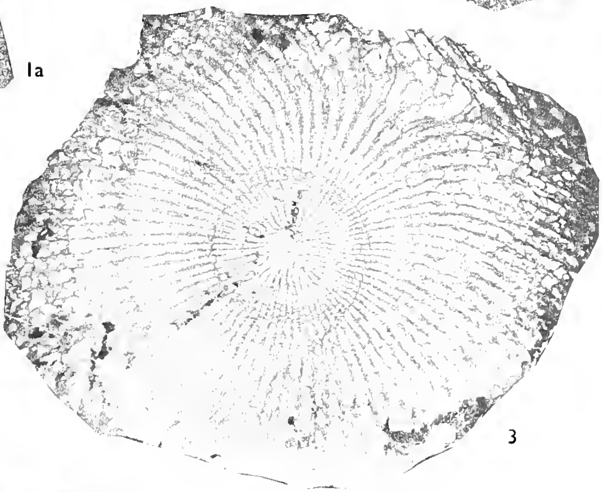
All figures ×2.

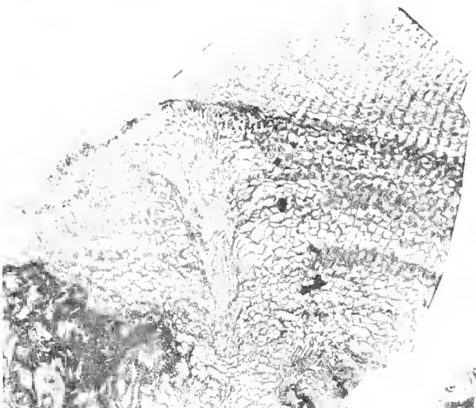
Fig. 1. *Australophyllum bilaterale* sp. nov. 1*a*, *b*, transverse and longitudinal sections, holotype SU 15158, loc. E–1.

Figs. 2–4. *Taimyrophyllum expansum* (Hill 1942). 2, longitudinal section, SU 14103, loc. Cr–111. 3, transverse section of a specimen with large Ts; holotype, SU 7290, loc. Cr–113. 4*a*, *b*, transverse and longitudinal sections of a specimen with small Ts; SU 14102, loc. Cr–111.


1a


1b


3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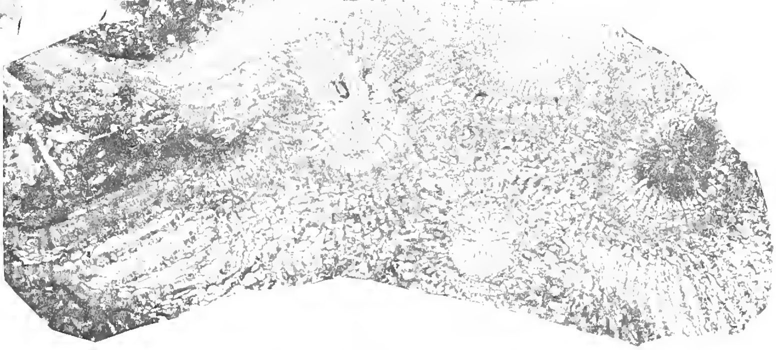
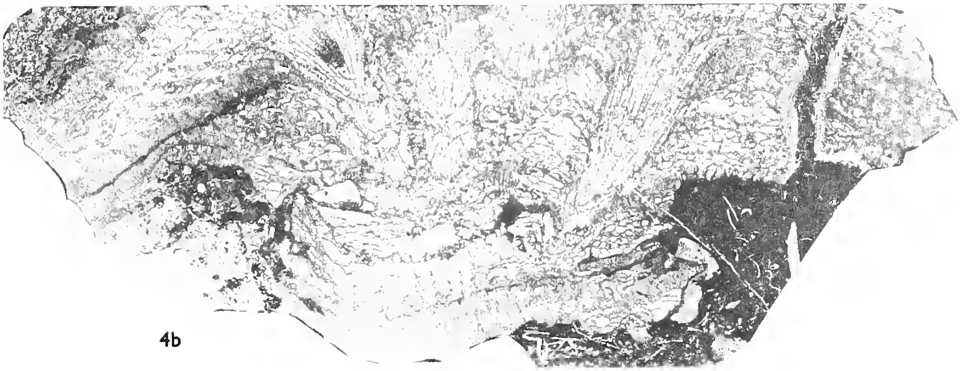
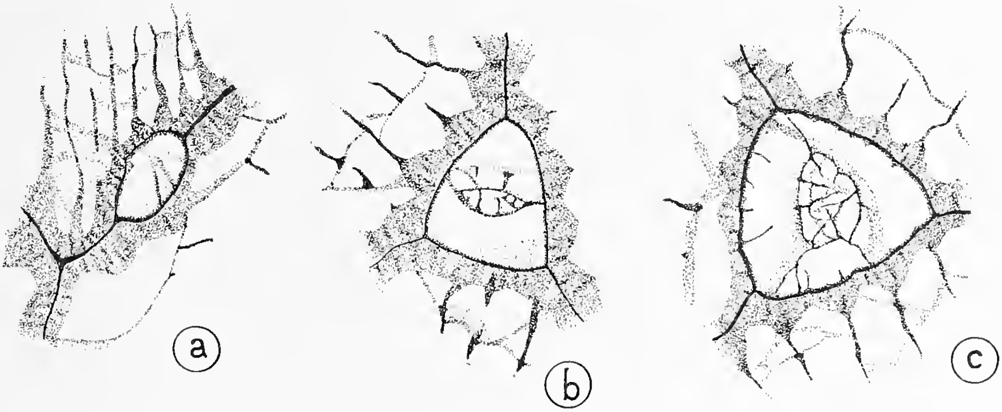

4a


4b

STRUSZ, Devonian Spongophyllidae from New South Wales

Variation. Only the holotype was well enough preserved for measurement. Reasonable plots were obtained for this for Dt:Dc, n:Dc, and n/Dc:Dc. (text-fig. 19). The first shows a slight change in slope at Dc = *circa* 12–13 mm. Dt changes gradually from about 0·3Dc in juveniles to about 0·2Dc for adults.

In the plots involving n, the change at Dc = 12 mm. cannot be seen; in n:Dc there is, however, apparently a change at about Dc = 8–9 mm. This does not show up very strongly on the plot n/Dc:Dc, which shows a gradual change in the ratio with increasing Dc.



TEXT-FIG. 20. *Australophyllum bilaterale* sp. nov. Transverse sections of holotype SU 15158, ×10, showing stages in ontogeny. (*a*) Dc = 1·4 mm., n = 4?; the smallest bud seen, forming between two adults, so suggesting it may be peripheral calical rather than intermural. (*b*) Dc = 2·0 mm., n = 6; a 'corner' bud; note the lack of septal bases peripherally. (*c*) Dc = 2·6 mm., n = 22 or 24?; in this bud, the minor septa are apparently just being introduced as very low ridges on the corallite walls.

Comparison. A. bilaterale is intermediate in size between *A. cyathophylloides* (the type species), and *A. giganteum* and *A. thomasae. A? spongophylloides*, from the Silurian of Yass, is almost as large, but has far fewer septa, and a very wide lonsdaleoid dissepimentarium. *A. bilaterale* is distinguished from all of these by the marked bilateral symmetry of its septal arrangement.

Known localities. Ct–17 (1 corallum), E–1 (1 corallum).

Genus TAIMYROPHYLLUM Chernyshev 1941

1941	*Taimyrophyllum* Chernyshev, pp. 12, 53.
1942*c*	*Eddastraea* Hill, p. 147.
1942*d*	*Eddastraea* Hill; Hill, p. 184.
1956	*Eddastraea* Hill; Hill, p. F306, in Moore.
1958	*Taimyrophyllum* Chernyshev; Bulvanker, p. 154.
1964	*Taimyrophyllum* Chernyshev 1941; Pedder, p. 436.

Type species. Taimyrophyllum speciosum Chernyshev 1941, pp. 12, 53, text-fig. 1, pl. 1, figs. 1–3, pl. 2, figs. 1–3, pl. 5, fig. 5; Tarei R., Taimyr, U.S.S.R.; Lower Devonian.

Diagnosis. See Pedder 1964, p. 436.

Remarks. The holotype has been refigured by Pedder (1964, pls. 63, 64).

Taimyrophyllum expansum (Hill 1942)

Plate 96, figs. 2–4

1942*d* *Eddastraea expansa* Hill, p. 184, pl. VI, figs. 5*a*, *b*.

Holotype. SU 7290 (Pl. 96, fig. 3). Type locality: Cr–113.

Diagnosis. *Taimyrophyllum* with few, rather large corallites, with very wide dissepimentaria, and with dilated septa. (Modified after Hill 1942.)

Description. From an examination of the holotype, and additional material, the following may be added to Hill's description:

(1) Dt is generally about 3–4 mm., reaching 6 mm. only in the holotype. Similarly, n is generally less than the 72 given by Hill; in SU 14102 it is 50–56.

(2) The tabulae are slightly to moderately sagging with upturned margins, and have a very shallow median depression.

(3) The outer parts of the septa are frequently modified by lateral dissepiments.

(4) The amount of septal dilatation is quite variable, from slight to very great.

(5) Dc cannot generally be accurately measured. In the additional material, Ts is highly variable, being generally 10–15 mm.

Comparison. All other species except *T. carinatum* Bulvanker 1958 have attenuate or only weakly dilated septa. That species differs from *T. expansum* in being markedly aphroid (see Bulvanker 1958, p. 155, pls. 76, 77). In other respects the two species are quite similar.

Known localities. Cr–100, Cr–111, Cr–113.

FOSSIL LOCALITIES

Localities are listed in the same way as in Strusz (1965*b*); those already listed there do not appear here. A full list of localities, together with detailed maps, may be found in Strusz (1963).

Parish of Bell, County of Ashburnam

Be–7: portion 175 (north end); grid reference 177.911 (Bathurst); Mandagery Ck., 150 yds. south-south-west of road crossing ('Crystal Springs'). Fossiliferous calcirudite.

Parish of Brymedura, Co. Ashburnam

Br–3: portion 73 (south); grid ref. 173.907 (Bathurst); in gully just west of road, and 50 yds. north of road junction. Calcarenite.

Br–10: junction, portion 81, 104, 105; grid ref. 174.899 (Bathurst); in road. Interbedded calcilutite and calcareous siltstone ('rubbly limestone').

Parish of Cardington, Co. Gordon

Ca–1: portion 106 (extreme north-east corner, near portion 136); grid ref. 179.935 (Dubbo); north-east of road. Thinly bedded fine calcarenite.

Parish of Curra, Co. Gordon

Cr–1: portion 103 (southeast); grid ref. 188.968 (Dubbo); about 120 yds. west of road, and about 50 yds. north of portion 97. Pellet—oölite calcarenite.

Cr–2: portion 150 (south-west corner); grid ref. 188.970 (Dubbo); near small abandoned quarry west of road. Pellet—oölite calcarenite.

Cr–5: portion 171 (centre, north-east side); grid ref. 184.968 (Dubbo); in Curra Ck. Thickly bedded calcarenite.

Cr–55: portion 172 (south-west); grid ref. 183.967 (Dubbo); south side of Wellington–Arthurville road, between Curra Ck. road junction and Fingerpost, 218 yds. north-east of junction of pors. 166, 167, 172, 173. 3-ft. band of rubbly calcarenite.

Cr–77: portion 99 (south-east); grid ref. 188.970 (Dubbo); 45 yds. west of portion 142, 120 yds. north of portion 100. Calcarenite.

Cr–86: portion 44 (south); grid ref. 187.966 (Dubbo); 65 yds. west of portion 48, 110 yds. north of southern boundary, portions 44, 84. Pelletal calcilutite.

Cr–89: portion 39; grid ref. 187.964 (Dubbo); 130 yds. south of portion 111, 250 yds. south-west of junction, portions 111, 39, and the Bell River. Biostromal limestone (about 20 ft. thick). Same horizon as Cr–94, –100, –111, –113.

Cr–103: portion 8; grid ref. 186.962 (Dubbo); 90 yds. north of portion 9, and 75 yds. west of road. Black, foetid fossiliferous pellet calcarenite.

Parish of Catombal, Co. Gordon

Ct–6: boundary of portions 75, 124; grid ref. 176.946 (Dubbo); 110 yds. east of junction, portions 38, 75, and 124. Ill-bedded fossiliferous calcirudite, possibly reef talus.

Ct–11: portion 40 (north-west); grid ref. 176.944 (Dubbo); in tributary of Back Ck., 210 yds. along creek east from portion 45 (= Bt/1838, measured section 'Bt', which see). Biohermal limestone.

Ct–13: portion 40 (north); grid ref. 176.944 (Dubbo); in creek, 400 yds. east of portion 45, and 140 yds. south of portion 124. Grey biohermal limestone with large coral colonies.

Ct–14: portion 40 (north); grid ref. *circa* 176.944 (Dubbo); large area of limestone around head of creek, about 500 to 600 yds. east of portion 45, and extending 180 yds. south from portion 124. Grey biohermal limestone.

Ct–15: portion 40 (north-west); grid ref. 176.944 (Dubbo); in gully, 90 to 100 yds. east of portion 45. Biohermal limestone.

Ct–16: portion 40 (north-west); grid ref. 176.944 (Dubbo); in gully, about 15 yds. east of portion 45. Pink biohermal limestone, with numerous *Favosites*, thamnoporids.

Ct–17: portion 45 (north); grid ref. 176.944 (Dubbo); in gully, 150 yds. west of portion 40. Bryozoan limestone (biohermal?).

Ct–22: portion 40 (east centre); grid ref. 176.944 (Dubbo); in gully, 160 yds. west of portion 57, and 520 yds. south of portion 124. Crinoidal biohermal limestone.

Ct–29: portion 40 (south-east corner); grid ref. 176.943 (Dubbo); near junction, portions 40, 41, and 57, and extending into portion 57 just north of that junction. Biohermal limestone.

Ct–36: portion 125 (south-east); grid ref. 176.941 (Dubbo); along north verge of road, extending 160 yds. north-west from portion 128. Thinly bedded fossiliferous calcarenite and lesser siltstone.

Ct–44: portion 113 (south-west corner); grid ref. 176.942 (Dubbo); in tributary of Sawpit Gully, 120 yds. east of portion 125, and 130 yds. north of portion 48. Olive-green calcareous siltstone.

Ct–45: portion 113; grid ref. 177.942 (Dubbo); in gully (as Ct–44), 200 yds. east of portion 125, and 150 yds. north of portion 48. Slightly fossiliferous olive-green calcareous siltstone.

Ct–50: portion 46 (north); grid ref. 176.941 (Dubbo); in gully 90 yds. west of junction of portions 31, 46, and 48, and 65 yds. east of portion 128. 'Rubbly limestone.'

Ct–55: portion 58 (north centre); grid ref. 177.939 (Dubbo); south bank of Loombah Ck., 90 yds. north of road, and 500 yds. west of junction of creek with portions 31, 58, and 77. Coarsely bedded calcarenite and minor calcirudite.

Parish of Cudal, Co. Ashburnam

Cu–2: portion 2; grid ref. *circa* 172.888 (Bathurst); large area of outcrop, just extending into portion 61, and between 370 and 700 yds. west of westernmost bend in Boree Ck. Calcarenite, calcilutite, and biostromal limestone.

Parish of Eurimbula, Co. Gordon

E–1: portion 127 (east); grid ref. 178.934 (Dubbo); in gully just west of road culvert, 500 yds. south of junction with road of portions 1, 24, and 127. 'Rubbly limestone.'

E–5: east junction, portions 98 and 160; grid ref. 178.932 (Dubbo); in gully about 170 yds. due west of road. Biostromal limestone (*circa* 10 ft.) over 'rubbly limestone.'

E–18: portion 67 (south-east); grid ref. *circa* 176.923 (Dubbo); north bank of gully, 100 to 180 yds. west of portion 52, and 200 yds. north of road. 'Rubbly limestone.'

E–24: portion 43 (east); grid ref. 180.927 (Dubbo); 70 to 150 yds. west of portion 151, and 430 yds. north of portion 63. Massive calcarenite, with thin interbedded fossiliferous shales.

E–30: portion 80; grid ref. 180.925 (Dubbo); in Blind Gully, 470 yds. east of portion 161, and 420 yds. north of portion 108. Biohermal limestone.

E–31: portion 80; grid ref. 180.925 (Dubbo); in Blind Gully, 370 yds. east of portion 161, and 400 yds. north of portion 108. Biohermal limestone.

E–37: portion 51 (north); grid ref. 178.923 (Dubbo); 190 yds. east of road, and 35 yds. south of portion 76. Calcirudite.

Parish of Geurie, Co. Lincoln

Ge–2: grid ref. 177.990 (Dubbo); north-east bank of railway cutting between portions 197 and 198, about 300 yds. north-west of Geurie town boundary. Thin beds of fossiliferous calcarenite in unfossiliferous pellet-oölite calcarenite.

Ge–7b: grid ref. 178.991 (Dubbo); south wall of abandoned quarry just north-east of town of Geurie. Calcarenite.

Ge–12: boundary of portions 57, 59; grid ref. *circa* 179.988 (Dubbo); outcrop about 200 yds. across. Calcarenite.

Parish of Gregra, Co. Ashburnam

Gg–2: portion 58 (north-east corner); grid ref. 179.897 (Bathurst); Walker's Ck., just west of road bridge. Thickly bedded calcirudite, with interbedded thin favositid biostromes.

Parish of Gundy, Co. Gordon

Gn–7: portion 131; grid ref. 183.972 (Dubbo); head of gully, 500 yds. north of portions. 130, 132, and 940 yds. east of portion 55. Thickly bedded calcarenite.

Parish of Mickety Mulga, Co. Lincoln

MM–1: grid ref. *circa* 181.987 (Dubbo); south side of Mitchell Highway, between portions 60 and 95, about 800 yds. north-west of turn-off to Combo railway siding (at junction of portions 96 and 208). Pellet calcarenite.

MM–5b: portion 82 (south); grid ref. 182.983 (Dubbo); west of north-easterly road through portion, and north of road to Ponto Falls. Thick layer of fossiliferous calcarenite within unfossiliferous silty calcilutites and calcarenites.

MM–7: portion 78 (south); grid ref. 180.982 (Dubbo); about 50 yds. north of road, and 160 to 170 yds. east of portion 54. Calcarenite.

MM–11: portion 206; grid ref. 181.984 (Dubbo); east side of road, 50 to 200 yds. south of junction, portions 59, 206, and 207; just east of portion 59 (portion 206, near portion 59, of Hill 1942*d*). Calcarenite.

MM–12: portion 247 (north-west corner); grid ref. 180.986 (Dubbo); east of portion 39, and south of road; large outcrop extending about 250 yds. east of portion boundary, and about 500 yds. south of road. Calcarenite.

Parish of Ponto, Co. Gordon

P–1: portion 14 (south-west corner); grid ref. 179.977 (Dubbo); hill to west of Mickety Trig. station, 130 to 550 yds. north of road, and 350 to 600 yds. west of portion 118. Calcirudite.

P–22: portion 142 (east centre); grid ref. 182.976 (Dubbo); 90 to 110 yds. west of eastern portion boundary, and about 750 yds. due north of road; just north of northern boundary, Water Reserve 33680. Fossiliferous calcarenite and biostromal limestone.

P–23: portion 142 (north-west); grid ref. 182.976 (Dubbo); in gully, 360 yds. east of access road to 'Macquarie Park', and 280 yds. south of portion 104. Calcarenite (6 in. beds).

P–25: portion 142; grid ref. 182.976 (Dubbo); just south of gully, 500 yds. due east of access road, and about 460 yds. south of portion 104. Thick biostromal complex.

P–38: portion 104; grid ref. 182.977 (Dubbo); 70 yds. south of gully, about 450 yds. west of access road, 350 yds. south of portion 141, and 420 yds. east of portion 62. Calcarenite.

P–40: portion 103; grid ref. 182.979 (Dubbo); small outcrop 12 feet east of fence (portion 79), at gate near small wheat silos, 'Macquarie Park'; about 330 yds. south of Macquarie River. Partly dolomitized biostromal limestone.

Wellington Caves area: Ph. Wellington, Co. Gordon

WC–4: portion 208 (centre); grid ref. 188.963 (Dubbo); 95 yds. north-east of north-east corner, portion 201, and 280 yds. east of portion 92. Pellet calcarenite, calcilutite.

WC–9: portion 46; grid ref. 189.965 (Dubbo); outcrop south of road to Wellington Caves, at turn-off from Mitchell Highway. Black calcarenite.

Measured section BR^3: portions 9, 10, and 80, ph. Curra; west bank of Bell River, south-west of Wellington Caves. Section started at junction of three portions, and measured west along gully.

BR^3/200: 200 ft. west of starting point. Black foetid pellet calcarenite.

BR^3/214: 214 ft. west of starting point. Thin fossiliferous layer in black foetid pellet calcarenite.

Measured section Bt: portions 40 and 45, ph. Catombal; section measured eastward along tributary of Back Ck., from fence at boundary of portions 38 and 45; grid ref. *circa* 175.944 (Dubbo).

Bt/430: grey, poorly bedded biohermal limestone with numerous dendroid bryozoa and laminar *Favosites*, above pink crinoidal calcarenite; 430 ft. from portion 38.

Bt/936: grey biohermal limestone with common digitate *Favosites*, stromatoporoids, *Fasciphyllum* sp. nov.; 946 ft. from portion 38.

Bt/1838: portion 40; pale grey biohermal limestone with common stromatoporoids, *Fasciphyllum* sp. nov.; 1848 ft. from portion 38; = Ct–11.

Measured section CAT: portion 29, and boundary between portions 41, 43, ph. Catombal; section measured east from grain silos to portion 41 (fence), then south along fence to corner, then east again. The section is about 1 mile south of section Bt.

CAT/2193: grey biostromal limestone with *Favosites*, stromatoporoids, *Teratophyllum* sp. nov.; 1160 ft. along fence from corner. The same horizon as locs. Ct–18, –28.

Measured section St: portion 53, ph. Eurimbula; section started at first outcrop in gully near gate, east of Cumnock–Molong road, and measured eastward; gully is a southern tributary of Spring Ck.

St/181: grey calcarenite 181 ft. from start (i.e. near top of exposed section); near top of a 500-ft. layer.

St/1125: black, foetid pellet calcarenite, with crowded *Favosites*, stromatoporoids, 1,125 ft. from start; 110-ft. bed, separated from that of St/181 by a 50-ft. bed of unfossiliferous calcarenite and calcilutite.

St/1821: top of 150-ft. bed of thinly bedded grey fossiliferous calcarenite; 1,821 ft. from start.

St/2565: 18 in. bed of grey fossiliferous calcarenite in poorly fossiliferous black foetid calcarenite, 2,565 ft. from start, and near end of section.

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THE LATE PRECAMBRIAN FOSSILS FROM EDIACARA, SOUTH AUSTRALIA

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ABSTRACT. New genera and species are described from the richly fossiliferous Late Precambrian strata in which a number of medusoid fossils were discovered by R. C. Sprigg in 1947 and from which various pennatulacean, annelid, and other fossils have been described since. The new genera and their type species are: *Medusinites asteroides* (Sprigg), *Mawsonites spriggi* sp. nov., *Conomedusites lobatus* sp. nov., *Lorenzinites rarus* sp. nov., *Kimberia quadrata* sp. nov., *Rugoconites enigmaticus* sp. nov., *Arborea arborea* (Glaessner), *Ovatoscutum concentricum* sp. nov., *Praecambridium sigillum* sp. nov. In addition, the new species *Cyclomedusa plana*, *Rangea longa*, *R. grandis*, *Dickinsonia elongata*, *D. tenuis*, and *Spriggina*? *ovata* are described. The synonymies of several genera and species are revised, and new morphological information on others, particularly *Tribrachidium heraldicum* Glaessner, is presented.

SINCE the first accounts of the discovery of new Late Precambrian fossils at Ediacara were published (Glaessner 1958, 1959*a*, *b*, 1960, 1961, 1962; Glaessner and Daily 1959), much interest in this fauna has been expressed in the literature, in discussions, in the form of requests for illustrations for publication in a great variety of books, and in many other ways. Collecting and indexing of specimens from this locality, now numbering over 1,400, was continued and the authors have carried out jointly their study and interpretation. A comprehensive publication on the accumulated material is in preparation. It will deal with its geological aspects, fossilization, systematics, biological, evolutionary, and biostratigraphic interpretations. Nine new genera and thirteen new species are described, the synonymy of others has been altered, and new material of some known species has revealed additional important characters. Some of these new data are now made available to those interested in the early history of metazoan evolution and relationships, pending completion of more comprehensive investigations.

The description of this unusual collection of remains of soft-bodied animals preserved in hard sandstone or quartzite requires a careful consideration of the circumstances of their fossilization so as to discriminate, as far as possible, between results of post-mortem alterations and original morphological characters. The general sedimentary environment of the Ediacara fauna can be described as shallow marine and littoral. The position of the shoreline at the time when deposition of the Pound Quartzite in the Adelaide Geosyncline and on its western shelf margin was about to end is not known. Occasional emergence of sandy shoals is proved by the occurrence of networks of drying cracks on some bedding planes of the fossiliferous strata. The sediment is dominantly arenaceous; cross-stratification indicates moving sand ripples, and ripple-marked bedding planes are common. In this environment the fossils would not have been preserved but for one important local feature. The sandstone, now partly altered to quartzite, is flaggy, and the sandy layers are separated by argillaceous laminae and thin lenses. They represent areas of temporary quiescent conditions between the shifting current tracks, where fine particles could settle until they were covered again by sand waves. The animal remains which came to rest on the muddy or silty flats and pool bottoms either made impressions in the sediment or were retained there bodily until covered with sand by the next shifting

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current. The sand, though partly coarse, must have had some of the qualities of a foundry sand to be able to produce more or less perfect casts and moulds of the underlying sediment surface and of the animal moulds, tracks, and remains on it. The clay lenses were subsequently highly compacted and altered and are now mostly only thin, lenticular partings between the quartzite flags. Most of these partings can be opened only by natural weathering. They reveal fossils mostly on the lower surfaces of the quartzite flags. The upper portions of the sandy sedimentation units had apparently only rarely the required composition and consistency to retain them.

This peculiar mode of fossilization, which explains the localization of fossils along a few miles of outcrop of a stratigraphic horizon which has now been mapped regionally over hundreds of miles, requires careful consideration of its implications for descriptive work. Existing terminology must be applied with care to the five observed states of preservation of these fossils. Most of the medusoid remains are preserved in the form of a flattened convex *cast* (1) on the lower surface of a quartzite slab of the original depression in the underlying sediment. Sand-filled hollows or decayed parts of the organisms are also preserved as casts but these are rare. The depression in the underlying stratum which corresponds to the cast is its *counterpart mould* (2) which reproduces the surface features of the cast as its mirror image. A superimposition of the features of the lower surface of the organism (as deposited), moulded on the underlying stratum, and of those of its upper surface, produces a *composite mould* (3) (McAlester 1962). Where a convex feature on the underlying surface, possibly the dead organism itself, is impressed into the lower surface of the overlying stratum, we speak of an impression or *external mould* (4). The corresponding natural cast of this impression which is occasionally seen on a sandy bed below is the *counterpart cast* (5). It will be noted in the systematic part that two of the genera here described as medusoid are known as external moulds, as are all known representatives of the genera *Spriggina*, *Parvancorina*, and *Tribrachidium*, though in the last genus one external mould of the lower surface is known, in addition to those of the upper surface of this and many other specimens. Uncertainties in the distinction between the two sides of flat bodies which are caused by these modes of preservation add to the difficulties of their morphological and functional analysis. The preferential preservation as casts or external moulds in various taxonomic groups can be seen as a function of their resistance to decay or of the toughness of their tissues. Fortunately, with very few exceptions, each species is represented by many specimens, so that accidents of fossilization can be recognized by comparison.

At the present stage of our inquiries we do not wish to introduce any suprageneric classifications. The medusoid fossils cannot be generally classified into Scyphozoa and Hydrozoa, though comparisons suggest that both taxa are represented. The two annelid genera described clearly belong to two widely different families, but the level of their separation will not be discussed here.

The geology of the Ediacara area has been the subject of very detailed studies by geologists of the South Australian Mines Department who have carried out a geochemical investigation of the metalliferous Lower Cambrian carbonate rocks at this locality. In the course of this work (Nixon 1963, 1964) the fossiliferous strata of the Pound Quartzite and the overlying Parachilna Formation (Dalgarno 1964) were mapped in detail.

For reasons which have been stated (Glaessner 1960, 1962, 1963*b*; H. and G. Termier

1960) the Ediacara fauna is considered as Late Precambrian, preceding stratigraphically and chronologically the appearance of the first known Lower Cambrian faunas. South Australian geologists have accepted this designation in their regional mapping. The composition of the fossiliferous formation makes it unlikely that it will ever be dated directly by radioactivity methods.

The fauna as known at present comprises the following 25 species. There are indications of the presence of additional species and of trace fossils which require further study.

Phylum Coelenterata

A. Medusoid

Ediacaria flindersi Sprigg
Beltanella gilesi Sprigg
Medusinites asteroides (Sprigg)
Cyclomedusa davidi Sprigg
C. radiata Sprigg
C. plana sp. nov.
Mawsonites spriggi gen. et sp. nov.
Conomedusites lobatus gen. et sp. nov.
Lorenzinites rarus gen. et sp. nov.
Pseudorhizostomites howchini Sprigg
Rugoconites enigmaticus gen. et sp. nov.
Kimberia quadrata gen. et sp. nov.
Ovatoscutum concentricum gen. et sp. nov.

B. Pennatulacean

Rangea longa sp. nov.
R. grandis sp. nov.
Pteridinium cf. simplex (Gürich)
Arborea arborea (Glaessner)

Phylum Annelida

Dickinsonia costata Sprigg
D. elongata sp. nov.
D. tenuis sp. nov.
Spriggina floundersi Glaessner
S. ? *ovata* sp. nov.

Phylum uncertain

Praecambridium sigillum gen. et sp. nov.
Parvancorina minchami Glaessner
Tribrachidium heraldicum Glaessner

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Cambridge facilitated the completion of this paper. The text figures were re-drawn by Miss M. Boyce (Adelaide). To all those who helped in this investigation we express our sincere thanks.

Depositories. Registered numbers prefixed P refer to specimens deposited in the South Australian Museum. Those prefixed T or F refer to specimens in the Geology Department, University of Adelaide.

SYSTEMATIC DESCRIPTIONS

Phylum Coelenterata

A. Medusoid fossils

Most of the medusoid fossils from Ediacara are preserved as more or less flattened convex casts on the lower surfaces of quartzite beds. In this preservation, a medusa could show the shape of the exumbrellar surface and often also remains of any marginal flange which, if present, could either spread around the entire periphery, or part of it, or it could be hidden under the body. Such a cast could also show the subumbrellar side on which one would expect oral or gastric structures, and a velum impression in hydroid medusae. Actually, no clearly defined structures of this kind have been seen since Sprigg (1947, 1949) interpreted in this manner some of the fossils described by him. The distinction between preservation of the exumbrellar or subumbrellar surface is not necessarily clear-cut, as a number of the medusoid fossils show signs of composite moulding of parts of both surfaces. It is possible that in some of them remains of radial grooving which do not reach the centre are to be considered as subumbrellar, while most of the concentric grooving, particularly in the central part, was exumbrellar. Gradual decay of the gelatinous bell during fossilization introduces further complications. It is more important to recognize the complexities of structural interpretation of ancient medusoid fossils than to attempt prematurely their placing in the existing system. Further comparative studies are required but some distinctive genera and species are here recorded.

Genus EDIACARIA Sprigg 1947

Type species. Ediacaria flindersi Sprigg 1947.

Characters as for type species.

Ediacaria flindersi Sprigg 1947

Plate 99, fig. 6

1947 *Ediacaria flindersi* Sprigg, p. 215, pl. 5, figs. 1, ?2, text-fig. 3.
1949 *Ediacaria flindersi* Sprigg, p. 83, pl. 10, fig. 2, text-fig. 5.
1949 *Madigania annulata* Sprigg (*partim*), p. 93, pl. 17, figs. 1, 2 (*non* pl. 16, figs. 1, 2).
1949 *Protodipleurosoma wardi* Sprigg, p. 79, pl. 9, fig. 2, text-fig. 3E.
1956 *Ediacaria flindersi* Sprigg (*partim*), *Protodipleurosoma wardi* Sprigg; Harrington and Moore, *in* Moore, p. F74, fig. 60 (1); p. F79, fig. 64.
1959 *Ediacaria flindersi* Sprigg; Glaessner, *in* Glaessner and Daily, p. 378.
1962 *Ediacaria* Sprigg; Glaessner, p. 483.

Material and preservation. Over 40 specimens are definitely assigned to this species, while 30 small specimens, 3 relatively uncompressed specimens, 5 composite moulds with rather strong radial furrows, and a number of fragments may belong here.

Most specimens are rather flat composite moulds dominated by exumbrellar structures but some are gently domed. Strong radial furrows on some specimens may indicate subumbrellar structures.

The species was gregarious; one slab measuring about 45 × 30 cm. bears parts of 9 specimens with radii from 30–120 mm.

Holotype. T1–2058.

Dimensions. This is the largest medusoid known from Ediacara. The largest complete specimen has a mean radius of 120 mm. but a fragment has a radius of 210 mm. and another fragment indicates a much larger specimen. The holotype has a mean radius of 50 mm.

Diagnosis. The surface (which is considered as exumbrellar) shows a central disc and an outer ring, without any marginal flange. The disc is often slightly elevated above the outer ring. The surface of the disc may be marked by a sharp annular furrow which does not necessarily run parallel with its outer boundary. It could indicate the edge of the gastric cavity. Some specimens show additional concentric grooves on the disc. Several of them may be grouped close to the centre. Arcuate folds marked by grooves parallel to the periphery may also occur on the outer ring. Radial furrows are mostly confined to it but they are not present in all specimens. Crenulations of the periphery are probably accidental. The radius of the central disc is from one-quarter to three-quarters of the total radius.

Remarks. One-quarter of the holotype is poorly preserved and superimposed on a small *Cyclomedusa* near the centre. This *Cyclomedusa* has caused distortion, straightening the annular furrows near the centre of the *Ediacaria*. It may be the sole cause of some of the straight furrows delimiting one side of the subtriangular structure which Sprigg (1949, p. 85) interpreted as a manubrium. The other furrows delimiting this structure are a radial and a concentric furrow, each in line with the normal furrows of the disc but exceptionally deep.

Sprigg (1947, 1949) described ‘three pendant pouches extending radially from the base of the manubrium’ in the position in which Harrington and Moore (*in* Moore 1956, p. F75) noted four ‘circular knobs’. One or two of these irregularities appear to be due to distortion by the *Cyclomedusa* and the specimen does not support clearly either of the quoted descriptions. The outer ring shows a number of partial concentric folds. The general morphology of a more corrugated outer ring and a smoother, more convex disc, both with a surface texture of fine, radial striae, indicates that this specimen is an exumbrellar surface. None of the radial or concentric markings on the central disc can be attributed with any probability to internal or subumbrellar structures. Many radial furrows occur near the margin of the outer ring but less than half of them cross it. Most of those that do, die out at the edge of the central disc but a few reach to, or just across, a partly doubled annular depression on the disc which Sprigg (1947) regarded as the outer edge of the ‘gastrovascular cavity’ or ‘stomach’. The radial depressions on the outer ring of the holotype are more numerous than those in any other specimen interpreted as an exumbrellar surface. They are deeper and less numerous than those on the subumbrellar surfaces tentatively assigned to *Ediacaria* (Sprigg 1947, pl. 5, fig. 2, and other specimens). There is very little branching or overlapping of the radial furrows despite the striking arrangement of canals drawn in restorations (Sprigg 1947, text-fig. 3A, B; 1949, text-fig. 5A–C).

The holotype of *Protodipleurosoma wardi* Sprigg (1949, pl. 9, fig. 2) is a composite mould. All its exumbrellar characteristics are those of *Ediacaria flindersi*. It differs in the relatively small size and elongate-oblate shape of the sharp furrow that may indicate its gastric cavity (Sprigg 1949, p. 79). The enclosed portion is slightly elevated as if the area had been filled with sand before compression. Groups of furrows radiate from opposite points. They are deepest adjacent to the sharp furrow, and shallow away from it. There is also a fine wrinkling across the surface with which the constriction across the 'stomach' shown by Sprigg (1949, text-fig. 3E) is associated. These furrows and wrinkling are probably both compressional features due to the flattened infilling of sand; there are no structures equivalent to them among the new specimens of medusoid fossils. Thus the 'radial canals' (Sprigg) are not a convincing taxonomic character. The study of '*Protodipleurosoma wardi*' shows that several partial concentric folds have been aligned as a ring canal in Sprigg's text-fig. 3E, while the new material of *Ediacaria* shows that the development of concentric furrows on the outer ring, varying in completeness and number, is common. The centre of the disc, where the area within the oblate furrow is least raised, shows faintly a small, circular structure such as is seen on many specimens of *Ediacaria*. The size of the infilled area is the only remaining distinction between *Protodipleurosoma* and *Ediacaria*. This character cannot be considered as taxonomically distinctive. *Protodipleurosoma wardi* Sprigg 1949 appears to be a composite mould of *Ediacaria flindersi* Sprigg 1947, and the name is suppressed as a junior synonym.

Genus BELTANELLA Sprigg 1947

Type species. *Beltanella gilesi* Sprigg 1947.

Beltanella gilesi Sprigg

1947 *Beltanella gilesi* Sprigg, p. 218, pl. 6, fig. 1, text-fig. 4A–C.
1949 *Beltanella gilesi* Sprigg; Sprigg, p. 81, pl. 10, fig. 1, text-fig. 4D–F.
1956 *Beltanella gilesi* Sprigg; Harrington and Moore, *in* Moore, p. F70, fig. 56.
1959 *Beltanella gilesi* Sprigg; Glaessner, *in* Glaessner and Daily, p. 378.
1962 *Beltanella* Sprigg; Glaessner, p. 483, pl. 1, fig. 3.

Holotype. T3–2056.

Description. The holotype is a convex cast, highest at one side of the central disc. The type figure (Sprigg 1947; reproduced by Sprigg 1949, Harrington and Moore *in* Moore 1956) shows three bosses regularly spaced near the margins of the central disc; these are the clearest, but alternative lighting (Glaessner 1962) shows a fourth boss between and to the centre from two others. This distorts the concentric furrow which occurs at mid-radius of the central disc. In the possession of these bosses *Beltanella gilesi* remains unique but its other characteristics are shared by several specimens which cannot be separated from *Ediacaria flindersi*.

Its outer flange appears narrower than the outer ring of *Ediacaria*; it is only 5–7 mm. wide over one-half of the circumference of *Beltanella*, but it widens out to a width of 13 mm. where the total radius is 56 mm. Even here, concentric folds show that it was not stretched. The mean diameter of the central disc is just over 80 mm., so that the proportions of this apparent 'outer flange' fall within those of the 'outer ring' of *Ediacaria*. Similarly, the central disc is fairly smooth, bearing a concentric furrow (here partly double) at mid-radius. The central structure is delimited by four annular furrows, the outer 12 mm. and the inner 4 mm. in mean diameter. It consists of two flat rings, each 1 mm. across, and a narrower inner ring; probably the innermost portion was a boss but it is now broken and a sharp-edged depression occupies the centre. The natural features of this central structure can be closely matched among the available material of *Ediacaria*. A structure that is not matched among the *Ediacaria* specimens is the double radial furrow delimiting a low ridge, which crosses from the outer edge of the central disc to the concentric furrow at mid-radius of the disc, and which is opposed by a low ridge and indications of a double furrow on the opposite side of the central disc. Sprigg (1947, 1949) reconstructed this as two of four paired radial canals at right angles, but evidence of the other two is lacking and the significance of this character is uncertain. A feature which has not been described is the faint radial furrowing extending towards the centre from the concentric furrow at mid-radius (*vide* Glaessner 1962, pl. 1, fig. 3). This is not present around the full circumference.

As the size, proportions, and main features of *Beltanella* are within the range of similar structures in *Ediacaria*, their distinctiveness hinges mainly on the presence in *Beltanella* of the 'ring' of bosses which have been considered as possible gonads. The slab on which the *Beltanella* occurs is exceptionally rich in medusoids; eight small specimens of *Cyclomedusa* (including two clumps of three each) and two other medusoids occur, besides many vague markings. There are very few places on it where so large an individual as the holotype of *Beltanella* would not over- or underlie some other specimen. The bosses, as Sprigg noted from the first, have concentric furrows on them. A small group of *Cyclomedusa* specimens superimposed on the holotype would satisfactorily explain both this structure and the distribution of bosses (Glaessner 1962, pl. 1, fig. 3), which does not fit the interpretation of eight regularly distributed gonads. On present evidence it is not possible to prove conclusively whether these bosses are *Cyclomedusa* specimens or parts of *Beltanella*. The discovery of one or more specimens showing such bosses on slabs not rich in *Cyclomedusa* would be a strong indication of the distinctiveness of *Beltanella* but in their continued absence the taxon must be regarded as doubtful and as a possible synonym of *Ediacaria*.

Genus MEDUSINITES gen. nov.

Type species. Medusina asteroides Sprigg 1949.

Characters of type species. This genus resembles *Protolyella* only in its smooth central area, but the surrounding outer ring lacks the numerous, close-set, irregular, radial grooves and ridges. '*Medusina*' *filamentis* Sprigg does not belong here but is connected with *Pseudorhizostomites howchini* Sprigg by transitional forms. *Medusina* Walcott 1898 is an objective synonym of *Spatangopsis* Torell 1870, a form unrelated to *Medusinites*.

Medusinites asteroides (Sprigg) 1949

Plate 97, figs. 1–5

1949 *Medusina asteroides* Sprigg, p. 90, pl. 3, fig. 3, text-fig. 7c.
1949 ?*Medusina mawsoni* Sprigg, p. 89, pl. 13, fig. 4, text-fig. 7b.
1956 *Protolyella asteroides* (Sprigg), ?*P. mawsoni* (Sprigg); Harrington and Moore, *in* Moore, p. F155, fig. 127 (1), ?(2).
1959 *Protolyella asteroides* (Sprigg), ?*P. mawsoni* (Sprigg); Glaessner, *in* Glaessner and Daily, p. 381.

Material and preservation. About 20 casts on the lower surfaces of quartzite slabs, many with counterpart moulds.

Dimensions. Specimens with diameters from about 1 to 5 cm. can be identified. Smaller and slightly larger specimens lacking distinctive characters may also belong here.

Diagnosis. Small circular bodies with a very narrow, generally distorted, marginal flange surrounding a large outer ring separated from a central disc by a deep annular furrow. The radius of the central disc is smaller than the width of the outer ring. Radial furrows may be preserved on it. Faint concentric markings are more common on the central disc than elsewhere.

Remarks. In closely similar medusae, even on the same rock-surface, the marginal flange may be fully displayed, partly folded below the specimen (as in the holotype of *M. asteroides*) or absent. Specimens without a flange and with a large central disc are not clearly distinct from *Medusina mawsoni* Sprigg and it therefore seems on present evidence that this form should be merged with *M. asteroides*. It is preferable to retain the name of the form which shows most distinguishing characters, and suppress *mawsoni* as a synonym.

Genus CYCLOMEDUSA Sprigg 1947

Type species. Cyclomedusa davidi Sprigg 1947.

1947 *Cyclomedusa* Sprigg, p. 220.
1949 *Cyclomedusa* Sprigg, p. 91.
1949 *Madigania* Sprigg, p. 93.
1949 *Tateana* Sprigg, p. 86.
1956 *Cyclomedusa* Sprigg; Harrington and Moore, *in* Moore, p. F153.
1956 *Ediacaria* Sprigg (*partim*); Harrington and Moore, ibid., p. F74, fig. 60 (4–5).
1956 *Madigania* Sprigg; Harrington and Moore, ibid., p. F154.
1958 *Spriggia* Southcott [= *Madigania* Sprigg 1949, *non* Whitley 1945], p. 59.
1959 *Cyclomedusa* Sprigg; Glaessner, *in* Glaessner and Daily, p. 378.
1959 *Spriggia* Southcott, *Tateana* Sprigg; Glaessner, ibid., p. 388.

Remarks. Cyclomedusa radiata Sprigg differs from the type species in its central boss-and-ring structure and more widely spaced deep radial furrows, with fewer concentric grooves. In several specimens of *Cyclomedusa*, however, the radial structures agree with typical forms of *C. radiata* but extend further toward the centre, which is developed as in *C. davidi*. *C. gigantea* Sprigg is represented only by its holotype, which is badly

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EXPLANATION OF PLATE 97

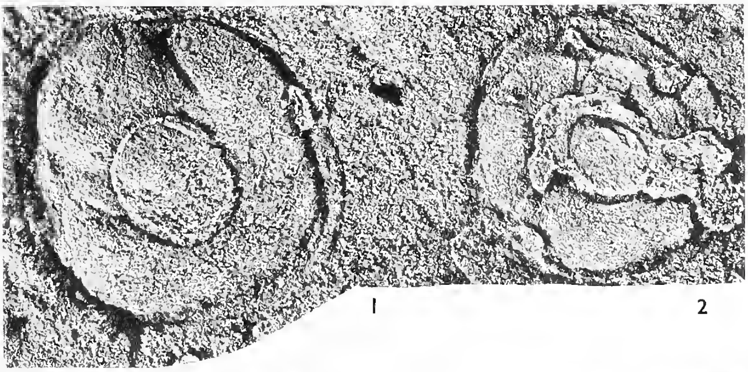
All figures ×1.

Figs. 1–5. *Medusinites asteroides* (Sprigg). 1–2, hypotypes, P13785–6, showing central disc, main annular furrow, outer ring, and marginal flange. 3, holotype, T40–2021, showing also few radial furrows. 4, holotype, T39, of '*Medusina mawsoni*' Sprigg. 5, hypotype, P13783, with numerous radial furrows on outer ring.

Figs. 6–7. *Kimberia quadrata* gen. et sp. nov. 6, holotype, P12734. 7, paratype, P12739. The deep groove x–y is probably accidental rather than structural. Outlines marked where only faintly recognizable on the specimens.

Fig. 8. *Ovatoscutum concentricum* gen. et sp. nov. Holotype, P13770. Arrow points to notch, centre, and radial suture. It ends where a faint discontinuity in the rock surface sculpture may indicate the edge of a smooth portion of the disc across the notch.

Fig. 9. *Tribrachidium heraldicum* Glaessner. Hypotype, F17021. A distorted natural mould showing impressions of bristles.



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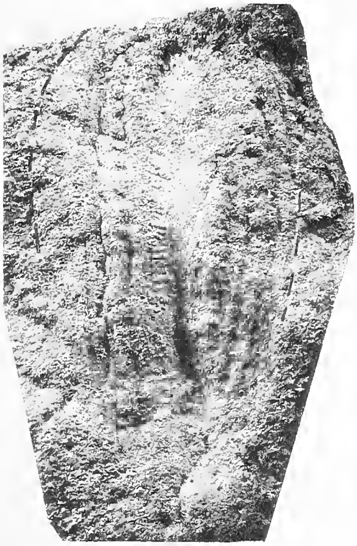

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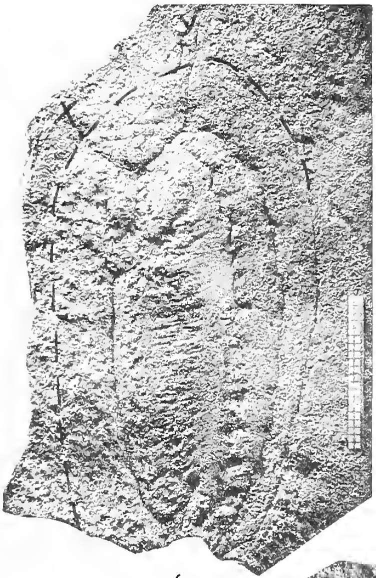

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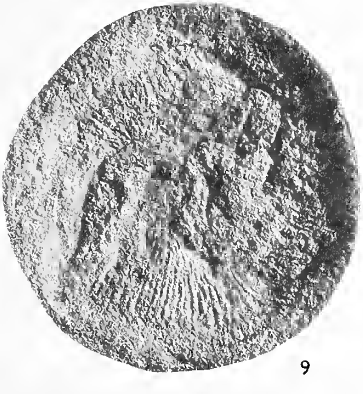

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GLAESSNER and WADE, Late Precambrian fossils from Ediacara, South Australia

weathered in the centre. Its specific distinctness from the type species is therefore questionable. The presence of areas with radial furrows on several specimens formerly placed in *Spriggia annulata* (Sprigg), including the holotype, makes its separation from *C. davidi* impracticable because of intergrading.

Cyclomedusa plana sp. nov.

Plate 98, figs. 1–3

1959 'Unidentified medusoid fossils', Glaessner, *in* Glaessner and Daily, pl. 45, fig. 2 (*partim*).

Material and preservation. 8 specimens, casts on the lower surfaces of quartzite slabs.

Holotype. P13778. *Paratypes.* P13779, P13780.

Diagnosis. Adult distinguished by a broad, flat disc (maximum known radius 12 cm.) surrounding a small, central, concentrically rugose cone rarely over 1 cm. in radius; radial furrows very fine when present. The central cone is sometimes duplicated by twinning.

Remarks. C. plana is distinguished from *C. davidi* in adult specimens by its smaller central cone and large disc with few or without concentric rugosities, and by its finer radial striations. The fineness of these, and the central cone, differentiate it from *C. radiata.*

Genus MAWSONITES gen. nov.

Type species. Mawsonites spriggi sp. nov.

Characters of type species. This genus is named after the late Sir Douglas Mawson, geologist and explorer, who inspired and led his students and colleagues in the study of the Flinders Ranges and the Ediacara area.

Mawsonites spriggi sp. nov.

Plate 99, figs. 1, 2

1958 'Unnamed jellyfish', Sprigg, *in* Best, pl. 6, fig. *b* (figured only).

Material. Four casts on the lower surfaces of quartzite slabs. The holotype retains an elevation of 5 mm. from the rock surface in places. The paratype and other specimens are flattened.

Holotype. F17009. *Paratypes.* F17016, F17019.

Dimensions. Diameter of holotype 110–125 mm., of paratype F17016 89 mm. (maximum), of paratype F17019 64–72 mm.

Diagnosis. Large, compressed, but in life presumably dome-shaped, becoming steeply conical near centre. Central conical part smooth-walled, truncated, and compressed in curved, overlapping folds in the holotype. The greater part of the surface is strongly sculptured with arcs of prominent, large, irregular, bosses which increase in size outwards, and merge into the peripheral zone which is dominated by large, irregular, radially elongate lobes separated by deep clefts. They form radial furrows on the outer half of the disc. Periphery lobate. A circular area bearing the conical centre and the enclosing one or two arcs of bosses was more compressible than the remainder of the bell and was enclosed by a shallow annular groove on the surface of the dome.

Remarks. The peculiar distribution of large bosses on the main body of the bell, and the lobate margin, set this form apart from other fossil and living medusae. The bosses must have been fairly solid to make such well-defined impressions in the underlying sediment. In its possession of a truncate, easily compressed, possibly hollow central cone with arcuate folds in its walls *Mawsonites* approaches *Cyclomedusa davidi* and *C. plana* in the Ediacara fauna, and the Stauromedusae among modern forms.

Genus CONOMEDUSITES gen. nov.

Type species. *Conomedusites lobatus* sp. nov.

Characters of type species.

Conomedusites lobatus sp. nov.

Plate 99, figs. 3, 4

Material and preservation. Three specimens, casts on the lower surfaces of quartzite slabs.

Holotype. P13789. *Paratypes*. P13788, P13790.

Dimensions. Diameter of holotype 21–22 mm., height 1·5 mm. Diameter of paratypes P13788 and P13790 15–18 and 19 mm. respectively, height 3 and 1 mm. respectively. It should be noted that the marginal flange is obscured in P13788.

Diagnosis. Small, convex body, composed of four almost equal lobes, delimited by sharply defined grooves that deepen outwards, separating adjacent lobes at the periphery, or above a broad, distorted, marginal flange with an entire margin. Further lobes may be intercalated peripherally by bifurcation of the four apical grooves.

Remarks. Only the aboral side of *C. lobatus* is known. It is distinguished by its conical shape from the exumbrellar view of the simpler specimens of *Brooksella alternata* Walcott (1898, pl. 1, fig. 4; re-figured by Harrington and Moore, *in* Moore 1956, fig. 11, 2*a–c*). There is no reason to assume that it was a related form as there is no trace of subumbrellar lobes. A resemblance to the Ordovician *Conchopeltis alternata* Walcott, a large, low, conical, tetramerous, presumably chitinous shell for which Moore and Harrington (*in* Moore 1956, pp. F32, F57) erected a new Family and Suborder in the Order Conulariida, could be fortuitous, for the marginal flanges preserved in two of the three specimens are apparently entire. *Conomedusites* is the only medusoid fossil from Ediacara with a clearly displayed tetrameral symmetry.

Genus LORENZINITES gen. nov.

Type species. *Lorenzinites rarus* sp. nov.

Characters of type species.

EXPLANATION OF PLATE 98

Figs. 1–3. *Cyclomedusa plana* sp. nov. 1, paratype, P13779, ×1·2. 2, holotype, P13778, ×1. 3, paratype, P13780, part of specimen with twinned centre, ×0·75. All specimens show the concentrically rugose small central area. Strong radial grooves in 1 and 3 are probably accidental.

Fig. 4. *Spriggina*? *ovata* sp. nov. Holotype, P13754, ×4.

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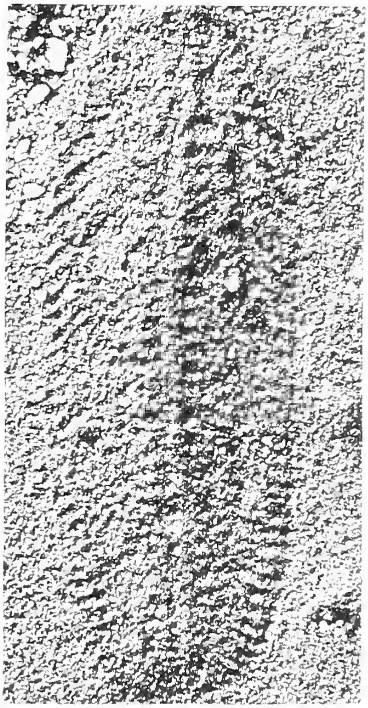

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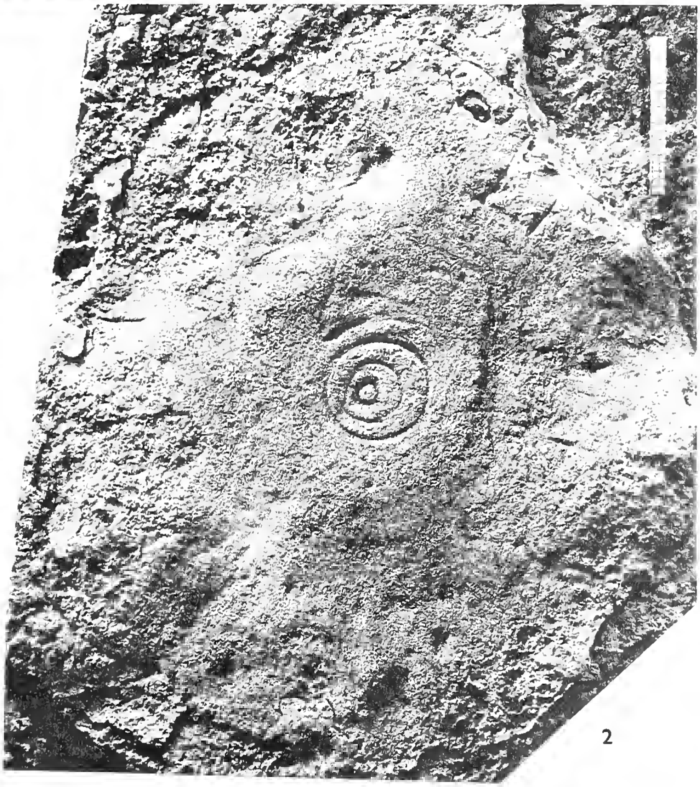

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GLAESSNER and WADE, Late Precambrian fossils from Ediacara, South Australia

Lorenzinites rarus sp. nov.

Plate 100, fig. 1

Material and preservation. A single specimen, an external mould on the base of a quartzite bed.

Holotype. P13784.

Dimensions. A disc with a diameter of 5–6 mm., surrounded by eleven radiating lobes 2–3 mm. long.

Diagnosis. A small central disc from which lobes (eleven in the only known specimen) radiate, broadened and flattened at the tips. The tips may bifurcate. The edge of the disc describes a series of arcs from the base of each lobe to the base of its neighbouring lobes.

Remarks. At first glance this structure resembles the problematic medusoid genus *Lorenzinia* but its lobes expand at the periphery of the fossil instead of being rounded off, and may bifurcate. Only eleven lobes are known. In this it resembles *Palaeosemaeostoma* Rüger, from the German Middle Jurassic, a genus classified as ?Trachylinida *incertae sedis* by Harrington and Moore (*in* Moore 1956, p. F76), but it lacks the raised narrow collar around the centre of the disc.

Like *Rugoconites enigmaticus* sp. nov., but unlike the other medusoid fossils which are casts, *L. rarus* is preserved as an external mould. This specimen resembles the centre of some specimens of *R. enigmaticus* but is much more regular. While its central disc is the size of the central ring-ridge of some specimens of *R. enigmaticus*, its lobes are smaller and more numerous than the innermost whorl of dichotomous radial ridges of this species. It is not likely to be a juvenile of *R. enigmaticus* because of their differing measurements and proportions, but it could be a related form.

Genus PSEUDORHIZOSTOMITES Sprigg 1949

Type species. Pseudorhizostomites howchini Sprigg 1949. Plate 103, figs. 2–4.

1949 *Pseudorhizostomites* Sprigg, p. 87, pl. 12, figs. 1, 3; text-fig. 6F–H.
1949 *Pseudorhopilema* Sprigg, p. 88, pl. 12, fig. 2; text-fig. 6E.
1949 *Medusina* Walcott (*partim*); Sprigg, p. 90, pl. 13, fig. 1; text-fig. 7D.
1956 *Pseudorhopilema* Sprigg, *Pseudorhizostomites* Sprigg; Harrington and Moore, *in* Moore, pp. F51, 52, fig. 41 (1–3).
1956 *Protolyella* Torell (*partim*); Harrington and Moore, ibid., p. F155, fig. 127 (7).
1959 *Pseudorhizostomites* Sprigg, *Pseudorhopilema* Sprigg; Glaessner, *in* Glaessner and Daily, pp. 381–2.

Material. Over 80 specimens, most of which are impressions on the bases of quartzite slabs; and occasional counterpart casts found on upper surfaces. The following descriptions are based on the impressions.

Description. The specimens are extremely variable in appearance. Although the small number available to Sprigg (1949) could be grouped in three apparent genera, such grouping is no longer practicable for the many intermediate and new forms which are now known.

The specimens, mostly under 7 cm. in diameter, consist of furrows which radiate outwards from a centre of variable shape. As they radiate, they split and become shallow, forming a zone of numerous very small furrows at the outer limits of many specimens. Only one specimen possesses a definite outer edge, a sharp groove preserved around half its circumference. Radial splitting and dendritic branching of the furrows are extremes of variation (Sprigg 1949, pl. 12, figs. 1–3; pl. 13, fig. 1).

Some rock specimens have been split vertically across these fossils accidentally, and others intentionally. In every example in which the lamina of quartzite immediately above the specimen had appreciable thickness (9 specimens) there were indications of post-depositional disturbance of sand grains above the centre, or above the deepest furrows. Plate 103, figs. 2–4 shows a specimen which has been split along a linear central furrow towards which all its other furrows converge. The main converging furrows can be traced into vertical flutes on the sides of a smooth-walled passage through the overlying lamina of quartzite. This passage ends on the next bedding plane. Although compaction during diagenesis has forced its sides into contiguity, the individual sand grains do not interlock. Another specimen with a linear central furrow shows a similar passage, while three with point-centres show very narrow, funnel-shaped lines of disturbance vertically above their centres, and more obscure disturbances are found in specimens with ill-defined centres or circular central furrows. All seem to have resulted from the escape of material from a decaying organism. The circular central furrows delimiting one to several rounded bosses of quartzite (e.g. '*Medusina*' *filamentis* Sprigg 1949, pl. 13, fig. 1) seem to result from the subsidence of the overlying sand-lamina during the escape of the organic matter, rather like the subsidence of the core of a ring-dyke. Forms such as that figured here and by Sprigg (1949, pl. 12, fig. 1, the holotype of *Pseudorhizostomites howchini*, and fig. 3*b*, *Pseudorhizostomites sp.*), which are more or less radial structures, seem to have been shaped largely by viscous flow towards the centre. These are the majority (over 40 specimens). The rather regular dichotomously branched form *Pseudorhopilema chapmani* Sprigg (Sprigg 1949, pl. 12, fig. 2) occurs in such numbers (about 20) that there is a possibility that some surface structures of the organism, in addition to post-mortem processes, influenced their formation.

While *Pseudorhizostomites howchini* is thus primarily based on a peculiar state of preservation of a decaying organism, it is unlikely to have been formed by the decay of any of the other medusoid organisms here described, with the exception, perhaps, of *Rugoconites*. It is likely to represent a morphologically distinctive though imperfectly known taxon. Reliable specific distinctions cannot be made within it at this time.

Genus RUGOCONITES gen. nov.

Type species. Rugoconites enigmaticus sp. nov.

Characters of type species.

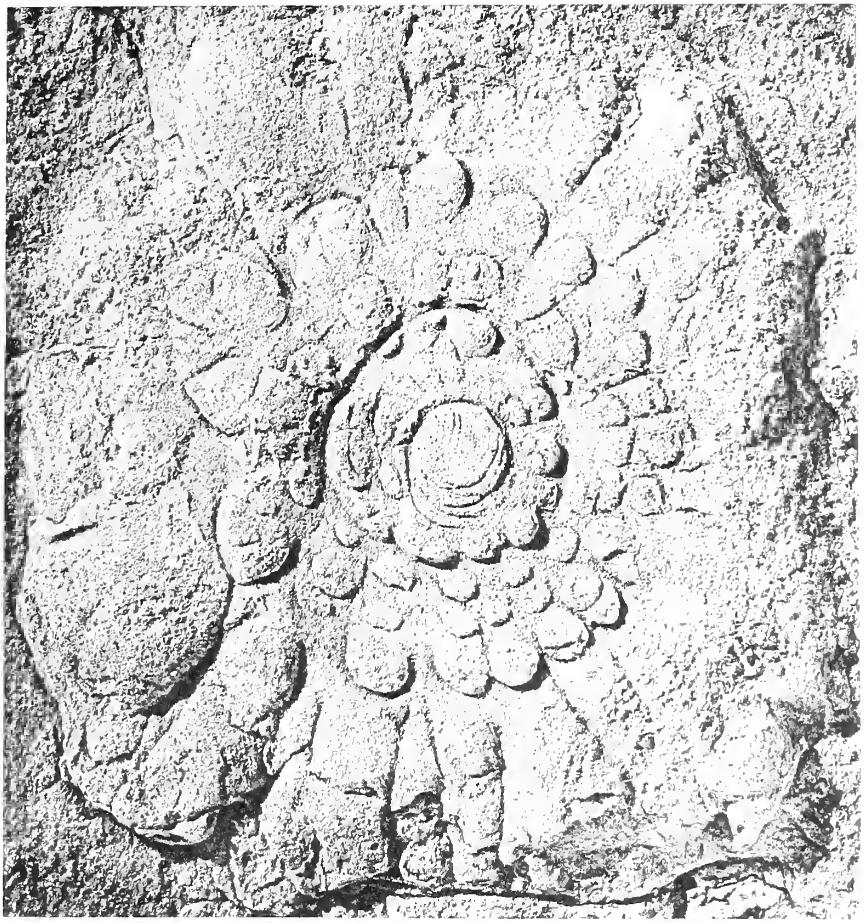
EXPLANATION OF PLATE 99

Figs. 1, 2. *Mawsonites spriggi* gen. et sp. nov. 1, holotype, F17009. 2, paratype, F17016, ×1. The smaller specimen is less strongly sculptured but the basic pattern is the same.

Figs. 3, 4. *Conomedusites lobatus* gen. et sp. nov. 3, holotype, P13789. 4, paratype, P13788, ×1.

Fig. 5. *Tribrachidium heraldicum* Glaessner. Latex cast of holotype, P12898, ×1.

Fig. 6. *Ediacaria flindersi* Sprigg. Hypotype, F17039, showing smooth outer ring and flattened central disc, marked only by an elliptical annular furrow, ×0·5.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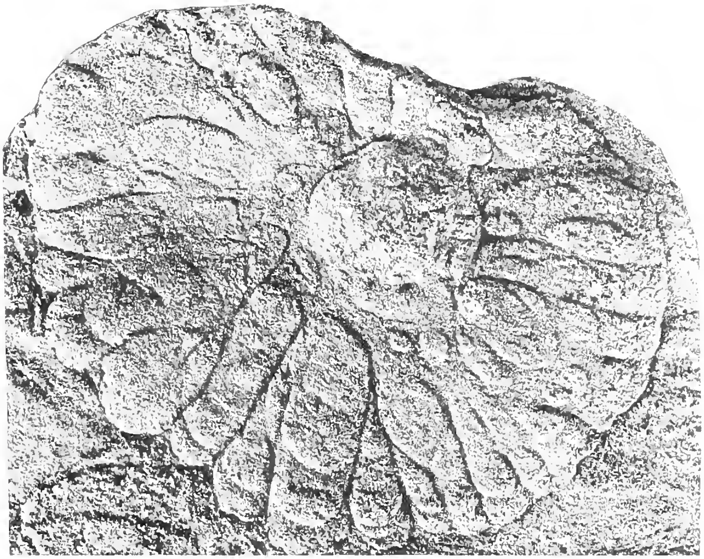
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GLAESSNER and WADE, Late Precambrian fossils from Ediacara, South Australia

Rugoconites enigmaticus sp. nov.

Plate 100, figs. 2, 3

Material and preservation. 16 impressions in the bases of quartzite flags. Large impressions are relatively (and often actually) flatter than small specimens and their inner parts are obscured by flattening. The following descriptions are based on latex casts of the impressions.

Holotype. P13781. *Paratype.* P13782.

Dimensions. The smallest specimen is 16 mm. in diameter; the largest, slightly oval, has an average diameter of 64 mm.

Diagnosis. Periphery circular to oval. A few radial ridges diverge from a small central elevation or polygonal ridge, and branch dichotomously one to three times. The last dichotomy is, in each individual, a constant distance inside the periphery, and the resultant ridges curve slightly to meet the periphery at a right angle.

Remarks. In its general form of dichotomous grooves in the rock surface *R. enigmaticus* resembles *Pseudorhopilema chapmani* Sprigg (1949). It differs from Sprigg's specimen and others since collected in usually having a definite periphery and in being much more regular in its branching. The branches ('ridges', as here described, corresponding to the 'grooves' of *P. chapmani* Sprigg 1949) are much thicker in the new form, and do not taper at their outer ends but are cut off sharply at, or just within, the periphery.

Genus KIMBERIA gen. nov.

Type species. Kimberia quadrata sp. nov.

Characters of type species. The genus is named after Mr. John Kimber, student, teacher, and collector who lost his life during an expedition to Central Australia in 1964.

Kimberia quadrata sp. nov.

Plate 97, figs. 6, 7

1959 'Problematic fossil, possibly belonging to the Siphonophora', Glaessner, *in* Glaessner and Daily, p. 391, pl. 47, fig. 9.

Material. Four nearly complete and two fragmentary specimens are known. All are very flat casts on the bases of quartzite slabs. Some portion of each specimen is broken off at the edge of the rock.

Holotype. P12734. *Paratype.* P12739.

Dimensions. Length of holotype 65 mm., width 36 mm.

Diagnosis. Ovate bodies, rounded at one end and with a smooth contour; internal structures represented by several longitudinal, distinct zones of two kinds, coarsely segmented or with fine, transverse, frill-like grooves bordering a smooth area.

Remarks. The bodies appear to have had the shape of a narrow bell which tapered a little more towards one truncate and presumably open end than at the opposite, rounded end. All are flattened and distorted in various ways, the truncate end of the bell being noticeably less resistant to compression than the rounded end. All known specimens have a frilled zone displayed centrally with segmented zones on either side. This suggests that the bells were either flattened at the frilled zones (squarish in life) or that the segmented zones supplied resilience so that the bodies preferentially lay on the area between two segmented zones. In this position the segmented zones would overlie one another and no specimen unequivocally shows how many there are, but there were more than two and no more than four. This seems the most probable number, as three segmented zones would not result in the frilled zone being displayed centrally. Even the two fragmental specimens seem to have been preserved in this position.

Various interpretations of the shape of this peculiar organism in life are possible. One line of argument leading to a tentative structural assessment is presented here. There is an obvious resemblance between the segmented zones of this species and the long gonads on four radial canals in some present-day medusae. These are principally found among the Carybdeida, Trachymedusina, and Leptomedusae. The gonads of the Carybdeida are paired, more lamellar, and less like tubes segmented by intermittent transverse creases than the segmented zones of *K. quadrata*; they are positioned in the corners of a more or less quadrate bell. The general shape of *K. quadrata* could have approximated that of *Carybdea marsupialis* Peron and Lesueur (Mayer 1910), but the segmented zones more closely resemble the gonads of, for example, adult Laodiceidae (Leptomedusae), which run from the stomach almost to the margin of the bell. It is difficult to relate the appearance of the frilled zone to these resemblances to structures of present-day medusae. Too little is known to justify the allocation of *K. quadrata* to one or other of the Leptomedusae, Trachymedusina, or Carybdeida, though the existence of most of its characters in one or more of these groups indicates its medusoid affinities.

Genus OVATOSCUTUM gen. nov.

Type species. Ovatoscutum concentricum sp. nov.

Characters of type species.

Ovatoscutum concentricum sp. nov.

Plate 97, figs. 8

Material. One external mould, flattened and showing some wrinkling but no fracturing. It is described from a latex cast.

Holotype. P13770.

Dimensions. Length 6·2 cm., width 6·1 cm. 35–40 concentric ribs.

Diagnosis. A large, rounded shield sculptured with strong concentric corrugation, which weakens adjacent to a triangular notch, where the outline of the shield is indistinct in the only known specimen. The centre of the sculpture, a minute, smooth, oval, convex area, is situated at a distance of about one-third of the length of the shield measured from a line across the extreme ends of the notch. The contour of the ribbing changes from

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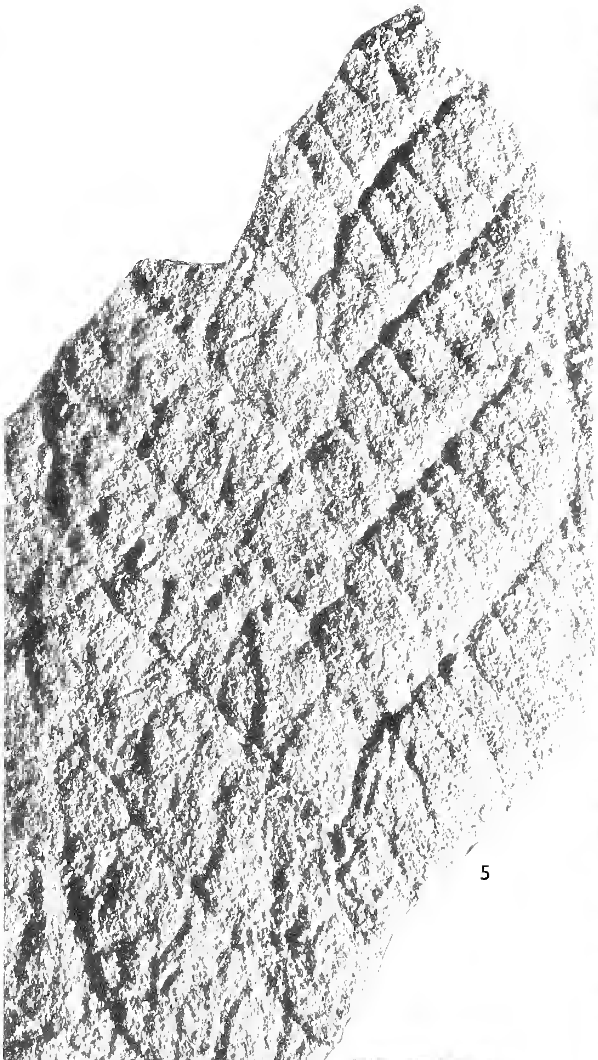
EXPLANATION OF PLATE 100

Fig. 1. *Lorenzinites rarus* gen. et sp. nov. Holotype, P13784, ×1·5.

Fig. 2, 3. *Rugoconites enigmaticus* gen. et sp. nov. 2, holotype, P13781. 3, paratype, P13782, one half broken off. Broken line marks faint outline of disc. ×1.

Fig. 4. *Rangea longa* sp. nov. Holotype, P13777, ×1.

Fig. 5. *Rangea grandis* sp. nov. Holotype, P12897, ×1.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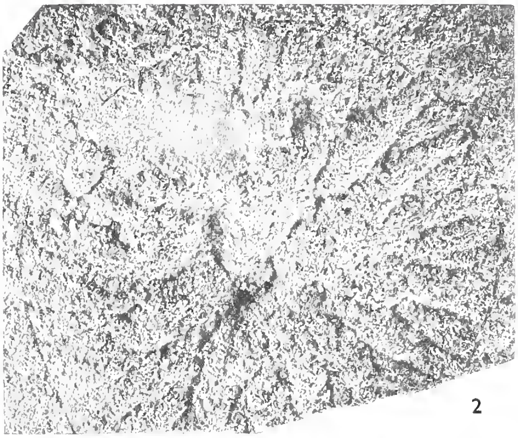
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GLAESSNER and WADE, Late Precambrian fossils from Ediacara, South Australia

distinctly elongate at a length of 2–2·5 cm. to almost equal in length and width, but it becomes sinuous rather than circular. A suture-like zone about 1 mm. wide extends through the centre from the tip of the notch towards the opposite margin.

Remarks. The shape, sculpture, and outline of the disc are somewhat distorted in the anterior portion, apparently through draping over an irregularity of the underlying surface. The ribs become wider and possibly more widely spaced towards the periphery. In some places they appear to be asymmetrical in profile, sloping more steeply towards the centre. The only radial lines are the suture-like zone where the profile of the ribs appears to be flatter and more evenly convex, and the edges of the notch, where the sculpture disappears along irregular and frayed-looking boundaries which are convex towards the median line. The notch does not extend to the centre.

The fossil is strikingly similar in outline and sculpture to *Plectodiscus cortlandensis* Caster, from the Upper Devonian of New York State (Caster 1942). It is only half as large as the holotype of this species and lacks the central cone described in much detail by Caster. He does not mention any notch but the sculpture appears to be absent in a triangular area between F and I (Caster 1942, pl. 1, fig. 1), corresponding in position to the notch in *Ovatoscutum*. The original substance of *P. cortlandensis* was described as 'tough and flexible'. This would also fit *O. concentricum*. Caster described the grooves between the ribs as 'asymmetrical, the steeper slope being consistently peripherad'.

P. cortlandensis was interpreted by Caster, as a result of detailed though 'speculative' interpretation, as a velellid float (pneumatophore). He examined other possibilities, such as an affinity with brachiopod shells, but found only superficial resemblances. Superficially, *Ovatoscutum* may also be thought to resemble a brachiopod shell, but it must have been quite flat, as the sculpture is not much distorted. The notch is unlike any brachiopod structure. The possibility of the suture-like zone being a hinge of a bivalved shell was also considered, but there is no discontinuity across this zone. Much of Caster's interpretation is concerned with proof of the existence of a 'sail' in *Plectodiscus*. No evidence of such a structure exists in *Ovatoscutum* which, if correctly identified as a pneumatophore of one of the Hydrozoa Chondrophorina, would have resembled that of the living *Porpita* rather than that of *Velella*. Harrington and Moore (*in* Moore 1956, p. F149) gave the following diagnosis of the Family Porpitidae Brandt, 1835: 'Corm highly vaulted or flattened disc-like, without crest or sails.' Ordovician to Devonian disc-like fossils assigned to this family have at least some radial sculptural elements. In this respect the new genus differs from all Porpitidae but this does not necessarily affect its tentative interpretation as a chondrophoran pneumatophore.

B. Pennatulacean Fossils

The interpretation of the genera *Rangea*, *Pteridinium*, and *Charnia* as representatives of the Order Pennatulacea (Anthozoa Octocorallia) was discussed in previous publications to which reference is made in the following systematic descriptions. New material confirms this assignment but does not yet permit a classification at family group level. The family Pteridiniidae Richter 1955 was based on a genus which is still incompletely known. It is not advisable to re-define it at this stage. The material from Ediacara which was previously placed in the species *Rangea arborea* Glaessner can now be separated into a species of *Rangea* (not including the holotype of *arborea*) and another species. Its markedly different characters had been considered earlier, on the evidence available from a limited number of specimens, as the result of post-mortem alteration of *Rangea*. The description of the genera and species now known requires a revision of descriptive terminology. For those genera which are close to Pennatulidae the terms applied to living forms can be used, although no polyps are discernible. But other genera deviate from living pennatulids and require new descriptive terms.

The body of all these fossils consists of a *rhachis* from which a leaf-like expansion (*frond*) spreads with bilateral symmetry, as a plant leaf spreads from its mid-rib. The term 'leaf' is not available, however, as in living pennatulids the numerous subordinate individual ridges which spread from, or are wrapped around, the rhachis are known as *polyp leaves*. They correspond to the *primary branches* which are delimited in fossils by *primary furrows* extending laterally from the sides of the rhachis or from the mid-line. In *Pennatula* the polyp leaves are deeply separated, so that there are no primary furrows, while in *Rangea* they are free only near the periphery (text-fig. 1*c*). In the species *arborea* they appear to have been rising above one surface of a *foliate base* (the main part of the frond), so that the term 'primary furrow' here becomes ambiguous. It could refer to a line on either side of the basal attachment of the polyp leaf or, since the polyp leaves may be flattened against the foliate base in fossilization, it could also refer to what in life was their free upper edge. The term *basal trace* is therefore used instead of primary furrow for this structural type. In *Pteridinium*, however, the primary branches are delimited by clear-cut primary furrows. In *Rangea* and *Charnia* the primary branches are clearly divided into *secondary branches* which correspond to the *anthosteles* in Pennatulacea. Such secondary branches and delimiting *secondary furrows* are also seen on the ventral side of *arborea*, but only very rarely and faintly in *Pteridinium*. The designation of the two sides of the foliate base as *dorsal* and *ventral* is conventional, as in all Pennatulacea, the rhachis often appearing as a wide track dorsally and as a narrow zigzag line between contiguous polyp leaves ventrally. The rhachis may extend downwards (in the living position) into a *stalk* which in Recent forms may end in a bulbous expansion. There are fossil specimens showing a long stalk with a pennatulacean fossil (like *Charnia* Ford) at one end, but there are also similar stalks ending in a round medusoid cast (like *Charniodiscus* Ford). No unquestionable fossil with a medusa-like base and a pennatulacean upper end has yet been found.

Genus RANGEA Gürich 1930

Type species. *Rangea schneiderhoehni* Gürich 1930.

The relations between the genera *Rangea*, *Charnia*, and *Pteridinium* require further study. A discussion of these general problems is beyond the scope of the present contribution.

Rangea longa sp. nov.

Plate 100, fig. 4; text-fig. 1

1959*a* *Rangea* sp. nov. (*partim*) Glaessner, pp. 1472–3.
1959 *Rangea arborea* (*partim*) Glaessner, *in* Glaessner and Daily, p. 383, pl. 45, fig. 1 (only).
1962 *Charnia* sp. b, Glaessner, pl. 1, fig. 5.

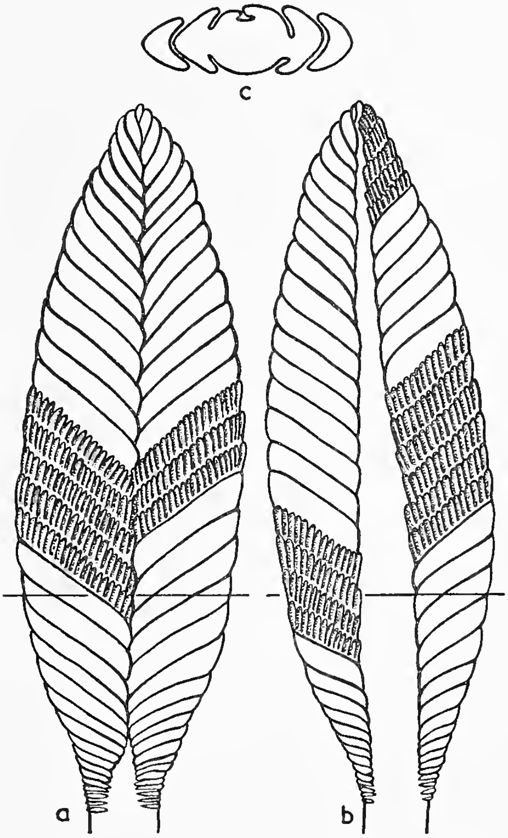
Material and preservation. Twelve specimens in good to fair preservation belong here. On one bedding plane they are preserved on the upper surfaces of rock slabs (Glaessner, *in* Glaessner and Daily 1959, pl. 45, fig. 1) but elsewhere they occur on lower surfaces; this is most common in all groups of fossils at Ediacara.

Holotype. P13777.

Dimensions. The holotype is 15 cm. long and about 6 cm. wide. The largest fragmentary specimen is 25 cm. long.

Diagnosis. Angle between axis and primary branches (polyp leaves) commonly acute, but it could evidently be modified by bending. Polyp leaves made up of secondary branches (anthosteles) of uniform appearance, elongated approximately at right angles to the free (upper) edges of the polyp leaves. The secondary branches are separated by furrows that are deeper at their upper ends. Twenty or more secondary branches in larger leaves, fewer in smaller leaves in every example.

Description. Outline of frond variable, from fusiform to very elongate. All specimens lie flat (or almost flat) on dorsal or ventral sides, indicating that their width must have exceeded their thickness prior to compression. The margins are lobate, the outwardly convex portions corresponding to the polyp leaves, and the indentations to the furrows between them. Normally these primary furrows are straight, lying at angles from 25° to 50° to the axis, the angles being steeper near the apex of the frond. The secondary furrows form approximately right angles with the upper edge of the polyp leaf. The largest number of these depressions counted is 17 but counts could not be made on complete leaves. The secondary furrows are most distinct near their upper ends, which could have divided the upper margin of the polyp leaves into separate lobes. In their position and varying degree of distinctiveness they correspond to the anthosteles of some modern pennatulids. In some specimens some secondary branches are transversely wrinkled. The width of the polyp leaves in the mid-portion of a frond is from about one-third to one-sixth of their length. Approximately 1:5 is the most common ratio.



TEXT-FIG. 1. *Rangea longa* sp. nov. Reconstruction based on the holotype and three other specimens, ×0·5 (approx.). *a*, ventral view; *b*, dorsal view; *c*, diagrammatic cross-section along transverse line,

Remarks. The most obvious differences between the type species *R. schneiderhoehni* and the Australian form are possibly due to preservation. They are the questionable 'outer flange' of the holotype of *R. schneiderhoehni* and the oblique angle which its secondary furrows make with the primary furrows. The African material consists, as far as we know, of only two specimens and is inadequate to elucidate which of its characters are diagnostic. No other material of this species has been obtained to date. Rather than doubtfully assign the better-known Australian material to the less well-known African species, we have described it as a new species. The holotype and other specimens from Ediacara of a species previously placed in *Rangea* can now be distinguished generically from *R. schneiderhoehni*, on the basis of new material. Some others are placed in *Pteridinium*. One unique specimen is considered as specifically distinct from *R. longa*.

Rangea grandis sp. nov.

Plate 100, fig. 5

1959*a* *Charnia sp.*, Glaessner, p. 1472, text-fig. 1*b*.
1959 *Rangea? sp.* (changed in addendum to *Charnia sp.*), Glaessner, *in* Glaessner and Daily, p. 397, pl. 46, fig. 2.
1961 *Charnia sp.*, Glaessner, p. 75, text-fig.
1962 *Charnia* sp. a, Glaessner, pp. 484–5, pl. 1, fig. 4.

Material and preservation. One fragment of the mid-portion of a large frond preserved as a cast on the lower surface of a rock slab.

Holotype. P12897.

Dimensions of holotype. Overall length of fragment approximately 160 mm., maximum measurable width 75 mm. The longer dimension of the lowest secondary branches (anthosteles) on either side is 20 mm., decreasing fairly regularly to 14 mm. in the highest pair of polyp leaves.

Diagnosis. Frond large. Ventral zigzag furrow irregular. Primary branches (polyp leaves) make an acute angle with the axis (30°–40° in the holotype). Secondary furrows divide the polyp leaves into secondary branches (anthosteles) with bluntly rounded tips but become shallow grooves across the lower one-half to two-thirds of the polyp leaves. The secondary branches are larger and fewer than in other species; they narrow somewhat towards the outer margins of the frond, and 13 is the greatest number known in one polyp leaf.

Remarks. *R. grandis* differs from *R. longa* and from *R. schneiderhoehni* in its much larger secondary branches (anthosteles), which are about three times as wide as the largest known in *R. longa*, and fewer in each primary branch. Diminishing width of the anthosteles away from the axial furrow has not been observed in *R. longa* or *R. schneiderhoehni*. Like *R. longa* and unlike *R. schneiderhoehni*, the secondary furrows of *R. grandis* are roughly at right angles to its primary furrows.

Genus PTERIDINIUM Gürich 1930

Type species. *Pteridinium simplex* (Gürich) 1930.

Topotype material of *Pteridinium simplex* was described by Glaessner (1963*a*).

Pteridinium cf. *simplex* (Gürich)

cf. 1929 'Nr. 1', Gürich, p. 85.
cf. 1930*a* 'Nr. 1' Gürich, pp. 671, 680, fig. 1.
cf. 1930*b* *Pteridinium simplex* Gürich, p. 637.

cf. 1933 *Pteridinium simplex* (Gürich); Gürich, p. 144, fig. 4*a–c*.
cf. 1955 *Pteridinium simplex* (Gürich); Richter, p. 246, pl. 1–6, pl. 7, fig. 11.
?1959 *Pteridinium* sp., Glaessner, *in* Glaessner and Daily, p. 382, pl. 46, figs. 3, 4.
cf. 1963 *Pteridinium simplex* (Gürich); Glaessner, p. 113, pl. 1, pl. 2, fig. 1.

Material and preservation. Two small and obscure specimens (P12744*a*, *b*, described in Glaessner 1959*a*), and four or five fragmentary larger specimens (collected 1964 by M. Wade). One of these (F17010A–C) is preserved as a generally convex cast (A) showing two fragments of a frond, with their median zones forming approximately a right angle. The margins of the larger fragment are obscured but appear to converge away from the smaller one which has the margins curled down giving a polygonal outline. There is a counterpart or natural mould (B) of this specimen, generally concave, showing the features of A in mirror image. A small piece of rock (C) was removed from this counterpart block. It shows a continuation of the larger fragment of A extending for 10–20 mm. along the median zone and actually overlying the left-hand side of the smaller specimen by about 10 mm. vertically. The two specimens could represent two individuals overlapping accidentally, or two fragments of the same individual. The other three specimens are convex casts, without counterparts. Two show short fragments of one side of the frond without the median zone. The lateral margin is preserved in one of them. The third fragment shows a short portion of the median zone and part of one lateral margin. As in the Nama quartzite from South-west Africa, the specimens are contorted and they are found on surfaces fractured by weathering. Only very small areas can be freed by further mechanical preparation.

Dimensions. The larger fragment of F17010 is about 80 mm. long, with a maximum width of about 55 mm. The smaller fragment is about 35 mm. long and up to 45 mm. wide. The other specimens are 48, 45·5, and 42 mm. The distances between primary furrows are 4–4·5 (F17010), 5·4, 2·3–3·5, and 5 mm.

Occurrence. Remains of *Pteridinium* were first recorded from the fossiliferous flaggy quartzites. Others have since been found in a massive quartzite on a low hill top about 3000 ft. north-north-east of the southernmost outcrop of these beds, some 60 ft. stratigraphically below the main fossiliferous beds. At this locality the rock outcrop is affected by later silcrete formation during weathering. *Pteridinium* is the only fossil found here.

Remarks. The new material from Ediacara obviously represents one species. The two specimens described earlier from the richly fossiliferous beds can be included in it only doubtfully, because of poor preservation. This material has been compared in detail with *P. simplex* from the Kuibis Quartzite of South-west Africa, as represented by about 18 specimens described by Richter (including the neotype of which a cast is available to us), 8 specimens lent by the Geological Survey of South Africa, and 8 specimens lent by the Museum of South-west Africa. Thirty-four specimens of this species are now known.

The characters of *P. simplex* and their variability have been comprehensively described by Richter (1955), who gave careful attention to the influence of peculiarities of preservation on the appearance of these fossils. Little can be added to his observations. Some additions, based on the South African Geological Survey material (Glaessner 1963) can be summarized as follows: (1) The presence of secondary furrows between the primary furrows, noted by Gürich but questioned by Richter, has been confirmed on one specimen. (2) The interpretation of the course of the primary furrows as 'forward and outward' as proposed by Richter has been questioned and a more transverse course with distal convexity assumed. Admittedly, this is still hypothetical and the true position of the proximal end has not been established beyond doubt in any specimen. (3) A broad (5 mm.) median zone was found in one specimen (No. 1), instead of the median narrow zigzag line, but here again there is no confirmation from other specimens. The removal of a piece of quartzite at the lower end of this specimen (as figured on pl. 2, fig. 1, Glaessner 1963) has revealed a part of a convex cast 70 mm. long along the median zone. Its lateral zone is separated from that of the originally described concave mould by up to 7 mm. of rock. This could be a 'lower surface' (as in Richter's pl. 2, fig. 3 and pl. 4, fig. 5*c*, x–x), but no less than four other interpretations of this specimen are possible, based on varying assumptions of folding-over and subsequent loss by erosion or lithification of half-specimens, as described in some of Richter's specimens in which duplication by apposition has occurred. Some of these interpretations would make it doubtful whether the broad median zone now visible on the mould is an original character of a single specimen. Two of the new specimens from Ediacara and five of the eight specimens of *P. simplex* from the Museum of South-West Africa again show only a narrow median zigzag line; in the others this region is not preserved or not clearly visible.

The material from Ediacara, like that from South-West Africa (with the one possible exception mentioned) shows identical aspects of *Pteridinium*, consisting of a leaf-shaped surface with a median zone developed as a narrow zigzag line from which primary furrows extend laterally, with slightly staggered placing of their origins. Measurements of the spacing of these furrows indicate a slightly greater width (5·0, 5·4 mm.) in two of the Ediacara specimens than in the African material, in which 4·7 mm. seems to be the widest and about 2 mm. the narrowest. No gradients of spacing along the frond length have been observed and too few reliable widths of fronds to which spacings could be related are observable to be significant for comparison. Another possibly diagnostic character of the Ediacara material is a convergence of primary furrows (and narrowing of primary branches) towards the margins of the fronds. This, however, was observed only on 5–6 primary branches, while others give only a general impression of greater curvature. The distinction between inner and outer lateral zones is weaker than in some South-West African specimens but this is a variable character.

The distinguishing characters of the few specimens of *Pteridinium* from Ediacara do not appear to be sufficiently diagnostic from those of the much more abundant material of *P. simplex* to establish a new species.

The interpretation of *Pteridinium* rests largely on its similarity with *Rangea* and *Arborea*. Richter had referred both forms to the Gorgonacea, assuming that the frequently observed apposition of specimens was indicative of the diagnostic branching of fronds in this group. The large number of specimens of *Pteridinium* now known, without a single branching one among them, disposes of his argument. Richter also concluded from the apposition and from the apparently sediment-infilled specimens that *Pteridinium* had a 'lower' surface which was virtually identical with the upper surface and in which ridges rising upwards corresponded in position to grooves, and depressions to the upwardly convex primary branches. This remains questionable. Alternatively, the 'lower' surface could have been featureless and perishable, leaving essentially an 'upper' lamina as the only potential fossil to represent a former somewhat *Renilla*-like organism.

Genus ARBOREA gen. nov.

Type species. Rangea arborea Glaessner 1959.

Diagnosis. Dorsal track broad, ventral track narrow to fairly broad, zigzag-shaped; rhachis extends downwards to form a stalk ending probably in a basal expansion. The rhachis extends laterally into a thin, smooth, foliate base forming a frond with entire margins. Lateral primary branches can be seen as ridges on both ventral and dorsal sides of the foliate base, but they do not project as much on the dorsal side as they do ventrally. The mainly ventral attachment of the foliate base to the rhachis produces in less compressed specimens triangular pocket-like hollows between the rhachis and each of the primary branches on the dorsal side. Flange-like polyp leaves showing grooves (secondary branches), apparently delimiting fused anthosteles, arise from each basal trace. They are probably confined to the ventral side and end before reaching the margin or on it. Their preservation in varying positions indicates that their free edges extended away from the foliate base in life. Sharp, straight, linear grooves on the rhachis ('median field') and primary branches can be interpreted as impressions of spicules.

Remarks. Abundant new material has led to a reinterpretation of the pennatulacean fossils from Ediacara. The forms with pronounced spicular impressions, formerly considered as distinguished from typical forms of *Rangea* mainly by their state of preservation, also possess flange-like and flexible primary branches which do not reach the leaf margins.

Arborea arborea (Glaessner) 1959

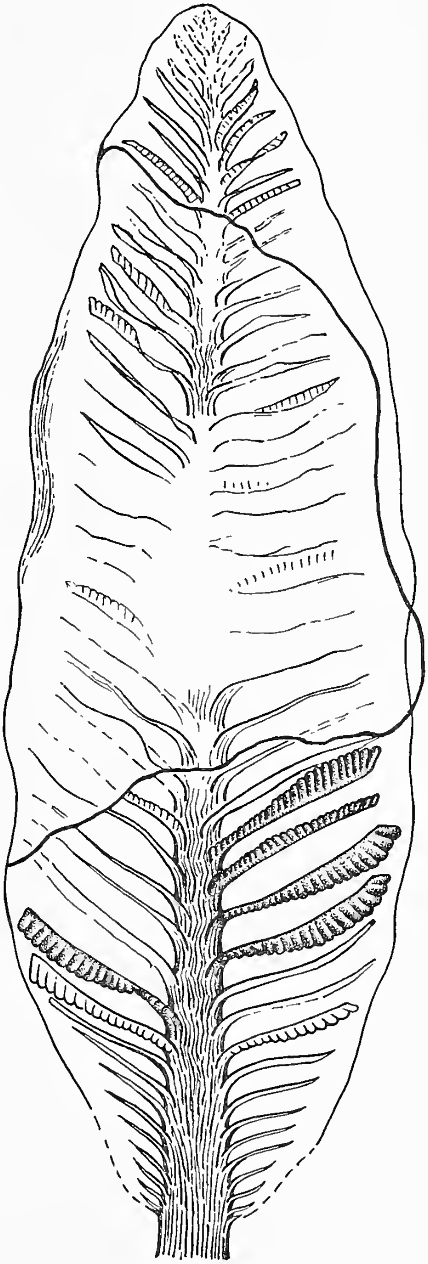
Plate 102, figs. 1, 2; text-fig. 2

1959*a* *Rangea* sp. nov. (*partim*) Glaessner, pp. 1472–3.
1959 *Rangea arborea* Glaessner, *in* Glaessner and Daily, p. 383, pl. 43, figs. 1–3, ?fig. 4; pl. 44, figs. 1–3; pl. 45, fig. 2 (part), ?pl. 46, fig. 1.

Material. 35 specimens.

Dimensions. The incomplete holotype (P12891) measures 15 cm. along the axis. Its greatest measurable half-width is 5·5 cm. The largest known specimen is about 60 cm. long and over 10 cm. wide.

Diagnosis. Spicules in the axis lie approximately longitudinally in the dorsal track, but zigzag from side to side of the ventral track at the insertions of primary branches. In the frond, spicules are approximately parallel to the primary branches.



TEXT-FIG. 2. *Arborea arborea* (Glaessner). Drawing of the holotype surrounded by reconstruction based on other specimens. ×0·5.

Remarks. The polyp leaves may be buried in a collapsed position, forming a ridge on the basal trace, with all structure blotted out, or they may be folded flat against the foliate base, upwards (i.e. towards the apex), or downwards (towards the stem). Composite moulds show the secondary branches (anthosteles) as convex projections and the secondary grooves as furrows. They were soft enough to collapse like medusae downwards into the sediment while those of *Rangea longa* (but not *R. grandis*) usually stood up long enough to produce external moulds at the base of the overlying sedimentary layer. This supports the supposition that they are often absent because of comparatively rapid disintegration of the polyp leaves which also brings the supporting spicules to the surface to form clear-cut impressions. As the polyp leaves of *Arborea* show more clearly on the ventral than on the dorsal side of a foliate base, this genus may be compared with *Renilla*, but in this living form there is no linear arrangement of the polyps on the surface of the foliate base.

Phylum Annelida

Genus DICKINSONIA Sprigg 1947

Type species. Dickinsonia costata Sprigg 1947.

This genus, representing the Family Dickinsoniidae Harrington and Moore 1956, differs from *Spinther* in the absence of the claw-like parapodia which this living genus uses in its predatory life on sponges. *Dickinsonia* was a free-living organism, apparently moving on the sediment or in the water above it by body undulations rather than by parapodial crawling. Specimens of *Dickinsonia* are preserved as moulds or casts. There are partly decayed specimens showing frayed edges and traces of longitudinal muscles, and specimens with multiple impressions of the peripheral margin resulting from contraction after the first contact with the substratum.

Dickinsonia costata Sprigg

Plate 101, fig. 4

1947 *Dickinsonia costata* Sprigg, p. 221, pl. 7, fig. 2.
1947 *Papilionata eyrei* Sprigg, p. 223, pl. 8, fig. 2.
1949 *Dickinsonia costata* Sprigg, *D. minima* Sprigg, p. 95, pl. 18, fig. 2; pl. 19, figs. 1, 2; pl. 20, figs. 1, 2; pl. 21, figs. 1–4; text-figs. 9, 10.
1955 *Dickinsonia spriggi* Harrington and Moore, p. 160.
1956 *Dickinsonia costata* Sprigg, *D. minima* Sprigg, *D. spriggi* Harrington and Moore, *in* Moore, p. F24, figs. 13–16.
1956 *Papilionata eyrei* Sprigg; Harrington and Moore, ibid., p. F159.
1959*b* *Dickinsonia costata* Sprigg, *D. minima* Sprigg; Glaessner, p. 526, fig. 4.
1959 *Dickinsonia costata* Sprigg; Glaessner, p. 379.

EXPLANATION OF PLATE 101

Figs. 1–3. *Pteridinium* cf. *simplex* (Gürich). 1, 2, counterpart casts and moulds of specimen F17010A–B above and possibly another specimen below. 3, same as 2 with part of cast (F17010C) which was removed in 2 to reveal underlying surface. × 1.

Fig. 4. *Dickinsonia costata* Sprigg. Hypotype, T53. Cast with faint segmental sculpture and with infilled intestinal caeca on antero-median part. × 1.

Fig. 5. *Tribrachidium heraldicum* Glaessner. Holotype, P12898, × 3. As the holotype is an external mould (impression), the direction of the curvature of the three arms is reversed from that in the animal as represented by latex casts (Pl. 99, fig. 5).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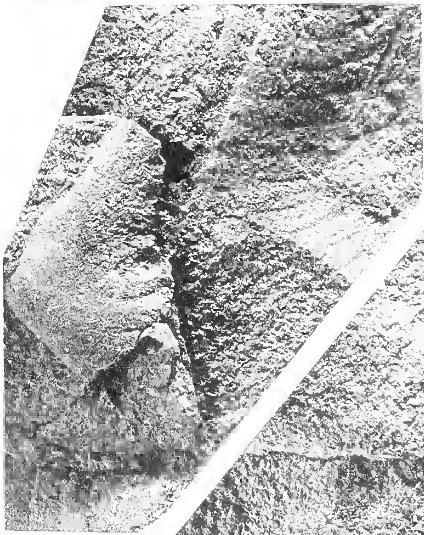
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2

GLAESSNER and WADE, Late Precambrian fossils from Ediacara, South Australia

1959 *Papilionata eyrei* Sprigg; Glaessner, p. 380.
1961 *Dickinsonia costata* Sprigg; Glaessner, p. 74, text-fig.
1962 *Dickinsonia* sp. Glaessner, pp. 484, 493, pl. 1, fig. 7.

Material. Approximately 250 specimens occur as impressions on the bases of beds; several have counterpart casts on the tops of the underlying beds.

Dimensions. Generally the length exceeds the width but the largest specimen is about 17 cm. long and 18·5 cm. wide, probably because of contraction. The smallest specimen is less than 1 cm. long.

Diagnosis. Broad, flat polychaet worms, growing to large size; with left and right halves of anterior body-segment fused together pre-orally; with intestinal caeca that branch dichotomously around pharynx; pharynx situated at centres of first few segments; segmental furrows depressed dorsally and ventrally; dorsal lamellae rarely fossilized.

Remarks. The discovery of a specimen of *D. costata* showing some intestinal caeca has established the position of these fossils among the annelids. The pattern of the caeca has increased the previously noted known resemblances of *Dickinsonia* to *Spinther*, the only other worm known with a similarly fused anterior body segment, which were indicated by Glaessner (1959*b*, 1961, 1962).

The specimen for which Harrington and Moore (1955) erected the species *D. spriggi* is badly preserved and has had most of its edges broken off at the margins of the rock. The lineation considered as the edge of the body by Harrington and Moore is a slight step fault in the rock, and the impression is markedly shallower on the down-thrown side than in the more axial portion of its body. This change of preservation occurs at differing distances from the axis. The faintly preserved furrows are not discrete marginal tentacles and this specimen does not provide evidence for the placing of *Dickinsonia* in a coelenterate 'Class Dipleurozoa' as proposed by Harrington and Moore. It is probably *D. costata* as Sprigg (1949) had thought. Numerous newly discovered specimens have bridged the apparent gap separating *D. costata* from *D. minima* Sprigg, which is accordingly placed in the synonymy of the type species.

Dickinsonia elongata sp. nov.

Plate 102, fig. 3

Material. One juvenile specimen with both anterior and posterior ends, one adult lacking anterior end and right side, three distorted adults lacking anterior ends, and many fragments, some very large.

Holotype. P13767.

Dimensions. The holotype, a juvenile specimen, is just over 16 cm. long; it has approximately 100 segments. The adult specimen, which is partly preserved on a broken slab, measures 33·5 cm. with 250 segments but appears to have been buried in a limp and stretched condition. The three distorted adults seem to have been at least 30–40 cm. long; one has 380 segments in about 31 cm., including the diminishing segments of the posterior end. Fragments of greater width suggest larger specimens still; one has 190 segments in a length of 19 cm., its half-width from periphery to median line tapering from 11 cm. to little more than 8 cm.

Diagnosis. Elongate, rounded anteriorly, tapering posteriorly. Only the anterior segments are appreciably shorter in the axial region than in the peripheral region. They are followed by up to several hundred similar segments of constant length and width, forming a long mid portion of the body. The proportion of width to length of these segments is about 100:1 or more.

Dickinsonia tenuis sp. nov.

Plate 103, fig. 1

Material and preservation. 16 specimens of good to poor preservation and a number of fragments. The segments are so short that the grain size of the sediment tends to blot them out. Some specimens are preserved as casts on the bases of quartzite slabs, others as external moulds.

Holotype. P13769*a*.

Dimensions. Not many specimens are well enough preserved for accurate measurements. The species is very variable in its proportions but the smaller forms are all relatively narrow (some being half as wide as long, others relatively wider) while most of the larger forms are not much longer than wide. The holotype is the largest specimen. It is almost complete but the posterior end is very faint. It is 19–21 cm. long and 15–16 cm. wide, the width probably being reduced a little by the position of the body. It had approximately 380 segments.

Diagnosis. Rounded to elongate outline, very short segments, numbering up to several hundred. They are three or more times as numerous as in specimens of *D. costata* or *D. elongata* of the same length.

Remarks. While the overall shape of *D. tenuis* is similar to that of *D. costata*, its very short segments clearly differentiate it from both *D. costata* and *D. elongata*. A contracted specimen shows the same pattern of ridges and grooves as a contracted *D. costata*. The preservation of several individuals as natural casts on the bases of quartzite slabs may indicate that the tissues of *D. tenuis* were less resistant to decay than those of *D. costata* and *D. elongata*, since in the Ediacara fossil beds natural casts on the lower surfaces of beds are otherwise known only among the medusoids.

Genus SPRIGGINA Glaessner 1958

Type species. Spriggina floundersi Glaessner 1958.

Studies of abundant new material of the species of *Spriggina* are in progress and will be reported later. A new species tentatively assigned to this genus is recorded here.

Spriggina? *ovata* sp. nov.

Plate 98, fig. 4

Material and preservation. Four external moulds. The fossils are here described from latex casts.

EXPLANATION OF PLATE 102

Figs. 1, 2. *Arborea arborea* (Glaessner). 1, Composite mould, hypotype, P13787, showing ventral narrow zigzag line above, wide dorsal rhachis below, with some lateral spicule impressions to the right and flattened primary branches (polyp leaves); secondary branches (anthosteles) on left side. 2, hypotype, F17018, composite mould with dominantly ventral aspect, showing primary and secondary branches. D marks lateral margins of rhachis on dorsal surface, preserved by composite moulding. The polyp leaves appear to be mostly turned upwards on the left and downwards on the right. ×1.

Fig. 3. *Dickinsonia elongata* sp. nov. Holotype, P13767. An impression (external mould) showing some distortion of the axial furrow (a ridge in the mould), due probably to the intestine or other internal organs. The surfaces of the segments are wrinkled by contraction of transverse muscles, with folds continuous across anterior segments but interrupted at segmental boundaries of the smaller middle and posterior segments. ×1.

Fig. 4. *Praecambridium sigillum* gen. et sp. nov. Holotype, P13794, ×5.

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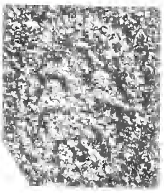

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GLAESSNER and WADE, Late Precambrian fossils from Ediacara, South Australia

Holotype. P13754.

Dimensions. In mm.

No.	*Length along axis*	*Max. width*	*No. of body segments*
P13754	22	8·5	about 40
P13755	19	8·0	about 40
P13757	31 approx.	11	probably nearly 50
P13756	broken at 24	15	23 present

Diagnosis. Elongate-oval polychaet worms. Prostomium arcuate, narrower than the broadest part of the body, which is a short distance behind it. The tapering postero-lateral processes of the prostomium possibly bear setae. Segments up to 50 or more, very short and broad, with parapodia apparently supported by bundles of long acicular setae. An axial groove is bounded on each segment by a pair of small ridges which are broadest and highest adaxially. On unflattened specimens the ridges terminate in a pair of small bosses adjacent to the parapodia, at least on the larger segments. A pair of small elongate ridges (such as teeth could form) occupy a near-axial position just behind the prostomium.

On the best-preserved and on one flattened specimen, long setae are attached to the segments, between the axis and the parapodia. These setae are generally oriented in backward-curving groups and tend to obscure the segmentation.

Remarks. In its arcuate prostomium with postero-lateral processes *S.*? *ovata* resembles *S. floundersi,* but its prostomium was not equally resilient and only its anterior edge is clearly preserved. A pair of large teeth was probably present, while there is no evidence of teeth in *S. floundersi.* There were no long dorsal setae in *S. floundersi.*

? Phylum uncertain

Genus PRAECAMBRIDIUM gen. nov.

Type species. Praecambridium sigillum sp. nov.

Characters of type species.

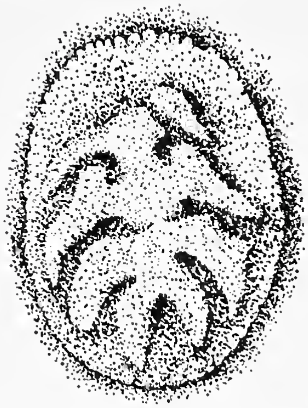
Praecambridium sigillum sp. nov.

Plate 102, fig. 4; text-fig. 3

Material and preservation. Seven moulds on the bases of quartzite slabs. Four specimens of good to fair preservation are on one slab, and three on isolated slabs. Two further isolated specimens show similar but less distinctive features. The species is here described from latex casts.

Holotype. P13794.

Diagnosis. Oval disc-shaped bodies less than 5 mm. in length and under 4 mm. wide. One is slightly conical, rising 0·15 to 0·2 mm. above the bedding plane; the remainder are flattened. The surfaces of the casts each bear three pairs of small raised lobes and an axial lobe. These lobes are more or less confluent in the centre. The axial lobe of the best-preserved specimen bears another pair of small lobes laterally. All the paired lobes taper to pointed outer ends which are directed towards one end of the disc. This is here considered the posterior end. The axial lobe is rounded at the opposite (anterior) end.



TEXT-FIG. 3. *Praecambridium sigillum* gen. et sp. nov. Holotype, P13794, × 10.

Remarks. The interpretation of these minute fossils is difficult. It seems reasonable to assume that the lobes are muscle impressions in a thin and probably rather soft shell. Like other Ediacara fossils some of these forms were distorted but they are not known to have broken. The fossils may be composite moulds of thin shells with segmental muscles, but they do not conform with the pattern of the Monoplacophora, as the muscle impressions (if they are correctly interpreted as such) were partly median. In this respect there is a resemblance with the description of the larger Cambrian genus *Cambridium* Horny 1957, but no close relationship is suggested.

A more striking resemblance is found with the Lower Cambrian genera *Mobergella* Hedström 1923, and *Discinella* Hall 1872. [The genus *Barella* Hedström 1930 is invalid. It was based on Barrande's 'opercule isolé H', from the middle Ordovician of Osek in Bohemia, which was recognized by Zazvorka in 1930 as an operculum of *Hyolithes paxillosus* Novak.] The difficult question of the status of these genera and their true nature is still undecided. It was reviewed recently by Åhman and Martinsson (1965) who also gave the first clear illustrations of *Mobergella holsti* (Moberg). Their final conclusion is as follows:

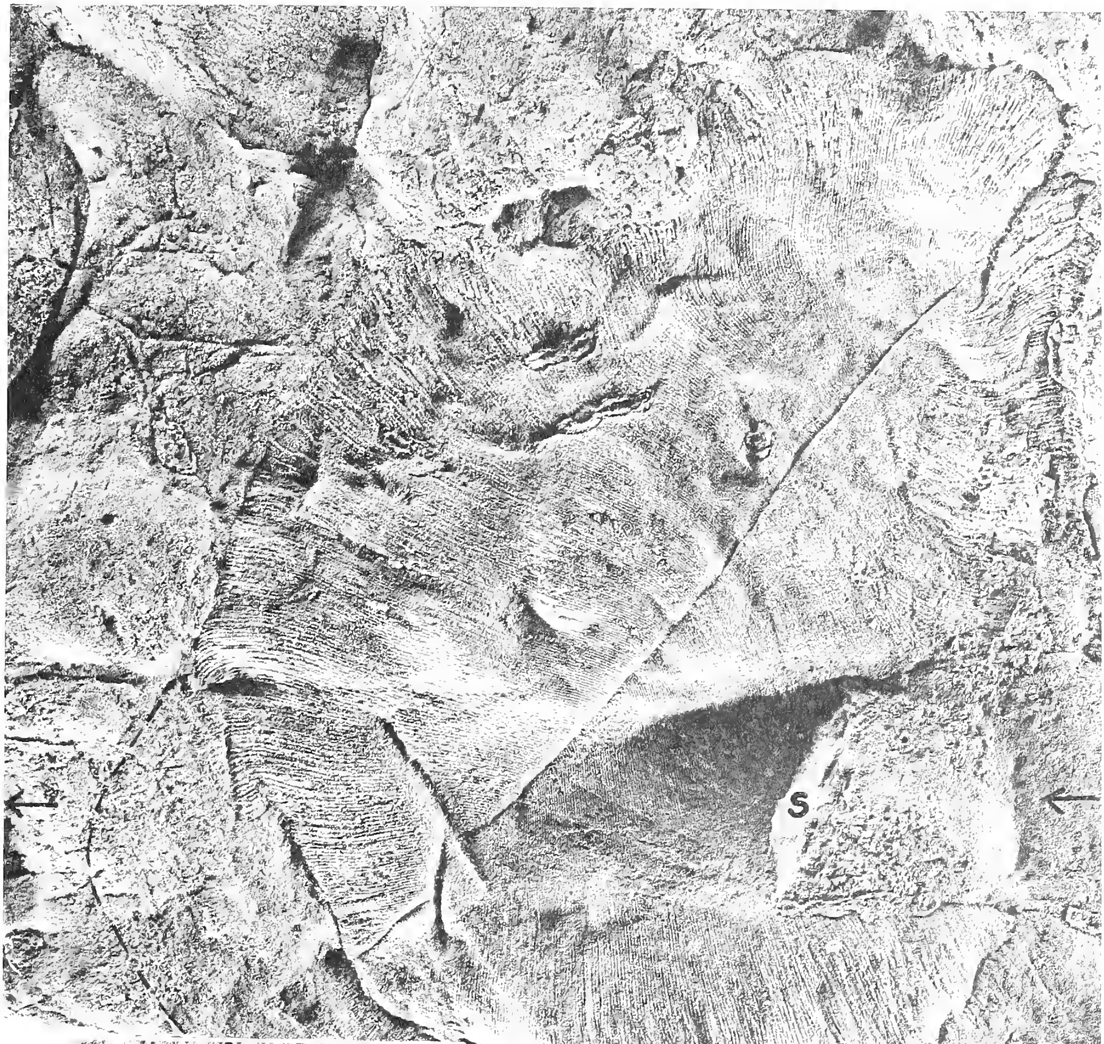
> As long as the number of muscle scars may be accepted as a distinctive character, this fossil should be called *Mobergella holsti* (Moberg). For the first time it has been found together with tubes with which it may be associated as an operculum, but the material leaves us without an absolutely convincing solution of the classical problem whether the disc has belonged to a sedentary hyolithellid or is the remains of a free-living mollusc. Without turning a blind eye on the latter interpretation we may state that the accumulated observations are very strongly in favour of the former one.

The new form has not been found together with *Hyolithellus*-like tubes. It is distinguished by its elongate-oval outline and by the pattern of the presumed muscle impressions, which show a concave curvature towards the posterior end of the disc, while in the known genera they are straight or concave anteriorly. They are confluent along an elongate median zone while in *Mobergella* and *Discinella* they merge at the apex in the anterior third of the length of the shell. No such eccentric apex is known in *Praecambridium*. Whatever will be the final decision about the systematic position of the problematic Cambrian genera, the new genus is morphologically distinct, differing from them more than they differ from each other, yet similar enough to be considered as probably related to them.

EXPLANATION OF PLATE 103

Fig. 1. *Dickinsonia tenuis* sp. nov. Holotype, P13792, × 0·8. The specimen is a cast on the lower surface of a bed. The anterior end is in the right upper corner. The body was deposited across a stem of a large but poorly preserved *Arborea* which was partly sand-filled (s). Arrows mark its centre line, pointing upward. Lateral branches begin to show on the rock about 5 cm. to the left and a bulbous expansion about 10 cm. to the right from the margins of the picture.

Figs. 2–4. *Pseudorhizostomites howchini* Sprigg. 2, Hypotype, F17011, view from the lower surface of the bed. 3, 4, views of the sides of the break seen across the specimen in 2, showing fluted surfaces of the passage above the centre furrow. Arrows point to the upper surface of the bed. × 1.



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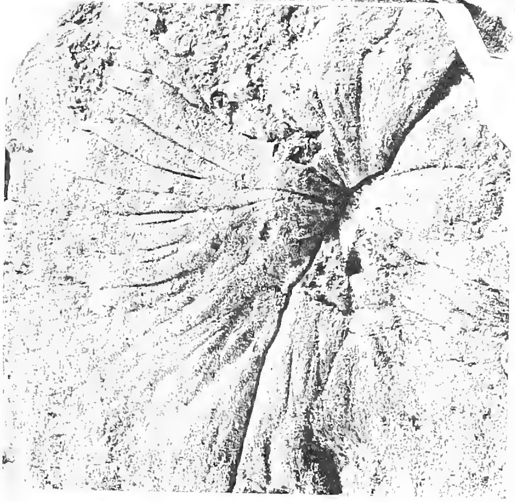

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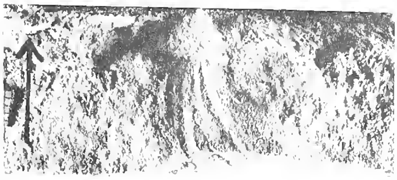

4

GLAESSNER and WADE, Late Precambrian fossils from Ediacara, South Australia

Genus PARVANCORINA Glaessner 1958

Type species. Parvancorina minchami Glaessner 1958.

Parvancorina minchami Glaessner 1958

1958 *Parvancorina minchami* Glaessner, p. 187, pl. 1, fig. 4.
1959 *Parvancorina minchami* Glaessner, p. 528, text-fig. 3.
1959 *Parvancorina minchami* Glaessner, *in* Glaessner and Daily, p. 380, pl. 47, figs. 5, 6.
1960 *Parvancorina minchami* Glaessner, pp. 60, 62.
1961 *Parvancorina minchami* Glaessner, p. 75, text-fig.
1962 *Parvancorina minchami* Glaessner, p. 484, pl. 1, fig. 9.

Dimensions. The largest specimen, obliquely deformed, is 26 mm. long and 27 mm. wide. Less deformed specimens are 25, 23, and 22 mm. long and, respectively, 21, 21, and 23 mm. wide. The smallest specimen is 3 mm. long and less than 2 mm. wide.

Diagnosis. Small shield-shaped fossils with an elevated, anchor-shaped, antero-median ridge bearing curved, linear postero-lateral appendages on its anterior arms and finer transverse appendages on its median bar.

Remarks. About 60 specimens of this form are now available, representing a wide range of sizes. Other specimens found recently have not shown any additional morphological characters. They show the growth range and the post-mortem deformation of the integument, which was pliable and possibly chitinous. It is not clear whether some feeble ridges on the inverted anterior portion of one specimen are reflected dorsal or independent ventral structures.

Genus TRIBRACHIDIUM Glaessner 1959

Type species. Tribrachidium heraldicum Glaessner 1959.

Tribrachidium heraldicum Glaessner 1959

Plate 97, fig. 9; Plate 99, fig. 5; Plate 101, fig. 5

1959 *T. heraldicum* Glaessner, *in* Glaessner and Daily, p. 389, pl. 47, figs. 7, 8.
1960 *T. heraldicum* Glaessner, pp. 60, 62.
1962 *T. heraldicum* Glaessner, p. 484, pl. 1, fig. 6.

Material and preservation. 40 specimens are available; 34 upper (oral) sides, one of which has a counterpart showing the lower (aboral) side. The aboral side is an almost featureless disc and this explains the failure to identify it when its casts or moulds occur alone. The remaining 5 specimens are composite moulds dominated by the rather resistant marginal zone of the body, which forms an outer ring.

The material occurs as impressions (external moulds) on the lower surfaces of quartzite slabs, with the exception of the one external mould of the aboral side which is separated from the overlying lamina only by a thin, sericitic parting and the space contained between the two laminae. Elsewhere on the same bedding plane the lower lamina remained sufficiently plastic during diagenesis to form a natural cast of the impression of another specimen in the upper lamina. Another natural cast of a different specimen of *Tribrachidium* is known from a rock with only a thin sericitic parting between the laminae. Thus all except one of the counterparts are natural casts of the mould on the overlying lamina, or composite moulds.

The species is described from latex casts of the external moulds.

Holotype. P12898.

Diagnosis. Disc-shaped fossils, slightly biconvex, with a steeply sloping margin; up to about 4 cm. in diameter. The diameter of the smallest specimen on which the edge of the disc can be seen, is 9 mm. The oral side has three raised brachia radiating from the centre and curving in a clockwise direction to become parallel to the periphery, and tapering to their extremities. The curve is more evenly rounded in small specimens and more angular in large ones. A small, central, Y-shaped groove which may represent the mouth is seen very rarely between the arms. Dome-shaped 'bullae' (Glaessner 1959 *b*) occupy part of each interbrachial space, each being attached to the neighbouring convexly curved side of an arm. The arms (brachia) and bullae are elevated above the oral surface and have resisted flattening to some extent. The distal two-thirds of each arm bears short stout tentacles on the outer side and tip. The number of tentacles is generally greater in larger specimens, and some appear to be arranged in alternating series. Fine, long, straight or gently curved bristles, all equal in width, extend from the crest and the concave curve of each arm towards the periphery and can also be seen extending from the surface of interbrachial spaces past the tip of an adjoining arm. They are not preserved in all specimens.

Only a few, shallow, concentric grooves occur on the aboral side. A wide marginal zone shows in composite moulds; though subject to some flattening, it does not transmit structures of the oral side, which suggests considerable resilience.

Remarks. A distorted specimen, the largest (Pl. 97, fig. 9), shows numerous bristles extending radially from the crests of the arms, which are unusually sharp in this specimen. They obscure the surface of the arms. The greatest number of bristles that can be counted as attached to one arm in this specimen is 40. The number of tentacles on the three arms appears to differ slightly in some individuals and to differ strongly between different individuals of the same size. In specimens over 2 cm. in diameter the number of tentacles on one arm appears to vary between 16 and 30, though the exact number has not been determined.

Glaessner (1959, 1960, 1962) has mentioned the superficial resemblance of *Tribrachidium* to certain Edrioasteroidea which show relics of tri-radial symmetry, but has discounted suggestions of relationship between *Tribrachidium* and echinoderms because of the complete absence of any traces of calcareous plates and of an ambulacral system. Since then the resemblance has been strengthened by the discovery of specimens with a central Y-shaped groove which could represent the mouth, and by the recognition of bristle-like appendages on the surface. These are straight or gently curved, thin, long and rather stiff but not brittle. In discussions with one of the present authors (M. F. G.), Professor H. B. Fell (Museum of Comparative Zoology, Harvard University) argued persuasively in favour of a relationship with echinoderms, considering the calcareous skeleton as not essential for it and suggesting that the bristles might be tube feet. It is difficult to see in the available material the precise manner of their attachment. They were certainly not attached in regular rows to the crests of the arms, as the casual inspection of an oddly preserved specimen (Pl. 97, fig. 9) might suggest. They can be seen to cross the arms from at least their inner margins, if not from the inter-brachial spaces. They could have arisen in positions adjacent to the arms or, alternatively, all over the body like the tube feet in *Holothuria*. They could have been respiratory organs, being stiff and flexible, rather than prehensile and capable of being bent by muscles like true tube feet.

Thus they could have been the kind of 'passive tube feet' which Nichols (1962, p. 152) suggests may have existed in Agelacrinidae. The basal surface of *Tribrachidium* was probably a tough membrane like that which Nichols (p. 153) believed could have existed in *Edrioaster* so that, as Bather had suggested earlier, it could have provided a sucker for temporary attachment as well as a muscular base for limpet-like movement. These new observations and suggestions provide a still tenuous line of argument connecting *Tribrachidium* with echinoderms, perhaps phylogenetically rather than taxonomically. The lophophore-like apparatus of tentacles will also have to be considered in future functional and phylogenetic interpretations of *Tribrachidium*, but these are beyond the scope of the present paper.

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ADDENDUM

Two additional important specimens were collected at Ediacara in August 1966. (1) A complete external mould of a dickinsoniid worm, 77 mm. long, shows very fine transverse grooving which is probably not segmental. Previously found specimens of this form were distorted or badly preserved. Though its anterior end is similar to *Dickinsonia*, the surface sculpture distinguishes this form specifically and possibly generically. (2) A specimen attributed to *Conomedusites* is twice as large as the previous specimens. It is a cast on the lower surface of a bed, with tentacles up to 14 mm. long around part of its periphery but without a marginal flange. It resembles the Ordovician *Conchopeltis alternata* Walcott 1876 (Moore and Harrington, *in* Moore 1956, p. F32, fig. 22, and p. F57) but shows no radial striation.

DISTRIBUTION OF SPORE AND POLLEN ASSEMBLAGES IN THE LOWER KITTANNING COAL OF WESTERN PENNSYLVANIA

D. HABIB

ABSTRACT. Palynological study of the Lower Kittanning coal seam of western Pennsylvania (Allegheny Series; lower Westphalian D) has revealed an orderly vertical and geographical distribution of spore and pollen assemblages.

Assemblages characterized by *Densosporites* and *Punctatisporites* (*P. obliquus*) occur in the uppermost zones where the seam is directly overlain by marine and restricted-marine faunal facies, respectively, of the Lower Kittanning shale. The greatest vertical variation of assemblages occurs at these localities. Where the seam is in direct contact with the overlying freshwater facies, however, it remains dominated throughout its thickness by assemblages rich in *Lycospora*. Fewer assemblages occur at these localities. Because of the distribution of spore and pollen assemblages in the seam and faunal facies in the overlying shale, a genetic relationship is suggested.

New taxa include two genera, *Spackmanites* and *Paleospora*, and thirty-three species.

THE Lower Kittanning coal seam in western Pennsylvania is one of the more readily identifiable and geographically extensive stratigraphic horizons of the Allegheny Series (middle Pennsylvanian age). Because it is easily recognized, variations in the biological, physical, and chemical properties of the seam and surrounding rocks have been investigated. The known variation in these properties has prompted investigation of the seam once again, this time to determine the vertical and geographic distribution of its spore and pollen assemblages. It was assumed at the beginning of this study that if distinctive spore and pollen assemblages at least partially represent *in situ* Lower Kittanning plant communities, then some distributional pattern of their assemblage zones should be discernible, in light of the known distributional pattern of other properties in the seam and juxtaposed rocks.

Methods of study. Vertical columns of the Lower Kittanning seam were collected from 15 localities in the western part of the state (text-fig. 1). A one-inch increment of coal was taken at three-inch levels in sequence in each column from the top downward. Where the bottom-most sample did not coincide with this interval, it was taken as an additional sample. The density of sampling sites was intended to cover a large area while keeping the geographic interval small.

Maceration of the samples consisted of oxidation in nitric acid or Schulze's solution, and subsequent treatment in 8% potassium hydroxide. The spore residue was then mounted on slides in glycerine jelly. Two hundred specimens were counted from each sample (100 per slide). The entire slide was examined at ×100 and/or ×450 magnification, in order to determine the total number of species per sample.

Geological setting. The Kittanning formation comprises the middle third of the Allegheny Series (Westphalian C–D). The formation is defined by three major coal horizons which are separated by two thicker and lithologically more variable detrital units. The lowermost coal seam, the Lower Kittanning, is overlain by the Lower Kittanning

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shale, a unit which separates the seam from the next overlying coal horizon by an interval of from 30 to 50 ft.

On the basis of the distribution of fossil invertebrates in the Lower Kittanning shale, Williams (1959) differentiated facies depicting marine, restricted-marine, and fresh-water environments of deposition. In a northwesterly direction across the sedimentary strike of the marine embayment, the fresh-water facies of the Lower Kittanning shale, represented by estherids, changes to restricted-marine (*Lingula*, *Aviculopecten*), and marine (*Mesolobus*, other calcareous brachiopods, gastropods) facies in respective order, before reverting through restricted-marine and fresh-water facies. Geochemical evidence corroborates the delimitation of marine and fresh-water facies. Degens *et al.* (1957, 1958) distinguished these facies by relative abundance of trace element assemblages. Greater concentrations of boron and rubidium were found in the marine shales, while gallium was found to be more abundant in the fresh-water shales. Williams and Keith (1963) subsequently showed a statistical relationship between the sulphur content of the seam and the facies of the directly overlying rocks (Lower Kittanning shale), the content being higher in the seam where it directly underlies ancient marine sediments. Weber *et al.* (1964) distinguished fresh-water siderite nodules in the Lower Kittanning shale from marine nodules through distinct differences in their carbon isotope ratios.

Sampling Sites

Station 1. Section exposed in a limestone quarry, 7 miles west of New Castle, Pennsylvania. The Vanport limestone is mined here and is exposed approximately 40–50 ft. below the Lower Kittanning seam. Marine shale overlies the seam, characterized by *Lingula* and *Mesolobus*.

Station 2. Section exposed in coal strip pit, 1 mile east of West Pittsburg, Pennsylvania. The seam is slightly thicker than that reported for the Lower Kittanning in this area.

Station 3. Section exposed in a road cut, on the east side of a toll bridge, 1 mile E. of Freedom, Pennsylvania. The marine facies of the Lower Kittanning shale is represented here by *Mesolobus*.

Station 4. Section exposed in a coal strip pit, 5 miles north-west of Harlansburg, Pennsylvania. The Lower Kittanning shale is characterized here by sandstone beds occurring 10 ft. above the seam.

Station 5. Section exposed in coal strip pit, 4 miles west of Slippery Rock, Pennsylvania. Plant remains prevail in the nonmarine facies of the Lower Kittanning shale. Sandstone beds occur 6 ft. above the seam.

Station 6. Section exposed in road cut 1 mile east of Nectarine, Pennsylvania. Thin irregularly bedded sandstone, with plant remains, lies just above the seam.

Station 7. Section exposed in strip pit, 1 mile north-north-west of West Freedom, Pennsylvania. The Vanport limestone is exposed approximately 40–50 ft. below the seam. The shale is characterized by interlaminated light and dark layers (varves), with abundant plant fragments.

Station 8. Type locality of the seam. Section exposed in a railroad cut above west bank of Allegheny River, outside of Kittanning, Pennsylvania. *Mesolobus* occurs in the shale a few inches above seam.

Station 9. Section exposed in strip pit 1 mile east of Turkey City, Pennsylvania. The Vanport limestone is exposed approximately 25 ft. below the seam.

Station 10. Section exposed in strip pit, on a hill 2 miles west of U.S. Route 68, and 15 miles south of Clarion, Pennsylvania. *Mesolobus* abounds in the upper portions of the shale, with *Lingula* just above the seam. Shale is interlaminated in the lower part.

Station 11. Section exposed in strip pit 2 miles south of Limestone, Pennsylvania. The shale contains *Lingula*.

Station 12. Section exposed in strip pit 1 mile west of Truittsburg, Pennsylvania. The shale contains abundant *Mesolobus* a few inches above the seam. The seam varies within the pit from 64 to 38 ins. in thickness, through a distance of 100 ft.

Station 13. Section exposed in road cut on north side of creek, just north of Worthville, Pennsylvania. *Lingula* occurs just above the seam, with *Mesolobus* predominant above.

Station 14. Section exposed in strip pit 0·25 miles north-east of Hamilton, Pennsylvania. *Aviculopecten* and *Lingula* are present just above the seam, with *Mesolobus* and other calcareous brachiopods prevalent above.

Station 15. Section exposed in strip pit 1 mile south of Curwensville, Pennsylvania. *Lingula* and *Aviculopecten* occur in the shale.

SYSTEMATIC DESCRIPTIONS

One hundred and forty species of spores and pollen, situated in 59 genera, were recognized. Of these 33 are formally described as new, and 14 are given lettered specific designations due to insufficient number of specimens. Two new genera, *Spackmanites* and *Paleospora*, are proposed. All slides used in this study are stored in the Organic Sediments Laboratory, The Pennsylvania State University. Position of specimens on the slides is indicated by the scale settings of an E. Leitz ortholux microscope, serial no. 448497. All measurements are given with reference to the maximum diameter of specimens. Wherever possible, holotypes were mounted as single grain wax mounts.

Anteturma SPORONITES (R. Pot.) Ibr. 1933
Genus RETICULATASPORITES Leschik 1955
Reticulatasporites aletoreticulus sp. nov.

Plate 104, fig. 1

Diagnosis. Alete spores; subcircular to circular in outline. Exine covered with concentric reticulation pattern; lacunae largest in centre and become smaller and more lenticular towards margin, as well as more low-lying; muri conversely become wider and more low-lying towards margin, eventually grading into exine. No evidence of tetrad scar. Exine approximately 1·5–2·0 μ thick. Size range (twelve specimens) 53 to 66 μ.

Holotype. Plate 104, fig. 1; 53 × 55 μ; slide LKC–2 (27–28) 1, coordinates 24·3 127·7.

Remarks. Spores of this species are characterized by the marginward diminution of its reticulate pattern. The species was observed only at Station 2, where it is confined to samples containing the *Lycospora-Guthoerlisporites erectus* assemblage. *Reticulatasporites aletoreticulus* sp. nov. resembles the detached caps of specimens of *Vestispora*, but could be distinguished in the Lower Kittanning seam by its larger size and ornamentational pattern.

Anteturma SPORITES H. Pot. 1893
Turma TRILETES Reinsch 1881
Subturma AZONOTRILETES Luber 1935
Infraturma LAEVIGATI (Benn. and Kidst.) R. Pot. 1956
Genus LEIOTRILETES Naumova ex Pot. and Kr. 1954
Leiotriletes sp. A

Plate 104, figs. 2, 3

Description. Trilete spores; triangular, with sharply rounded radial corners and concave or slightly convex (due to folding) inter-radial margins. Exine one micron thick or less; essentially levigate. Trilete mark distinct and slightly raised; it extends almost to radial corners; contact area defined by faintly sinuous ('wrinkled') curvaturae which turn in inter-radially toward juncture of sutures. Two specimens, 41×41 μ, and 36×38 μ (folded).

Remarks. Shape and thickness of spore coat relate the two specimens to *Leiotriletes ornatus* Naum. and *L. tumidus* Butt. and Will. They are distinguished, however, by their unique curvaturae. The specimens were observed only at Stations 5 and 7; both are present in zones containing the *Thymospora pseudothiessseni* assemblage.

Genus CALAMOSPORA S. W. and B. 1944

Calamospora multiplicata sp. nov.

Plate 104, figs. 6, 7

Diagnosis. Trilete spores; roundly elliptical in outline. Exine smooth, one micron thick or less. From 3 to 9 curving, slender folds criss-cross exine in concentric and radial directions; they are typically long and slender. Trilete mark short, extending less than one-half radius; lips very thin and only slightly raised; contact area present, but only slightly darker than remaining exine. Size range (twenty-five specimens) 43–60 μ.

Holotype. Plate 104, fig. 6; 55×41 μ; slide LKC–10 (13–14) 2, 43·9 113·9.

Remarks. *Calamospora multiplicata* sp. nov. is present at every locality; it is most common in the *Thymospora pseudothiesseni* and *Lycospora-Guthoerlisporites erectus* assemblages. The species is distinguished from other species of *Calamospora* in the Lower Kittanning seam by its size, roundly elliptical outline, and disposition of folds.

Calamospora elliptica sp. nov.

Plate 104, figs. 9, 10

Diagnosis. Trilete spores; elliptical to subelliptical-elongate in both polar and equatorial views. Exine not over 1·5 μ thick; generally smooth, although the slightly darker contact area may be slightly pitted; contact area not delimited by any specialized curvaturae. Secondary folds always present, usually grouped near margin; relatively long, slender,

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EXPLANATION OF PLATE 104

All figures ×500.

Fig. 1. *Reticulatasporites aletoreticulus* sp. nov., holotype.

Figs. 2–3. *Leiotriletes* sp. A.

Figs. 4–5, 8. *Calamospora pseudotriangulara* sp. nov. 4, Holotype. 5, Proximal polar view with well-developed contact area. 8, Thin dark folds attending the sutures prominent.

Figs. 6–7. *Calamospora multiplicata* sp. nov. 6, Holotype; slightly corroded but shows short trilete mark and contact area. 7, Specimen with open trilete mark but which shows typical orientation of folds.

Figs. 9–10. *Calamospora elliptica* sp. nov. 9, Holotype; thick lips border trilete mark. 10, Equatorial view.

Figs. 11–14. *Punctatisporites obliquus* Kos.; note size variation, and nature of trilete mark.

Figs. 15, 18. *Punctatisporites globulosus* sp. nov. 15, Holotype; lines of weakness extend longitudinally from sutures on to distal surface. 18, Ruptured specimen, with triangular gap which extends to distal hemisphere.

Figs. 16–17. *Punctatisporites sphaerorigidus* sp. nov. 16, Holotype; thick irregular fold on distal surface. 17, Specimen with T-shaped trilete mark.


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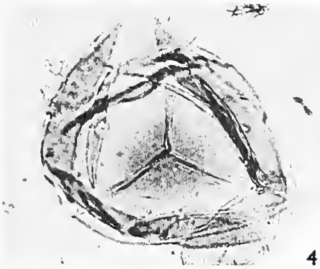
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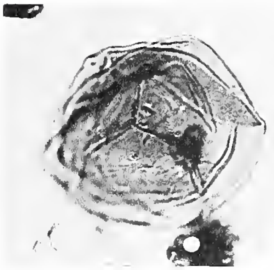
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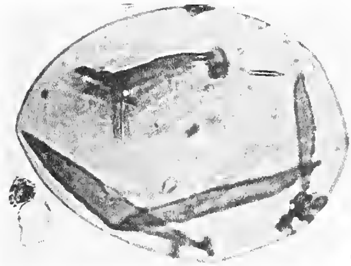
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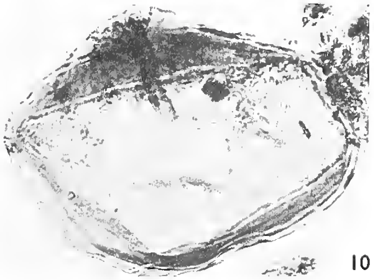
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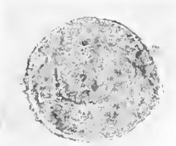
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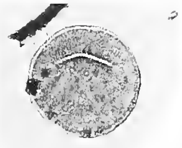
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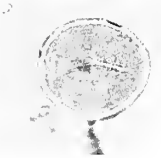
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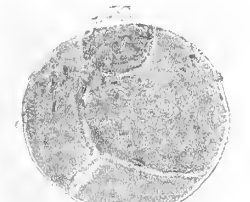
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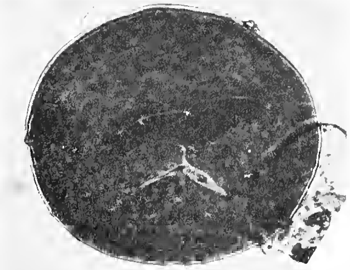
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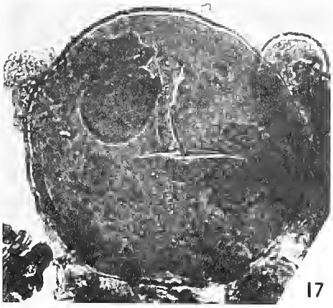
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HABIB, Pennsylvanian miospores

and smoothly tapering. Trilete mark distinct, extends about one-half radius bordered by thick, raised lips. Size range (ten specimens) 80–100 μ.

Holotype. Plate 104, fig. 9; 85×65 μ; slide LKC–10M–4, 37·7 128·5.

Remarks. The elliptical outline, long slender folds, and short thickly bordered trilete mark distinguish this species.

Calamospora pseudotriangulara sp. nov.

Plate 104, figs. 4–5, 8

Diagnosis. Trilete spores; subcircular to triangular in polar view, the outline appearing triangular because of the large folds. Trilete mark distinct, extends from one-half to two-thirds radius; thin but dark and distinct folds border it; contact area present, barely discerned to very distinct. Large sharply tapering folds run peripherally and often, because of their orientation, make the species appear triangular; largest peripheral folds most often occur inter-radially. Exine less than one micron thick, levigate. Size range (twenty specimens) 63–82 μ.

Holotype. Plate 104, fig. 4; 75×63 μ; slide LKC–8 (36–37) 1, 30·2 127·1.

Remarks. The species is most common in the upper half of zones containing the *Lycospora-Guthoerlisporites erectus* assemblage. It was not found at Station 13. *Calamospora pseudotriangulara* sp. nov. is easily distinguished from other related species by its size, triangular outline, thin exine, and long sutures bordered by thin, distinct folds.

Genus PUNCTATISPORITES Ibr. emend. Pot. and Kr. 1954

Punctatisporites obliquus Kosanke

Plate 104, figs. 11–14

Remarks. Because a very close relationship was observed between this species and *Laevigatosporites globosus* Schem., they were counted together. Except for only a slight difference in size ranges, the two species are very similar, and perhaps should be conspecific. The true nature of the suture in either species is in doubt. Schemel (1951, p. 747) noted the similarity between the species and admitted that if the nature of the suture could not be determined, it would be doubtful to which species and genus the specimens belong.

Punctatisporites sphaerorigidus sp. nov.

Plate 104, figs. 16, 17

Diagnosis. Trilete spores; circular to subcircular in outline, occasionally appearing obliquely compressed, due to the presence of a thick fold. Exine generally smooth, but may be irregularly pitted in localized areas; up to 5–6 μ thick in polar view. Trilete mark distinct and frequently open, extends about one-half radius or less; lips present but only slightly raised; occasionally the trilete mark assumes a T-shape. Single large compression fold, in some specimens accompanied by a smaller fold, usually present, restricted to distal hemisphere. Size range (twenty-five specimens) 75–98 μ.

Holotype. Plate 104, fig. 16; 83×74 μ; slide LKC–2 (12–13) 1, 22·1 123·4.

Remarks. The species rarely exceeded one per cent in any sample. It was observed most frequently in zones containing the *Punctatisporites obliquus* and *Thymospora pseudothiessenii* assemblages. *Punctatisporites sphaerorigidus* sp. nov. is distinguished by its size, thick exine, and relatively short trilete mark. It differs from *P. obesus* (Loose) Pot. & Kr., which also occurs in the seam, by its shorter trilete mark, smaller size, and relatively thicker exine.

Punctatisporites globulosus sp. nov.

Plate 104, figs. 15, 18

Diagnosis. Trilete spores; elliptical to subcircular in outline. Exine covered over its entire surface by dense, very closely spaced punctae; occasionally, probably due to locally unornamented areas, a few low-lying (1 μ or less) rounded protuberances emerge from the spore outline. Trilete mark distinct, and extends over one-half radius; lips distinct, slightly raised; extending radially from the end of each suture is a thin line along which the spores tend to rupture; ruptured specimens collapse usually to more elliptical outline with opened trilete mark forming triangular outline and extending well on to distal hemisphere. Size range (twenty-five specimens) 45–60 μ.

Holotype. Plate 104, fig. 15; 56×53 μ; slide LKC–6 (15–16) 1, 20·6 118·0.

Remarks. The species was most frequently encountered in zones containing the *Punctatisporites obliquus* assemblage, although it rarely exceeded two per cent.

Punctatisporites globulosus sp. nov. differs from other species of *Punctatisporites* by its lines of weakness along which the specimens tend to rupture.

Punctatisporites ellipticus sp. nov.

Plate 105, fig. 1

Diagnosis. Trilete spores; distinctly elliptical in outline. Exine about one micron thick; ornamented with minute but distinct, equidistant punctae which, as seen on the outline, could also be considered coni. Trilete mark distinct; extends from one-half to two-thirds radius; lips thin and slightly upturned. Size range (fifteen specimens) 55–65 μ.

Holotype. Plate 105, fig. 1; 60×43 μ; slide LKC–2 (12–13) 1, 33 113·6.

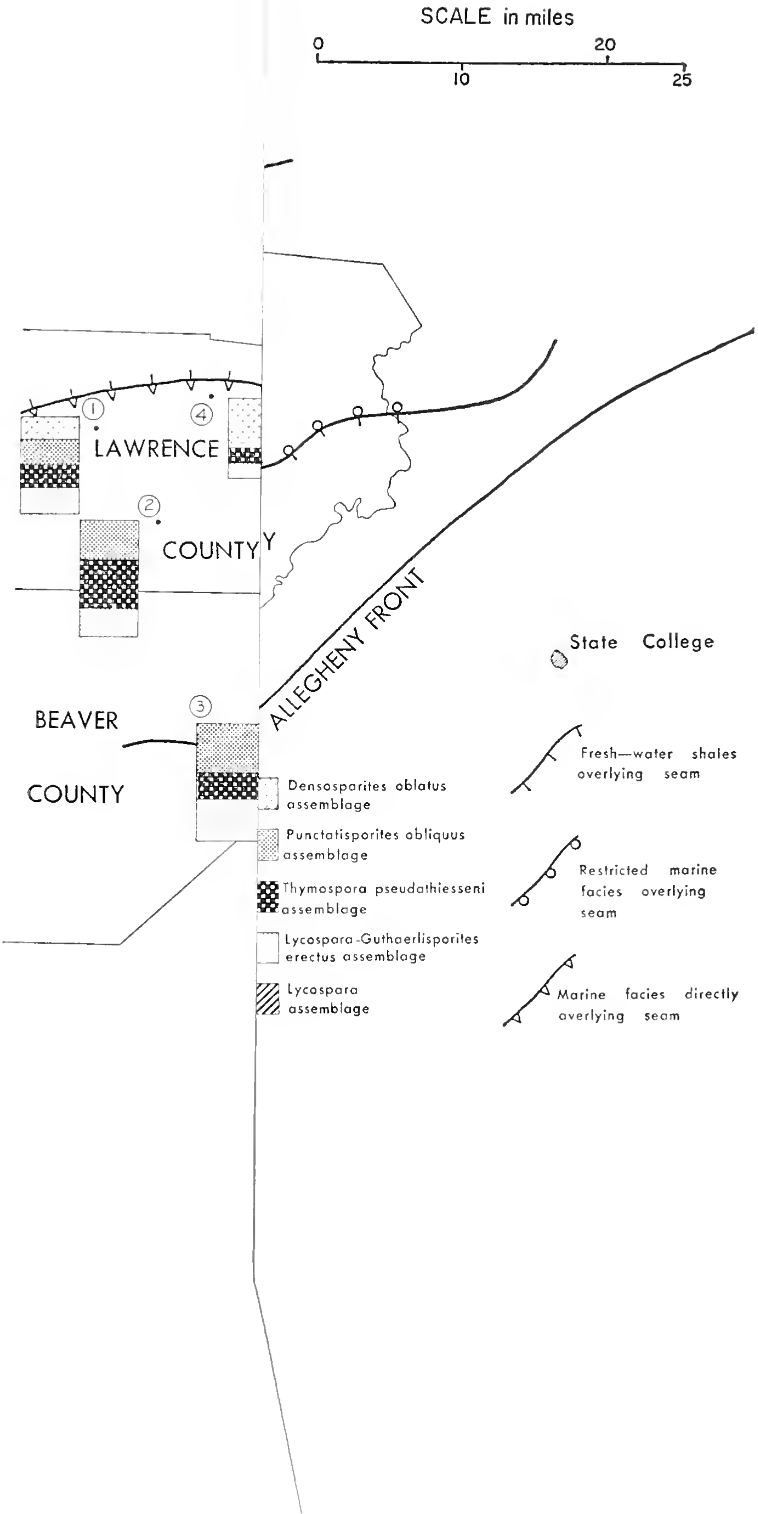
Remarks. This species is similar to *P. globulosus* sp. nov. but differs in its more elliptical outline and trilete mark. It was encountered most frequently in *Punctatisporites obliquus* assemblage zones.

Infraturma APICULATI (Benn. and Kidst.) R. Pot. 1956
Subinfraturma GRANULATI Dyb. and Jach. 1957
Genus GRANISPORITES Dyb. and Jach. 1957

Granisporites medius Dyb. and Jach.

Plate 105, figs. 2–3, 5

Remarks. This species is very similar to those ascribed to *Granasporites* Alpern, the essential difference being the presence of trilete mark in *Granisporites medius*. Occasionally, specimens were observed in tetrads (e.g. Pl. 105, fig. 5).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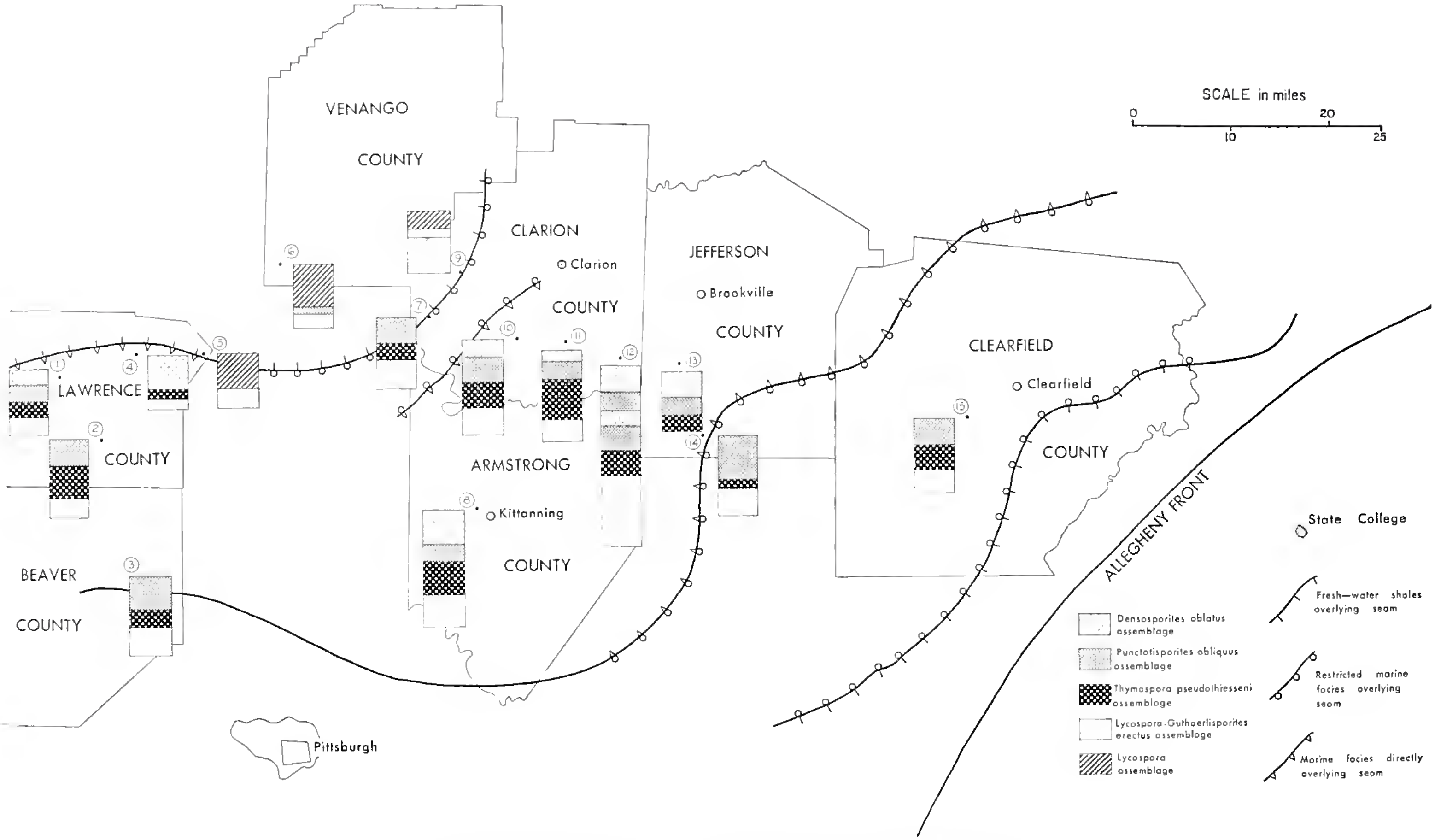
Densosparites oblatus assemblage
Punctatisporites obliquus assemblage
Thymospora pseudathiesseni assemblage
Lycospora-Guthaerlisporites erectus assemblage
Lycospora assemblage
Fresh—water shales overlying seam
Restricted marine facies overlying seam
Marine facies directly overlying seam



TEXT-FIG. 1. Geographic distribution of spore and pollen assemblages in the Lower Kittanning coal. Faunal facies boundaries from Williams (1959) and Williams and Keith (1963).

Subinfraturma VERRUCATI Dyb. and Jach. 1957

Genus CONVERRUCOSISPORITES Pot. and Kr. 1954

Converrucosisporites pseudovalvus sp. nov.

Plate 105, figs. 4, 7

Diagnosis. Trilete spores; triangular in polar view, with slightly convex to straight interradial margins and subangular to subrounded radial corners. Exine covered with rounded low-lying (approx. 2 μ high) verrucae which give the margin a roughened appearance; verrucae all about the same size and evenly distributed, tending, however, to become more numerous and slightly larger at radial corners; occasionally verrucae tend to align themselves concentrically. Trilete mark distinct, extends almost completely to radial corners; lips thin and only very slightly raised. Size range (five specimens) 38–50 μ.

Holotype. (Plate 105, fig. 4; 38 × 38 μ; slide LKC–8 (36–37), wax mount 33.

Remarks. Confined to the *Lycospora-Guthoerlisporites erectus* assemblage zones at Stations 8 and 11. *Converrucosisporites pseudovalvus* sp. nov. is distinguished from related species by the presence of larger and more numerous verrucae at the radial corners.

Genus SCHOPFITES Kosanke 1950

Schopfites grossus sp. nov.

Plate 105, fig. 6

Diagnosis. Trilete spores; outline in polar view usually elliptical, but may be near circular. Exine covered subequatorially and distally by short (to 3 μ) but very wide (up to 10 μ) verrucate processes; it is free of this ornamentation only in a small area of the proximal face, near the trilete mark; wall distinct, 3–6 μ thick. Trilete mark extends over one-half radius; usually closed but may be open, producing an irregular gap. Size range (fifteen specimens) 84–116 μ.

Holotype. Plate 105, fig. 6; 93 × 70 μ; slide LKC–10 (7–8) 2, 34·6 113·2.

Remarks. Although this species was rarely counted, it was observed more regularly in zones of the *Thymospora pseudothiesseni* assemblage.

Genus VERRUCOSISPORITES Ibr. emend. Smith *et al.* 1964

Verrucosisporites compactus sp. nov.

Plate 105, fig. 8

Diagnosis. Trilete spores; elliptical in both polar and equatorial views. Trilete mark extends from between one-half to two-thirds radius, frequently torn open to form an irregular gap; in some specimens, when not open, obscured by ornamentation; lips very thin and only slightly turned up. Exine covered with relatively large (to 3 μ in width) but low, rounded verrucae with only slightly flattened apices; verrucae closely distributed throughout surface, slightly higher than 1 μ. Size range (nine specimens) 45–53 μ.

Holotype. Plate 105, fig. 8; 48 × 37 μ; slide LKC–12 (5–6) 1, 25·1 129·5.

Remarks. This species was never counted. It differs from the other species of *Verrucosisporites* by its small size and relatively large verrucae.

Subinfraturma NODATI Dyb. and Jach. 1957

Genus LOPHOTRILETES Naum. ex Pot. and Kr. 1954

Lophotriletes interruptus sp. nov.

Plate 105, fig. 12

Diagnosis. Trilete spores; triangular in polar view with round to semicircular radial corners and gently to strongly concave inter-radial margins. Exine approximately one micron thick, covered by relatively large (about 3 μ by 3 μ) pointed to rounded coni. Trilete mark extends almost to the margin, usually closed and with thin lips. Size range (ten specimens) 28–38 μ.

Holotype. Plate 105, fig. 12; 28 × 28 μ; slide LKC–4 (18–19) 1, 26·2 116·3.

Remarks. This species was very rarely encountered.

Genus PLANISPORITES Knox emend. Pot. and Kr. 1954

Planisporites? sp. A

Plate 105, fig. 9

Description. Trilete spore; roundly triangular, with broadly rounded radial corners and gently convex inter-radial margins. Exine slightly more than 1 μ thick, covered over its surface by coni 2·5–3 μ high and wide at their base; the coni number 42 at the margin. Trilete mark thin and very straight, extends almost to the margin; very thin but distinct raised lips attend the sutures. Arcuate thickenings in exine present in proximal hemisphere inter-radial and distinctly convex. Specimen 75 × 73 μ.

Remarks. The single specimen is very similar to *P. granifer*, differing only in the presence of the arcuate thickenings.

EXPLANATION OF PLATE 105

All figures × 500.

Fig. 1. *Punctatisporites ellipticus* sp. nov., holotype.

Figs. 2–3, 5. *Granisporites medius* Dyb. and Jach. 2, trilete mark present, although indistinct. 3, Two sutures torn, the third indistinct. 5, Tetrad.

Figs. 4, 7. *Converrucosisporites pseudovalvus* sp. nov. 4, Holotype. 7, Verrucae tend to be concentrically oriented.

Fig. 6. *Schopfites grossus* sp. nov., holotype.

Fig. 8. *Verrucosisporites compactus* sp. nov., holotype.

Fig. 9. *Planisporites*? sp. A; note presence of arcuate ridges.

Figs. 10–11. *Acanthotriletes dimorphus* sp. nov. 10, Holotype; processes mostly blunted. 11, specimen with mostly spinose ornamentation.

Fig. 12. *Lophotriletes interruptus* sp. nov., holotype.

Figs. 13–14. *Acanthotriletes flexuus* sp. nov. 13, holotype.

Fig. 15. *Acanthotriletes tenuis* sp. nov., holotype.

Figs. 16, 20. *Knoxisporites* sp. A. 16, Paired ridges distinct.

Figs. 17–18. *Spackmanites ellipticus* gen. et sp. nov. 17, holotype. 18, Rudimentary trilete mark can be seen.

Fig. 19. *Spackmanites facierugosus* (Loose) comb. nov.

STATION NUMBERS	Reticulatasporites aletoreticulus	Leiotriletes sphaerotriangulus	Leiotriletes gulaferus	Leiotriletes Sp. A	Calamospora straminea	Calamospora pedat lus	Camalospor s lacunosus	Cal iculatisporites punctatus	Dictyotriletes mediareticulatus	Dictyotriletes densoreticulatus	Camptotriletes corrugatus	Knoxisporites Sp. A	Vestispora levigata	Vestispora profunda	Vestispora fenestrata	Triquitrites bransonii	Triquitrites minutus	Triquitrites spinosus	Triquitrites exiguus	Triquitrites additus	Triquitrites praetextus	Triquitrites cheilus	Triquitrites magnificus
1					X	X		X	X				X	X	X	X	X		X	X		X	
2	X	X	X		X			X	X				X	X	X	X	X		X			X	
3					X			X					X		X	X	X		X			X	
4					X		X	X					X			X	X		X	X		X	
5		X	X	X	X	X		X					X		X	X	X		X	X		X	
6					X	X		X		X			X		X	X	X	X	X	X		X	
7		X	X	X	X	X		X				X	X	X	X	X	X	X	X		X	X	
8		X			X	X		X		X			X		X	X	X		X	X		X	
9					X			X	X				X		X	X	X		X	X		X	X
10		X			X	X	X	X	X				X	X	X	X	X	X	X	X	X	X	
11		X			X			X	X				X	X	X	X			X			X	X
12					X		X	X	X		X		X		X	X	X	X	X	X	X	X	X
13		X	X		X	X		X	X				X	X		X	X		X	X		X	X
14		X	X		X			X	X				X	X	X	X	X		X	X		X	
15		X			X			X					X		X	X	X		X	X		X	

STATION NUMBERS	Triquitrites Sp. A	Moareisporites inusitatus	Ahrensisporites guerickei	Ahrensisporites vagus	Stenozonotriletes facilis	Crassispora kosanke is	Lycospora is	Lyc es diversiformis	Florinites pellucidus	Florinites occultus	Vesicaspora wilsonii	Vesicaspora saarensis	Camplexisporites polymorphus	Complexisporites chalonerii	Kosankeisporites elegans	Pityosporites kittanningensis	Alisporites symmetricus	Bisaccate Sp. A	Bisaccate Sp. B	Bisaccate Sp. C	Bisaccate Sp. D	Alatisporites pottsvillensis	Schopfipollenites Sp. A
1		X	X			X	X	X	X		X				X	X							
2		X				X	X	X	X		X			X									
3		X		X		X	X	X	X	X	X												
4		X		X	X	X	X	X	X		X												
5						X	X	X	X	X	X												
6		X				X	X	X	X		X												
7		X				X	X	X	X		X	X		X		X				X			
8		X		X		X	X	X	X		X		X	X					X	X	X		
9	X	X	X	X	X	X	X	X	X	X	X					X						X	
10		X	X	X		X	X	X	X	X	X					X		X			X		
11		X				X	X	X	X	X	X	X											X
12		X		X		X	X	X	X	X	X					X	X					X	
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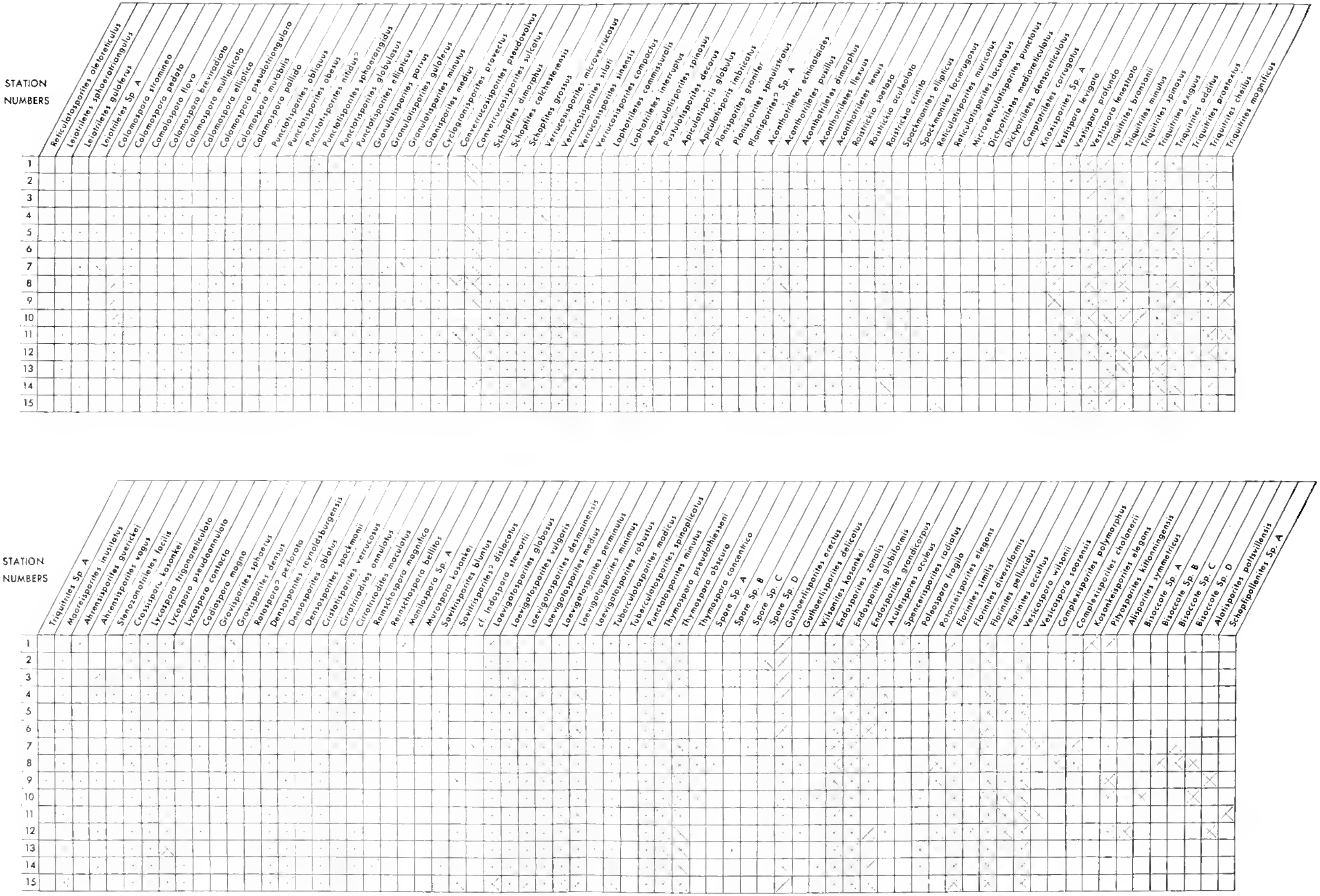
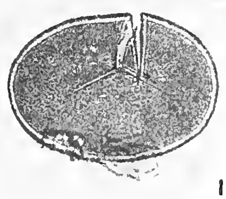


TEXT-FIG. 2. Presence of spore and pollen species in the Lower Kittanning coal.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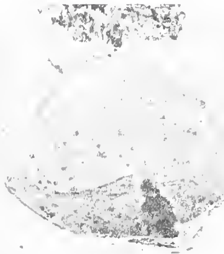
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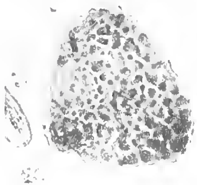
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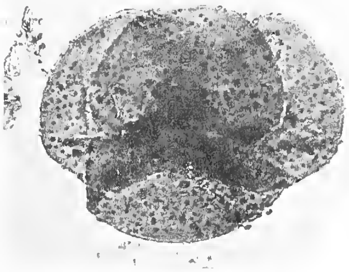
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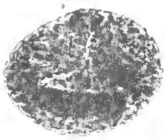
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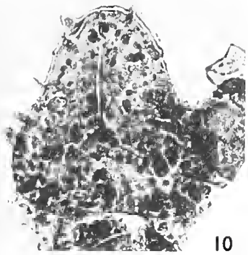
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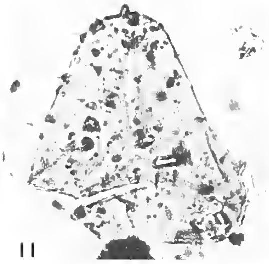
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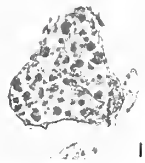
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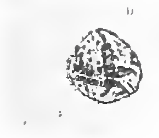
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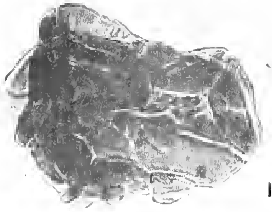
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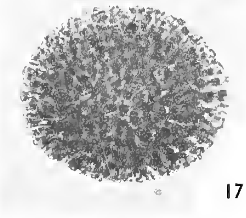
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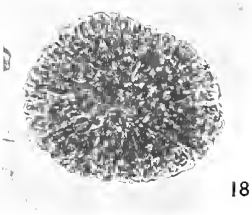
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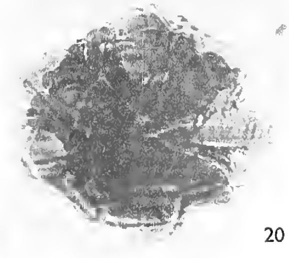
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HABIB, Pennsylvanian miospores

Genus ACANTHOTRILETES Naum. ex Pot. and Kr. 1954

Acanthotriletes dimorphus sp. nov.

Plate 105, figs. 10, 11

Diagrams. Trilete spores; roundly triangular, with broadly rounded radial corners and straight to gently concave (most often) or convex inter-radial margins. Exine 1–2 μ thick, covered with setaceous projections of essentially two types: (1) spine-like, broad-based (to 2 μ) projections which taper rapidly to a sharp point, (2) rod-like projections, about 1·5 or 2 μ wide, with rounded or flattened distal ends. Ornamentation usually evenly distributed, with up to 25 projections from the outline; ratio of blunted to spinose projections varies from 1:3 to 3:1. Trilete mark extends more than two-thirds radius; frequently open with upturned lips, occasionally torn. Size range (twenty specimens) 48–65 μ.

Holotype. Plate 105, fig. 10; 58 × 57 μ; slide LKC–10 (8–9), wax mount 15.

Remarks. The species is irregularly distributed in the seam although it was found more often in zones containing the *Thymospora pseudothiesseni* and *Lycospora-Guthoerlisporites erectus* assemblages.

Acanthotriletes flexuus sp. nov.

Plate 105, figs. 13, 14

Description: Trilete spores; triangular in outline. Exine less than 1 μ thick, covered with evenly distributed closely packed sharp spines up to 3 μ high; because of the thinness, the exine is almost invariably torn and/or folded. Trilete mark distinct, extends over two-thirds radius, it is attended by very dark thin folds. Size range (eight specimens) 22–32 μ.

Holotype. Plate 105, fig. 13; 30 × 28 μ; slide LKC–2 (8–9), 33·6 110·4.

Acanthotriletes tenuis sp. nov.

Plate 105, fig. 15

Diagnosis. Trilete spores; roundly triangular in polar view, with rounded radial corners and straight to convex inter-radial margins. Exine about 1–2 μ thick, sparsely covered by slender, gently tapering spines, never exceeding a height twice their width, and up to 4 μ high; about 15 to 20 spines are present at the outline, although in a few specimens only 8 or 9; the spines tend to group inter-radially at the equator, although they are also present at the radial corners. Trilete mark distinct, extends at least two-thirds radius; lips very thin and ill-defined. Size range (fifteen specimens) 33–41 μ.

Holotype. Plate 105, fig. 15; 33 × 33 μ; slide LKC–12 (8–9) 1, 28·5 126·7.

Remarks. The species was observed from only three localities. It is distinguished mainly by its very sparse, small, gently tapering spines.

Subinfraturma BACULATI Dyb. and Jach. 1957

Genus SPACKMANITES gen. nov.

Type species. S. ellipticus sp. nov.

Diagnosis. Trilete spores; overall outline circular to elliptical. Spore body almost completely obscured by the presence of long, very closely packed rod-shaped or club-shaped baculate processes, each of which is near-straight sided and approximately twice as long as wide; no appreciable thickening of the bacula occurs at the bases; they are evenly distributed over the entire surface of the exine, so much so that they are almost always appressed to one another at the bases; in most cases the bacula are partially fused, either at the base or at the distal ends; bacula usually rounded at the apices, or flat, with indentations. Trilete mark usually short, or may even be represented only by a triangular gap in the exine; usually can be seen only with careful focusing. Size range 30–70 μ.

Remarks. Spackmanites is characterized by closely spaced, long bacula which are tightly appressed to each other and even partially fused, the effect of which is to obscure the outline of the spore body. The genus most closely resembles *Verrucosisporites* and *Raistrickia*; it differs from the former in the lack of verrucae, and from the latter in the tight packing and partial fusing of the bacula.

Spackmanites ellipticus sp. nov.

Plate 105, figs. 17, 18

Diagnosis. Trilete spores; distinctly elliptical to oval in outline. Exine profusely covered with rod-like bacula which in some cases fuse with each other near their bases; bacula typically smoothly truncated or slightly indented at their distal terminations; many bacula thicken distally, appearing club-shaped in profile. Trilete mark short, with sutures of unequal lengths; frequently torn to form an irregular triangular gap. Size range (twenty specimens) 50–67 μ; exclusive of ornamentation, 34–49 μ.

Holotype. Plate 105, fig. 17; 60×51 μ (42×36 μ); slide LKC–12 (63–64), wax mount 39.

Remarks. The truncated and slightly indented bacula, which are partially fused, distinguish this species. It rarely exceeded one per cent in any zone, being found most frequently in those containing the *Lycospora-Guthoerlisporites erectus* assemblage.

Spackmanites facierugosus (Loose) comb. nov.

Plate 105, fig. 19

1934 *Reticulatisporites facierugosus* Loose, p. 155, pl. 7, fig. 26.
1954 *Verrucososporites facierugosus* (Loose); Butterworth and Williams, p. 754, pl. 18, fig. 6, text-fig. 1, 3.

Remarks. An excellent description of the species is given in Butterworth and Williams (1954, p. 754). Its more circular outline, less densely packed bacula with rounded apices, separates this species from *S. ellipticus*. *Spackmanites facierugosus* is usually restricted to samples of the *Lycospora-Guthoerlisporites erectus* assemblage. It was rarely counted.

Infraturma MURORNATI Pot. and Kr. 1954

Genus KNOXISPORITES Pot. and Kr. 1954

Knoxisporites sp. A

Plate 105, figs. 16, 20

Description. Trilete spores; outline distinctly polygonal. Exine characterized by thick ridges, approximately 3 μ wide, paired at polygonal corners but then separate, with each ridge continuing around the peripheral area; exine otherwise about 2 μ thick, levigate. Two specimens described, measure about 75 μ; similar to *Knoxisporites cinctus* (Lub. and Waltz) Butt. and Will. but differ in size and opening out of paired ridges. Specimens were recovered from the *Lycospora-Guthoerlisporites erectus* assemblage zone at Station 7.

Turma ZONALES (Benn. and Kidst.) R. Pot. 1956
Subturma AURITOTRILETES Pot. and Kr. 1954
Infraturma AURICULATI (Schopf) Pot. and Kr. 1954
Genus TRIQUITRITES Wilson and Coe 1940

Triquitrites cheilus sp. nov.

Plate 106, figs. 1, 2

Diagnosis. Trilete spores; triangular in polar view, with gently to markedly concave inter-radial margins and rounded, extending radial corners. Trilete mark distinct and extends to just short of the corners; it is bordered by wide, thick, and darkened lips (to 7 μ wide) which are raised. At the radial extremities round to flattened valvae are present, which tend to grade in transitionally towards the polar area. Inter-radial margin bordered by a relatively thin (to 2 μ wide), sometimes indistinct, ridge which thickens radially into the valvae. Exine levigate, with tendency to become irregular; approximately 2 μ thick. Size range (fifteen specimens) 45–60 μ.

Holotype. Plate 106, fig. 1; 53×51 μ; slide LKC–6 (1–2) 1, 40·6 124·3.

Remarks. The species is ubiquitously distributed, but rarely exceeds one per cent in any assemblage zone.

Triquitrites magnificus sp. nov.

Plate 106, fig. 3

Diagnosis. Trilete spores; isodiametric triangular in polar view. Trilete mark distinct and almost always open; extends almost to radial margins and attended by relatively wide (to 5 μ) lips that are slightly raised. Radial corners consist of flattened or stubby, thick valvae. Ornamentation of rather long digitated, somewhat sinuous baculate processes on an otherwise levigate exine. Projections, usually confined to areas of lips and valvae, about 10–15 μ long and near straight-sided. Size range (seven specimens) 58–78 μ.

Holotype. Plate 106, fig. 3; 75×78 μ; slide LKC–13 (18–19) 1, 36·0 107·9.

Remarks. This rare species was never counted. *Triquitrites magnificus* sp. nov. differs from *T. cheilus* sp. nov. in the possession of baculate processes, and from other species of *Triquitrites* in the concentration of processes at the lips and valvae.

Triquitrites sp. A

Plate 106, fig. 4

Description. Trilete spore; triangular in polar view, with convex inter-radial margins and angular radial corners. Trilete mark extends almost to radial corners; lips well-defined, slightly upturned. Radial corners thickened by rectangular to square-shaped valvae which grade in towards the polar area. Ornamentation of scattered lobed cristae, radially disposed; cristae low-lying, wider (to 5 μ) than high (to 3 μ), they are confined to distal and equatorial areas. Specimen 75×68 μ.

Remarks. Triquitrites sp. A resembles *T. crassus* Kos. but has its ornamentation restricted to the distal and equatorial areas of the exine.

Genus AHRENSISPORITES Pot. and Kr. 1954

Ahrensisporites vagus sp. nov.

Plate 106, fig. 5

Diagnosis. Trilete spores; triangular in polar view, with rounded radial corners and gently concave to convex inter-radial margins. Kyrtome best developed in inter-radial area and can always be traced to radial corners where, however, it is distinguished occasionally only with oil magnification; inner part raised inter-radially to form distinct thickening. Trilete mark distinct, extends approximately three-fourths radius; usually open, with thin lips. Exine smooth to minutely pitted. Size range (twenty specimens) 38–55 μ.

Holotype. Plate 106, fig. 5; 49×41 μ; slide LKC–12 (8–9), wax mount LK–10.

Remarks. This species is characterized by the indistinct development of the kyrtome at the radial corners. It was commonly encountered in samples of the *Densosporites oblatus* and *Punctatisporites obliquus* assemblages, and rare elsewhere.

Subturma ZONOTRILETES Waltz 1935

Infraturma CINGULATI Pot. and Kr. 1954

Genus CRASSISPORA Bhardwaj 1957

Crassispora kosankei (Pot. and Kr.) Bhardwaj

Plate 106, figs. 9–10, 13

Remarks. Some representatives of *Crassispora kosankei* observed in this study displayed a high degree of crassitudo development. The species was encountered in tetrads in rare instances. It is present at every locality, becoming most abundant in the upper portions of zones containing the *Lycospora-Guthoerlisporites erectus* assemblage.

Genus LYCOSPORA S. W. and B. 1944

Lycospora contacta sp. nov.

Plate 106, figs. 6, 8

Diagnosis. Trilete spores; roundly triangular to rounded in polar view and hemispherical in equatorial view. Exine approximately 1 μ thick, covered over its surface by very small (probably less than 1 μ) rounded grana. Equatorial crassitudinous thickening, 3–5 μ wide, grades irregularly towards polar area; indents most markedly at radial extension of trilete mark. Trilete mark distinct, straight, passes through indented crassitudinous thickening to margin; lips thin but distinct, slightly upturned. Size range (twelve specimens) 30–35 μ.

Holotype. Plate 106, fig. 6; 32×32 μ; slide LKC–12 (36–37) 1, 31·8 124·4.

Remarks. The species was very rarely counted, but was observed most frequently in samples of the *Thymospora pseudothiesseni* and *Lycospora-Guthoerlisporites erectus* assemblages. *Lycospora contacta* sp. nov. is distinguished by the irregular thickening at the margin which extends towards the polar area at the radial corners.

Genus GRAVISPORITES Bhard. 1954

Gravisporites densus sp. nov.

Plate 106, fig. 11

Diagnosis. Trilete spores; subcircular to oval in polar view, but often triangular and even pentagonal due to folding around the rigid trilete mark. Trilete mark distinct and rigid because of thick, wide (to 5 μ), elevated ridges. Exine usually folds around trilete mark; crassitudo distinct, to 4 μ wide, usually folded; exine 1–2 μ thick, irregularly surfaced with grana of various sizes. Size range (nine specimens) 45–55 μ.

Holotype. Plate 106, fig. 11; 53×48 μ; slide LKC–10 (30–31) 2, 39·6 122·6.

Remarks. The species was only very rarely encountered.

Genus ROTASPORA Schemel 1950

Rotaspora? perforata sp. nov.

Plate 106, fig. 7

Diagnosis. Trilete spores; roundly triangular in polar view; outline in some specimens accentuated by protrusion of trilete sutures. Cingulum smooth, but characterized by relatively large perforations aligned along its periphery, forming a peripheral rim. Central body slightly more rounded than cingulum, but still retains triangular outline; appears detached from cingulum, being connected solely by the sutures; ornamentation minutely punctate or scabrate. Trilete mark prominent; raised and extends to outer margin of cingulum. Size range (five specimens) 28–35 μ.

Holotype. Plate 106, fig. 7; 28×26 μ; slide LKC–7 (9–10) 1, 18·0 125·0.

Remarks. This species is distinguished by its distinctly perforated cingulum. It is only provisionally assigned to *Rotaspora* on the basis of the presence of a rim (?) at the outer margin of the cingulum. The actual occurrence of a rim is not firmly established, as it may be the result solely of the marginal alignment of perforations. Were this to be the case, the species would be better assigned to *Lycospora*.

Genus DENSOSPORITES Berry emend. S. W. and B.

Densosporites oblatus sp. nov.

Plate 106, figs. 12, 14

Diagnosis. Trilete (?) spores; oblate triangular in polar view, the radial corners rounded but always retaining some angularity. Cingulum occupies from one-third to one-half the area of the proximal surface of the central body, appears bizonate, becoming appreciably darker at its inner margin; ornamented by radiating, prostrate spines up to 5 μ; spines taper to sharp point; they vary from one or two per specimen to over fifty; in overmacerated specimens, many spines destroyed, leaving radial pits in cingulum. Central body smooth to distinctly punctate; punctae, when they occur, restricted to proximal surface; verrucae, up to 8 μ wide, on distal surface. No evidence of trilete mark. Size range (twenty-five specimens) 57–70 μ.

Holotype. Plate 106, fig. 12; 68 × 66 μ; slide LKC–10 (2–3) 1, 16 113·3.

Remarks. This species is very similar to *D. sphaerotriangularis* Kos., differing only in the presence of tapering prostrate spines and slightly larger size.

Densosporites spackmanii sp. nov.

Plate 106, figs. 15 *a*, *b*

Diagnosis. Trilete (?) spores; distinctly triangular in polar view, with a very irregular outline. Cingulum heavily sculptured by irregular flaps which appear imbricate; it is expressed on the outer margin by deeply cut crenulations, the outer portion of which forms a mammoid sculpture; it occupies approximately 30% or more of proximal area of central body. Central body more circular in outline; smooth to punctate on proximal surface, distal surface covered with 15 to 25 large verrucae. Distinct trilete mark lacking, although very faint trace can be seen on several specimens. Size range (nine specimens) 48–63 μ.

Holotype. Plate 106, fig. 15; 58 × 61 μ; slide LKC–10 (3–4) 3, 30·8 114·9.

Remarks. The heavily sculptured cingulum and distal verrucae distinguish this species. Only nine specimens were found. *Densosporites spackmanii* sp. nov. closely resembles

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EXPLANATION OF PLATE 106

All figures × 500.

Figs. 1–4. *Triquitrites* spp. 1–2. *T. cheilus* sp. nov. 1, Holotype. 3, *T. magnificus* sp. nov., holotype. 4, *T.* sp. A. Distal focus; distinct cristae.

Fig. 5. *Ahrensisporites vagus* sp. nov., holotype; ill-defined radial extensions of kyrtome.

Figs. 6, 8. *Lycospora contacta* sp. nov. 6, holotype; polar indentation of crassitudinous margin at radial corners well-expressed.

Fig. 7. *Rotaspora*? *perforata* sp. nov., holotype.

Figs. 9–10, 13. *Crassispora kosankei* (Pot. and Kr.) Bharad. Specimens possess very well-developed crassitudinous thickenings. 9, Polar view; triangular gap. 10, Equatorial view; well-developed crassitudo. 13, Tetrad; area of contact in each specimen, upper specimen in focus.

Fig. 11. *Gravisporites densus* sp. nov. holotype.

Figs. 12, 14. *Densosporites oblatus* sp. nov. 12, holotype; prostrate radiating spines and distal verrucae. 14, Verrucae slightly smaller.

Fig. 15. *Densosporites spackmanii* sp. nov., holotype; *a*, Proximal focus, structured cingulum, and proximally punctate spore body. *b*, Distal focus, large verrucae.

Fig. 16. *Cristatisporites verrucosus* (Dyb. and Jach.) comb. nov.

Fig. 17. *Monilospora* sp. A; trilete very faint but extends almost to outer margin of spore.

Fig. 18. *Savitrisporites bluntus* sp. nov., holotype.

Fig. 19. *Thymospora concentrica* sp. nov., holotype.


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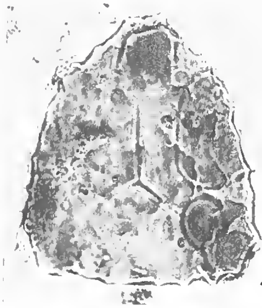
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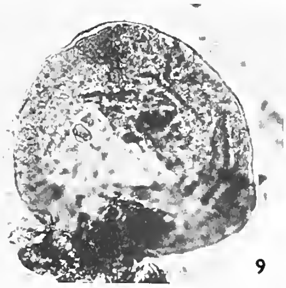
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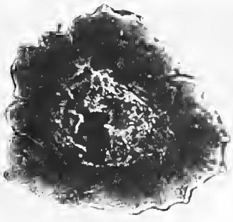
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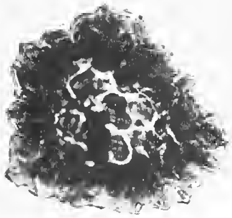
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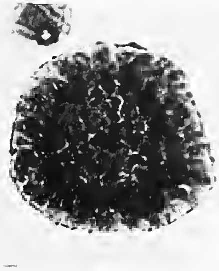
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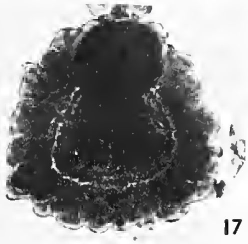
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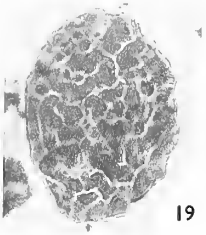
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HABIB, Pennsylvanian miospores

species of *Asperispora* Stapl. and Janson. It is provisionally placed in *Densosporites*, however, because of the distinct verrucae on the distal surface and lack of distinctive sutural ridges.

Genus CRISTATISPORITES Pot. and Kr. 1954

Cristatisporites verrucosus (Dyb. and Jach.) comb. nov.

Plate 106, fig. 16

1957 *Densosporites verrucosus* Dybova and Jachowicz, p. 166, pl. 50, figs. 1–4.

Remarks. The presence of radially aligned verrucae which are fused at their bases (Potonie and Kremp's 'kammen') warrants the inclusion of this species in *Cristatisporites*.

Genus MONILOSPORA Hacq. and Barss emend. Staplin 1960

Monilospora sp. A

Plate 106, fig. 17

Description. Trilete spore; roundly triangular in polar view, with convex inter-radial margins and roundly angular radial corners. Capsula, where it projects beyond central body, from 13 to 19 μ wide; it is characterized by a strongly crenulated outer margin, giving the specimen a rather serrated overall outline; it is very thin (less than 1 μ) where it encloses the proximal and distal hemispheres of the central body. Central body roundly triangular, with gently concave inter-radial margins; smooth, and approximately as thick (approx. 2 μ) as the inner margin of the free portion of the capsula. Trilete mark indistinct, but easily seen with careful focusing; extends almost to outer margin of capsula. Specimen 66×56 μ, central body 39×38 μ.

Remarks. Single specimen from Station 1.

Genus SAVITRISPORITES Bhardwaj 1956

Remarks. Bhardwaj's diagnosis and schematic illustration (1956, pp. 127–8, text-fig. 3*a*, *b*) of *Savitrisporites* distinguish it as a patellate spore genus. It differs from other patellate genera described here in its slightly thickened angles (Bhardwaj, p. 127).

Savitrisporites bluntus sp. nov.

Plate 106, fig. 18.

Diagnosis. Trilete spores; isodiametric triangular in polar view, with slightly thickened, truncated or rectangular radial corners and straight to gently concave or convex inter-radial margins. Patella 3–6 μ wide at equator, characterized by a gently crenulated equatorial margin which extends on to the distal surface to form a reticulum in polar view with wide (approx. 3 μ) but ill-defined muri and smaller lacunae. Proximal surface smooth. Trilete mark distinct, extends almost to inner margin of patella; usually open, with thin, raised lips. Size range (fifteen specimens) 30–38 μ.

Holotype. Plate 106, fig. 18; 37×35 μ; slide LKC–12 (7–8) 1, 24·2 118·9.

Remarks. This species is distinguished by its blunted isodiametric shape and small size. It was encountered most frequently in zones containing *Thymospora pseudothiesseni* and *Punctatisporites obliquus* assemblages.

Turma MONOLETES Ibr. 1933
Subturma AZONOMONOLETES Luber 1935
Infraturma SCULPTATOMONOLETI Dyb. and Jach. 1957
Genus TUBERCULATOSPORITES Imgrund 1952
Tuberculatosporites spinoplicatus sp. nov.

Plate 107, figs. 1–3

Diagnosis. Monolete spores; roundly elliptical to bean-shaped in outline. Exine 1–2 μ thick, somewhat loosely covered with flimsy, usually curved, spinose projections which are best seen at the outline; from 10 to 20 of the processes present at the outline; each process characterized by from 2 to 5 small, radiating folds at its base; processes 2–10 μ long and vary in side view from almost straight-sided with a length of more than twice its width, to relatively short with tapering sides. Monolete mark distinct, almost always open, but may be folded along its entire length; extends almost the entire length of the spore body; lips thin, slightly raised. Size range (twelve specimens) 106–126 μ.

Holotype. Plate 107, fig. 1; 119×81 μ; slide LKC–1 (6–7), wax mount 31.

Remarks. The presence of radiating small folds at the base of spinose protrusions makes this species unique. Specimens corresponding to this species were observed also in samples from the Cherokee coals of southeastern Kansas.

Genus THYMOSPORA Wilson and Venkatachala 1964
Thymospora concentrica sp. nov.

Plate 106, fig. 19

Diagnosis. Monolete spores; elliptical outline. Exine relatively thick, over 2 μ; ornamented throughout by thick, low-lying (approx. 3 μ high) verrucae which commonly fuse into sinuous, elongate vermiculae; in some specimens, the ornamentation is near-concentric. Monolete mark over two-thirds length of spore body; it is usually obscured by ornamentation, but can be observed with careful focusing. Size range (ten specimens) 60–90 μ.

Holotype. Plate 106, fig. 19; 61×43 μ; slide LKC–8 (24–25) 1, 29·9 117·1.

Remarks. This species is distinguished by its coarse ornamentation and large size.

INCERTAE SEDIS
Spore sp. A

Plate 107, fig. 4

Description. Trilete spore; oval in outline. Crassitudinous thickening at periphery, up to 7 μ wide. Exine otherwise approximately 1–2 μ thick, covered with very thin, curving, radially branching cristae, which are low-lying (approx. 1 μ high). Very short, irregular trilete mark is present, though indistinct; it is accentuated by a darkened contact area. A relatively large lenticular fold trends the length of the specimen. Size 58×48 μ.

Remarks. The presence of a crassitudinous thickening relates this specimen to *Crassispora*.

Spore sp. B

Plate 107, fig. 5 *a*, *b*

Description. Trilete spore; roundly elliptical in polar view. Exine approximately 1 μ thick, covered with sparsely distributed clusters of small hemispherical grana, each cluster of 15 to 25 grana. Triangular-shaped opening, with flaps folded back, indicating a torn trilete mark. Size 76×66 μ.

Remarks. Specimen is characterized by its clustered grana, and is otherwise very similar to species of *Granisporites*.

Spore sp. C

Plate 107, fig. 7 *a*, *b*

Description. Trilete spore; triangular in polar view, with near straight-sided inter-radial margins and sharply rounded radial corners. Exine approximately 2·5 μ thick, and characterized by an irregularly serrated equatorial outline; surface irregular but apparently without a distinct ornamentation pattern. On the distal surface, three deep but thin grooves approximately 23 μ long form an incomplete triangle. Width of specimen external to grooves about 12 μ. Trilete mark distinct, slightly wavy, extends almost to the radial margins; lips developed but not prominent. Size 48×41 μ.

Remarks. Specimen appears to be unique in its possession of oriented grooves on the distal surface.

Spore sp. D

Plate 107, fig. 6

Description. Trilete spore; roundly triangular, with convex inter-radial margins and broadly angular radial corners. Central body roundly triangular, generally smooth and very thin, probably, less than 1 μ; eight to ten large (to 5 μ wide) papillate-type thickenings aggregated in proximal polar area. Covering entire central body, except for a torn gap on proximal side, is a capsulate (?) structure; it is covered over its entire surface with short, tapering spines, not over 3 μ high; spines broad-based. Trilete mark extends, on the outer structure, almost to the outer margin of the specimen. Size 51×51 μ, central body 35×35 μ.

Remarks. The presence of a capsulate-like thickening relates this specimen closely to *Monilospora*.

Anteturma POLLENITES R. Pot. 1931
Turma SACCITES Erdtman 1947
Subturma MONOSACCITES (Chitaley) Pot. and Kr. 1954
Infraturma TRILETESACCITI Leschik 1955
Subinfraturma INTRORNATI Butt. and Will. 1958
Genus GUTHOERLISPORITES Bhardwaj 1954

Guthoerlisporites erectus sp. nov.

Plate 107, fig. 8

Diagnosis. Monosaccate, trilete pollen grains; overall outline oval to elliptical in proximo-distal and oblique orientations. Central body circular to subcircular, probably less than 1 μ thick, with a smooth surface; numerous slender folds concentrically disposed about periphery; outline vague. Saccus covers most of proximal surface of central body, thereby leaving only a somewhat indistinct outline of the latter structure; externally levigate and internally moderately reticulate; a darkening of the peripheral region occurs on most specimens. Trilete mark confined to area of central body, thin but straight and distinct; it extends from about one-half the distance to the margin to almost touching it; folds commonly continue the trace of the sutures, to the outline of the central body; lips very thin. Size range (thirty specimens) 60–89 μ; central body 38–43 μ.

Holotype. Plate 107, fig. 8; 81 × 69 μ; slide LKC–11 (24–25) 2, 21·2 115·2.

Remarks. This species is distinguished from *Guthoerlisporites magnificus*, the type species, by its smaller size, and tendency of folds to continue the sutures of the trilete mark to the wall of the central body.

Guthoerlisporites delicatus (Kos.) comb. nov.

Plate 107, fig. 9

1950 *Wilsonia delicata* Kosanke 1950, pp. 54–55, pl. 14, fig. 4.
1959 *Wilsonites delicatus* (Kos.); Kosanke, p. 700.

Remarks. Kosanke (1950, p. 54) distinguished *Wilsonites* partly by its vaguely defined central body being either completely covered or largely covered by the saccus. His illustration of the holotype of this species, as well as all the specimens of it encountered in this study, shows a rather distinct central body. Acknowledging that *Wilsonites* and *Guthoerlisporites* are closely related genera, this species is placed in *Guthoerlisporites* on the basis of its distinct central body.

Subinfraturma EXTRORNATI Butt. and Will. 1958

Genus ENDOSPORITES Wils. and Coe 1940

Endosporites globiformis (Ibr.) S. W. and B.

Plate 107, fig. 10

1932 *Sporonites globiformis* Ibrahim, p. 447, pl. 14, fig. 5.
1944 *Endosporites globiformis* (Ibr.) Schopf, Wilson, and Bentall, p. 45.
1940 *Endosporites ornatus* Wilson and Coe, p. 184, fig. 2.

EXPLANATION OF PLATE 107

All figures × 500.

Figs. 1–3. *Tuberculatosporites spinoplicatus* sp. nov. 1, holotype. 2, specimen with somewhat angular outline, due to ornamentation; well-developed radiating folds at bases of spines. 3, three distinct folds radiate from base of a spine.

Figs. 4–7. Unnamed spores. 4, sp. A; contact area present, although ill-defined. 5, sp. B; *a*, Distal focus; clusters of grana. *b*, Proximal focus; triangular gap. 6, sp. C. 7, sp. D; *a*, Proximal focus; slightly undulating trilete mark; *b*, Distal focus, triangularly oriented grooves prominent.

Fig. 8. *Guthoerlisporites erectus* sp. nov. holotype.

Fig. 9. *Guthoerlisporites delicatus* (Kos.) comb. nov.

Fig. 10. *Endosporites globiformis* (Ibr.) S. W. and B.

Figs. 11–12. *Endosporites grandicorpus* sp. nov. 11, holotype. 12, distinct apical papillae.


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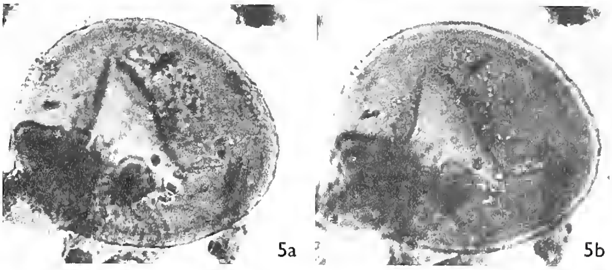
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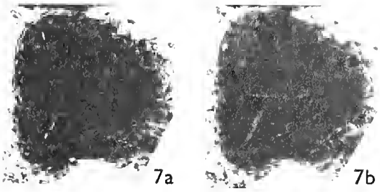
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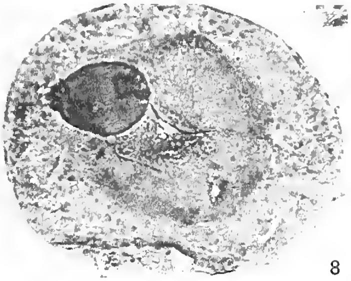
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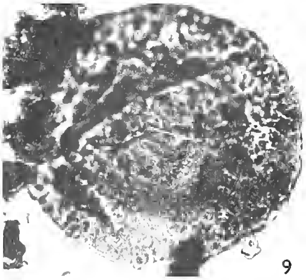
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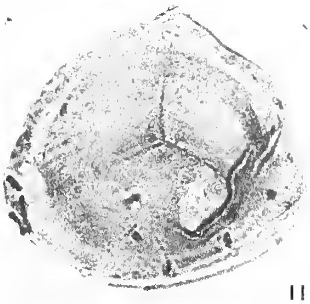
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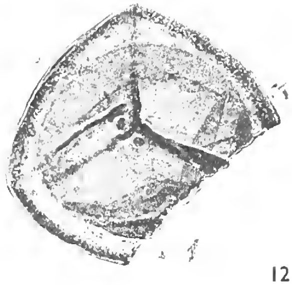
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HABIB, Pennsylvanian miospores

Remarks. Endosporites ornatus is here considered a junior synonym of *E. globiformis*, primarily on the basis of Chaloner's (1958) description of the microspores in the lycopod cone species *Polysporia mirabilis*. Although specimens of both species of *Sporae dispersae* could morphologically be distinguished, they invariably occurred in the same samples, and gradational specimens were observed.

Endosporites grandicorpus sp. nov.

Plate 107, figs. 11, 12

Diagnosis. Monosaccate trilete spores; overall outline roundly triangular in polar view, with distinctly angular radial corners. Central body circular to sub-circular; it occupies most of the area of the specimens, extending seven-tenths the radius or more; less than 1 μ thick; very commonly a number of small, lenticular folds criss-cross its distal hemisphere. Saccus sharply and densely punctate, showing best at the periphery; a distinct limbiate thickening occurs at the periphery, approximately 3–4 μ wide, attached to central body on proximal side. Trilete mark distinct, extends to margin of saccus. Apical papillae located inter-radially on proximal side, a phenomenon common in lycopod microspores. Size range (seven specimens) 65–81 μ; central body 60–73 μ.

Holotype. Plate 107, fig. 11; 80 × 72 μ; slide LKC–7 (9–10), wax mount 36.

Remarks. This species is distinguished by its relatively large central body, oblate triangular outline, and strongly differentiated limbus. It occurs most frequently in zones containing the *Thymospora pseudothiesseni* assemblage.

Infraturma VESICULOMONORADITI (Pant) Bhardwaj 1956

Genus PALEOSPORA gen. nov.

Type species. Paleospora fragila sp. nov.

Diagnosis. Elliptical to subcircular monosaccate grain with a longitudinal slit. Central body elliptical to circular and occupies an area about one-half or more of the enclosing saccus; in some cases it carries long, thin, concentric folds. Saccus thin, less distinctive than central body and very commonly folded or torn. A longitudinal fissure extends from over one-half to the complete length of the saccus; it forms a line along which entire specimens are commonly folded. An equatorial enclosing flange is the most prominent structure, and appears to hold the shape of the flimsy specimens; it is relatively wider than the saccus. The single described species ranges upward in size from 150 microns.

Remarks. This genus is distinguished from *Potonieisporites* by its distinct flange, and from *Spencerisporites* by its longitudinal fissure.

Paleospora fragila sp. nov.

Plate 108, figs. 1, 2

Diagnosis. Monosaccate spores or pollen with a straight longitudinal fissure confined to the area of the saccus; elliptical in outline. Central body more roundly elliptical, 1 μ or less thick; it is enclosed by a closely appressing saccus with which it conforms in outline. Both saccus and central body appear very flimsy and are almost always folded in several directions; they both appear to be essentially unornamented. Flange in an equatorial zonate structure of about the same thickness (approx. 1 μ) throughout its width; it is the most prominent and most highly ornamented structure; the ornamentation consists of very low-lying (approx. 1 μ or less high) irregularly radiating corrugations or cristae, which become more distinctive toward the outer margin. Longitudinal fissure open in all observed specimens, ranging from a thin slit to a wide gap which participates in folds which, when they occur, run the entire length of the body. Size range (twenty-five specimens) 150–195 μ; saccus 105–140 μ; flange width 15–25 μ.

Holotype. Plate 108, fig. 1; 161 × 93 μ; slide LKC–2 (21–22) 2, 36·5 115·2.

Remarks. This species does not appear to be restricted to any particular assemblage zone.

Genus POTONIEISPORITES Bhardwaj 1954

Potonieisporites elegans (Wils. and Kos.) emend.

Plate 108, fig. 3

1944 *Florinites elegans* Wilson and Kosanke, p. 330, fig. 3.
1964 *Potonieisporites elegans* (Wils. and Kos.); Wilson and Venkatachala, pp. 67–68.

Emended diagnosis. Monosaccate pollen grains; roundly elliptical in overall outline. Central body distinct, elliptical to circular in outline, characterized by prominent crescentic or lenticular folds which commonly transect each other, though on opposite sides of the central body, at angles approaching ninety degrees; the transverse folds, always two, appear confined to the distal hemisphere at or near the juncture of central body and saccus; the longitudinal folds, also two, are present on the proximal (free) hemisphere of the central body and trend along the maximum dimension of the body; ornamentation minutely punctate to granulose. Saccus externally levigate and internally moderately infra-reticulate, attached to central body only on its distal side. Tetrad mark prominent on proximal (free) side of saccus; it is essentially straight longitudinal, but occasionally T-shaped with a much reduced third suture, or even symmetrically (Y-shape) trilete.

EXPLANATION OF PLATE 108

All figures × 500.

Figs. 1–2. *Paleospora fragila* gen. et sp. nov. 1, holotype.

Fig. 3. *Potonieisporites elegans* Wils. and Kos. emend. Monolete mark continued across saccus by folds, optically superimposed on distally attached central body.

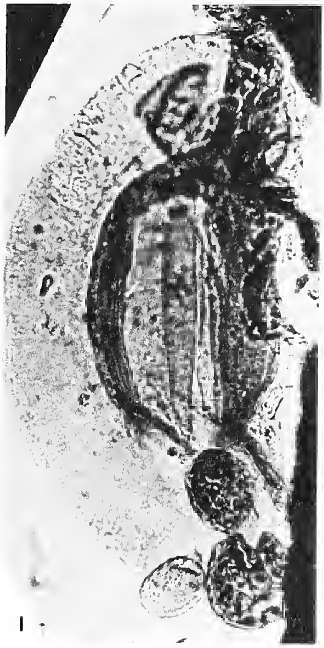
Figs. 4–5. *Florinites occultus* sp. nov. 4, holotype; irregular gap at contact of central body and distal surface of saccus, and radiating folds. 5*a*, Distal focus, showing contact of central body and saccus; saccus torn around thick central body. 5*b*, Proximal focus, showing rudimentary trilete mark on saccus.

Figs. 6–8. *Vesicaspora wilsonii* Schemel. 6, Polar view, showing vague central body. 7, Oblique view; continuation of saccus across central body illustrated by folds. 8, Equatorial view, showing orientation of saccus, proximally protruding central body, and tenuitas-like membrane crossing saccus distally.

Fig. 9. *Vesicaspora saarensis* (Bharad.) comb. nov.

Fig. 10. *Complexisporites chalonerii* sp. nov. Holotype.

Figs. 11–12. *Pityosporites kittanningensis* sp. nov. 11, holotype.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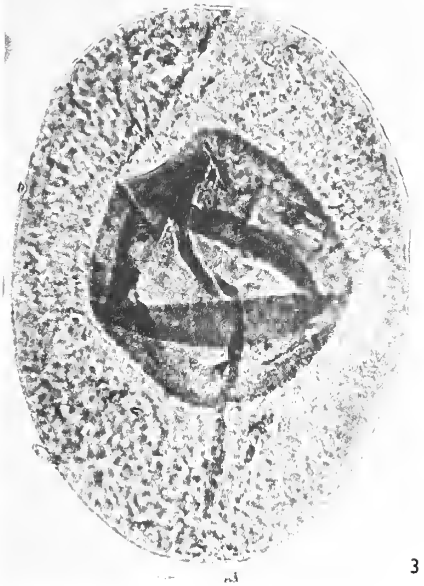
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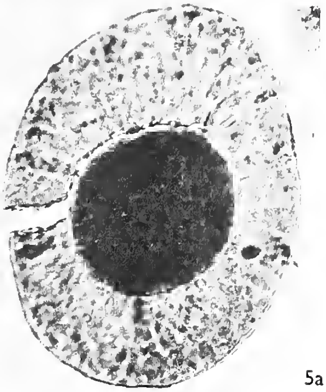
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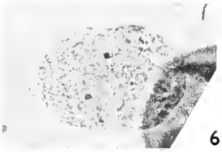
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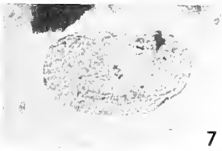
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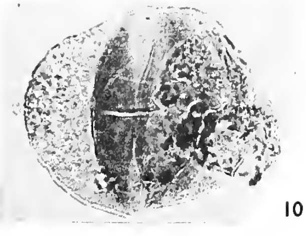
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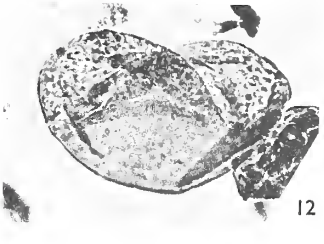
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HABIB, Pennsylvanian miospores

Dimensions. (Twenty-five specimens) 135–215 μ; central body 85–110 μ.

Remarks. This species is formally emended because of the additional information provided by numerous specimens present in the Lower Kittanning seam. These specimens agree in every respect to the species recombined by Wilson and Venkatachala (1964) and have demonstrated that the suture is confined to the saccus on the proximal (free of any contact with the central body) side. In a specimen illustrated in Plate 108, fig. 3, the suture and attendant minor folds pass across the central body and its transverse and longitudinal pairs of folds without disturbing them. This seems possible only when the suture is superimposed on the central body optically from another surface. Because no mention of the actual position of the tetrad suture is given in the generic diagnosis by Bhardwaj (1954, pp. 19–20), this species is retained in *Potonieisporites*.

This species is almost invariably restricted to the bottom-most samples in the Lower Kittanning seam.

Infraturma ALETESACCITI Leschik 1955

Genus FLORINITES S. W. and B. 1944

Florinites occultus sp. nov.

Plate 108, figs. 4, 5 *a*, *b*

Diagnosis. Monosaccate pollen grains; roundly elliptical to subcircular outline. Central body circular to oval, very thick and dark, probably over 2·5 μ thick; an irregularly spinose or conate ornamentation is distinct at its outline. Saccus externally levigate and internally coarsely reticulate, reticulation pattern radiating out from area of central body; attached distally to central body, proximal side free; junction with saccus on distal side attended by an irregular gap, exposing central body; in some specimens, it is concentrically torn around the central body, presumably because of the latter structure's thickness. A tetrad scar was observed in only one specimen (Plate 108, fig. 5 *a*, *b*), where a short, irregular trilete mark is present on the proximal (free) side of the saccus. Size range (eight specimens) 60–106 μ; central body 35–80 μ.

Holotype. Plate 108, fig. 5 *a*, *b*; 91×76 μ; slide LKC–12 (51–52), wax mount 21.

Remarks. This species is distinguished by its thick, dark central body. It occurs most frequently in zones containing the *Lycospora-Guthoerlisporites erectus* assemblage, most usually in the bottom-most samples.

Genus VESICASPORA Schemel emend. Wils. and Venkat. 1963

Vesicaspora wilsonii Schemel emend. Wils. and Venkat. 1963

Plate 108, figs. 6–8

Remarks. Specimens of this species present in the Lower Kittanning coal demonstrate well the morphological reinterpretation by Wilson and Venkatachala (1963).

Vesicaspora saarensis (Bhard.) comb. nov.

Plate 108, fig. 9

1957 *Alisporites saarensis* Bhardwaj, p. 117, pl. 31, figs. 14–15.

Remarks. The species described by Bhardwaj (1957) as *Alisporites saarensis* differs from previously described species of *Vesicaspora* by its slightly darker central body.

Subturma DISACCITES Cookson 1947

Genus COMPLEXISPORITES Jizba 1962

Complexisporites chalonerii sp. nov.

Plate 108, fig. 10

Diagnosis. Striate, capped, bisaccate pollen; roundly elliptical to oval in outline, the width of either saccus never exceeding that of the central body. Central body smooth, not accentuated by an equatorial thickening; subcircular to slightly transversely elongated, outline obscured by attachment folds of sacci. Sacci externally levigate and internally infrareticulate, distally inclined, attached distally to central body near the polar area and proximally in a subequatorial position; distinct folds define their distal attachment to central body. Relatively narrow (approx. 6–8 μ) germinal furrow lies parallel to sacci bases. On the proximal side of the central body, a vaguely defined, but always present, cap is defined by a circular groove; within the cap, from 26 to 35 μ in diameter, is a straight longitudinal fissure, running the length of the cap; it is attended on either side by from one to three less distinct striae; in some specimens the striae could be distinguished only with careful focusing. Size range (six specimens) 63–86 μ.

Holotype. Plate 108, fig. 10; 66×56 μ; slide LKC–7 (18–19) 1, 22·5 114·3.

Remarks. This species is placed in *Complexisporites* Jizba on the basis of its striated proximal cap. It differs from *C. polymorphus*, the type species, mainly in the structure of the cap. This species also has sacci which are more distally inclined. It occurs with *C. polymorphus* in the Lower Kittanning coal, in the lower samples of the *Lycospora-Guthoerlisporites erectus* assemblage.

Genus PITYOSPORITES Seward emend. Manum 1960

Remarks. Alete, bisaccate grains with distal orientation of sacci are assigned to *Pityosporites* (Sew.) Manum in this study. These grains are similar to *Klausipollenites* Jansonius, especially in the crescentic to semicircular outline of the sacci, but can be distinguished from this genus by their distal attachment of sacci closer to the polar area of the central body, and narrower germinal furrow.

Pityosporites kittanningensis sp. nov.

Plate 108, figs. 11, 12

Diagnosis. Alete, bisaccate pollen; central body almost circular, but appears transversely elongated due to the mode of saccus attachment; sacci crescentic, free margin circumscribing more than half the outline of a circle. Central body indistinct, probably not more than 1 μ thick, characterized by subequatorial, convexly crescentic thickenings at proximal bases of sacci; surface smooth to minutely punctate, punctae being observed only with high magnification oil objective. Sacci distally inclined at angles from 20 to 30 degrees, attached proximally to central body in a near equatorial position, and distally in polar area; in smooth continuity with the central body so that in equatorial view they help purvey the 'boomerang' effect typical of the genus; externally levigate and internally infrareticulate; no evidence of a thickening at their outer margin. Germinal furrow relatively thin and only vaguely defined, always present, elongated parallel to distal attachment of sacci bases. Size range (ten specimens) 60–78 μ; central body 36–58 μ.

Holotype. Plate 108, fig. 11; 70×47 μ; slide LKC–12 (51–52) 1, 26·8 116·0.

Remarks. This species is distinguished from closely allied species by its size and less distinct central body. Almost all specimens were recovered from the lower portions of the Lower Kittanning seam.

Genus ALISPORITES Daugherty emend. Pot. and Kr. 1954

Alisporites symmetricus sp. nov.

Plate 109, figs. 1–3

Diagnosis. Alete, bisaccate pollen; elliptical to elongate-elliptical in polar and equatorial views. Central body indistinct; outline discerned in some specimens only with careful focusing; approximately 1 μ thick, smooth to minutely punctate; greatest diameter along the greatest dimension of the specimens. Sacci attached proximally in subequatorial position and distally nearer the polar area; they appear to be of about the same thickness as the central body and are moderately infrareticulate without any distinct radial orientation. Connecting the two sacci distally is a very thin (probably less than 1 μ) germinal furrow which when observed in equatorial view is always split open, 12–30 μ wide, oriented parallel to the sacci bases; unornamented and much lighter in colour than either central body or sacci. The sacci are not pendant, but are isodiametrically opposed. Size range (eight specimens) 73–91 μ.

Holotype. Plate 109, fig. 1; 81×58 μ; slide LKC–12 (63–64), wax mount 39.

Remarks. This species is smaller than most species of *Alisporites*. It was found only in the lowermost samples of the seam.

Bisaccate sp. A

Plate 109, fig. 4

Description. Fissured, bisaccate pollen grain; elliptical in outline, with the central body at least as wide as the sacci which, in turn, are widest at their bases. Central body 71 μ in diameter, almost circular, although not sharply defined; without appreciably distinct wall, minutely granulose. Sacci externally levigate and internally moderately reticulate, attached distally very close to polar area of central body, and proximally in a subequatorial position; distal attachment marked by distinct primary folds which are convexly lenticular and extend the entire distance of the bases. Relatively narrow germinal furrow, about 7 μ wide, parallel to the primary folds; a narrow but very distinct fold runs almost its entire longest dimension. On the proximal surface of the central body is a very distinct longitudinal fissure 23 μ long, bordered by thick raised lips. Size 91×71 μ.

Remarks. This specimen is distinguished by its large central body and bordered longitudinal fissure.

Bisaccate sp. B

Plate 109, fig. 5 *a*, *b*

Description. Two alete, bisaccate pollen grains; elliptical or dumb-bell shaped in outline, the central body circular with sacci somewhat hemispherical. Central body very vaguely defined, probably very thin and smooth. Sacci attached distally by thickened areas near polar area of central body; attached proximally, although very vaguely, in a subequatorial position; externally levigate and internally incompletely reticulate, the ornamentation appearing more vermiculate or verrucate; the effect of the ornamentation gives the specimens a roughened outline; a darkened peripheral zone occurs at the outline. Relatively wide but thin furrow between sacci bases on distal side. Specimens 64 × 50 μ (Plate 109, fig. 5 *a*, *b*) and 61 × 43 μ.

Remarks. The two specimens are distinguished by their coarse ornamentation and dumb-bell shape.

Bisaccate sp. C

Plate 109, figs. 6, 7 *a*, *b*

Description. Two striate, bisaccate pollen grains; elliptical in polar view, with hemispherical sacci wider than the central body. Sacci attached to indistinct central body in polar area on distal side, and subequatorially on proximal side. On proximal side of central body, well-defined cap distinguished by circular groove; cap striate, six to seven distinct striae, a few split longitudinally for part of their length. Central body roundly elliptical, smooth; sacci externally levigate and internally microreticulate. Relatively narrow germinal furrow parallels the sacci bases. Specimens 89 × 62 μ (fig. 6) and 76 × 60 μ (fig. 7).

Remarks. The proximally located striate cap relates these specimens to *Complexisporites*; however, the podocarpitidaceous sacci-central body relationship relate them closely to *Striatopodocarpites*. Only these two specimens were found, in the lowermost samples containing the *Lycospora-Guthoerlisporites erectus* assemblage at Stations 7 and 8.

Bisaccate sp. D

Plate 109, figs. 8 *a*, *b* and 9

Description. Two striate, bisaccate pollen grains; sacci circumscribe an outline greater than one-half that of a circle, and with a width greater than that of the central body. Central body characterized by thick (to 8 μ wide at outline) sinuous wall; on its proximal side, from two to four relatively wide (approx. 3 μ) but somewhat less sinuous thickenings are separated by striae; usually one or two thickenings are more conspicuous than the others. Sacci externally levigate and internally finely reticulate; long, slender, straight folds radiate out from area of central body, presumably due to thickness of central body; sacci attached distally and proximally to central body in subequatorial positions, being probably only very slightly distally inclined. On the distal surface, a

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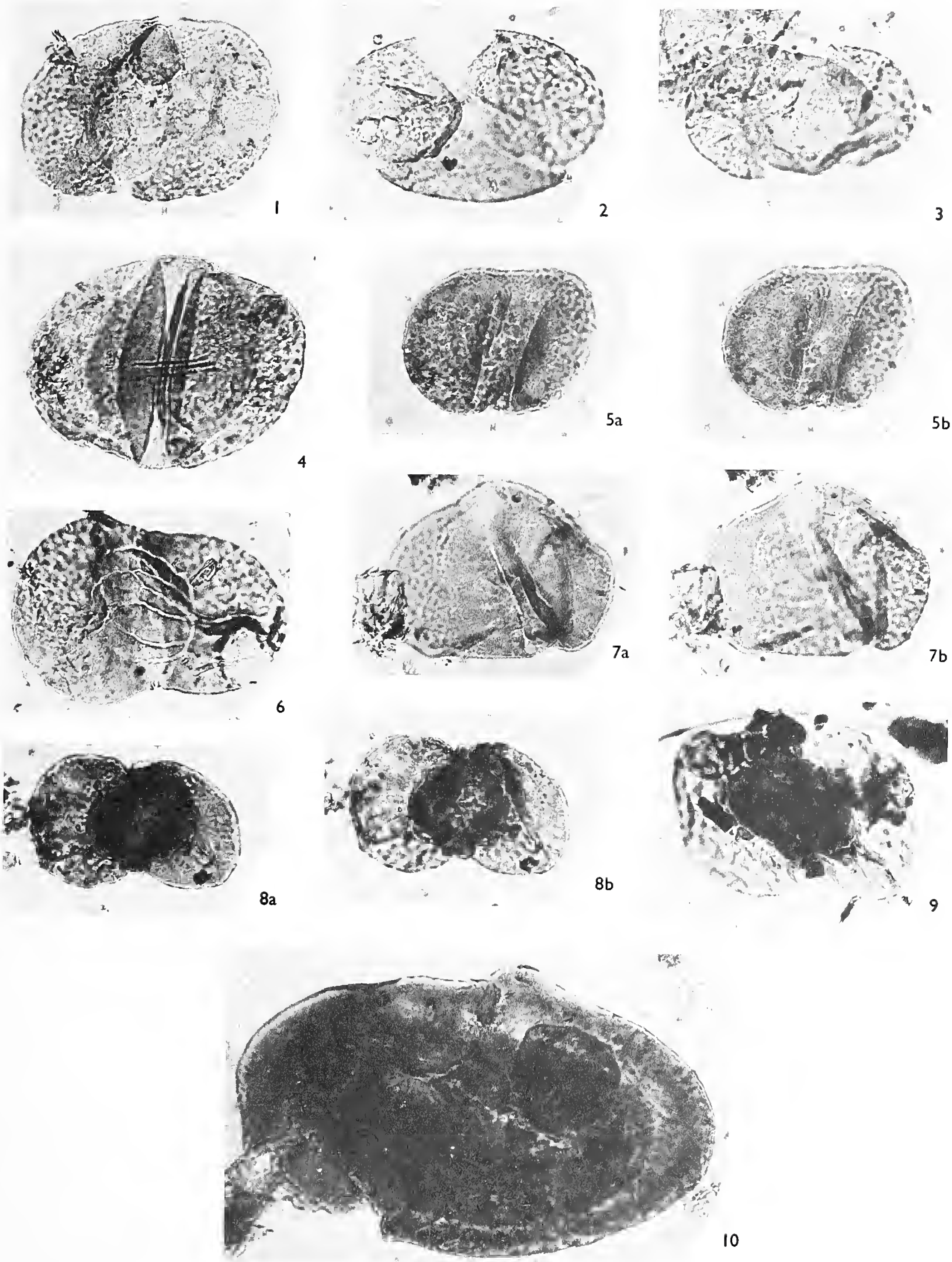
EXPLANATION OF PLATE 109

All figures × 500.
Figs. 1–3. *Alisporites symmetricus* sp. nov. 1, holotype.
Figs. 4–9. Bisaccate spp. 4, Sp. A. 5, Sp. B; *a*, distal focus; *b*, proximal focus. 6–7, Sp. C. 8–9, Sp. D.
Fig. 10. *Schopfipollenites* sp. A.



HABIB, Pennsylvanian miospores

wide unornamented germinal furrow. Specimens, 71×45 μ (fig. 8 *a*, *b*) and 80×60 μ (fig. 9).

Remarks. The striate central body and larger sacci relate these specimens closely to *Striatopodocarpites.*

Turma PLICATES Naumova emend. R. Pot. 1960
Subturma PRAECOLPATES Pot. and Kr. 1954
Genus SCHOPFIPOLLENITES Pot. and Kr. 1954

Schopfipollenites sp. A

Plate 109, fig. 10

Description. Monolete, prepollen grain; elongate-elliptical outline. Specimen bordered by thick flange-like structure approximately 8–10 μ wide, thickest nearest the polar area, and thinning rapidly towards the outer margin. Two centrally located thick primary folds extend longitudinally, each 25 μ long; located on the distal surface, they taper in opposite directions, joining with each other at their terminations. Monolete mark slightly bent, extends over two-thirds length. Exine densely but very minutely punctate, probably over 2 μ thick. Specimen 179×109 μ.

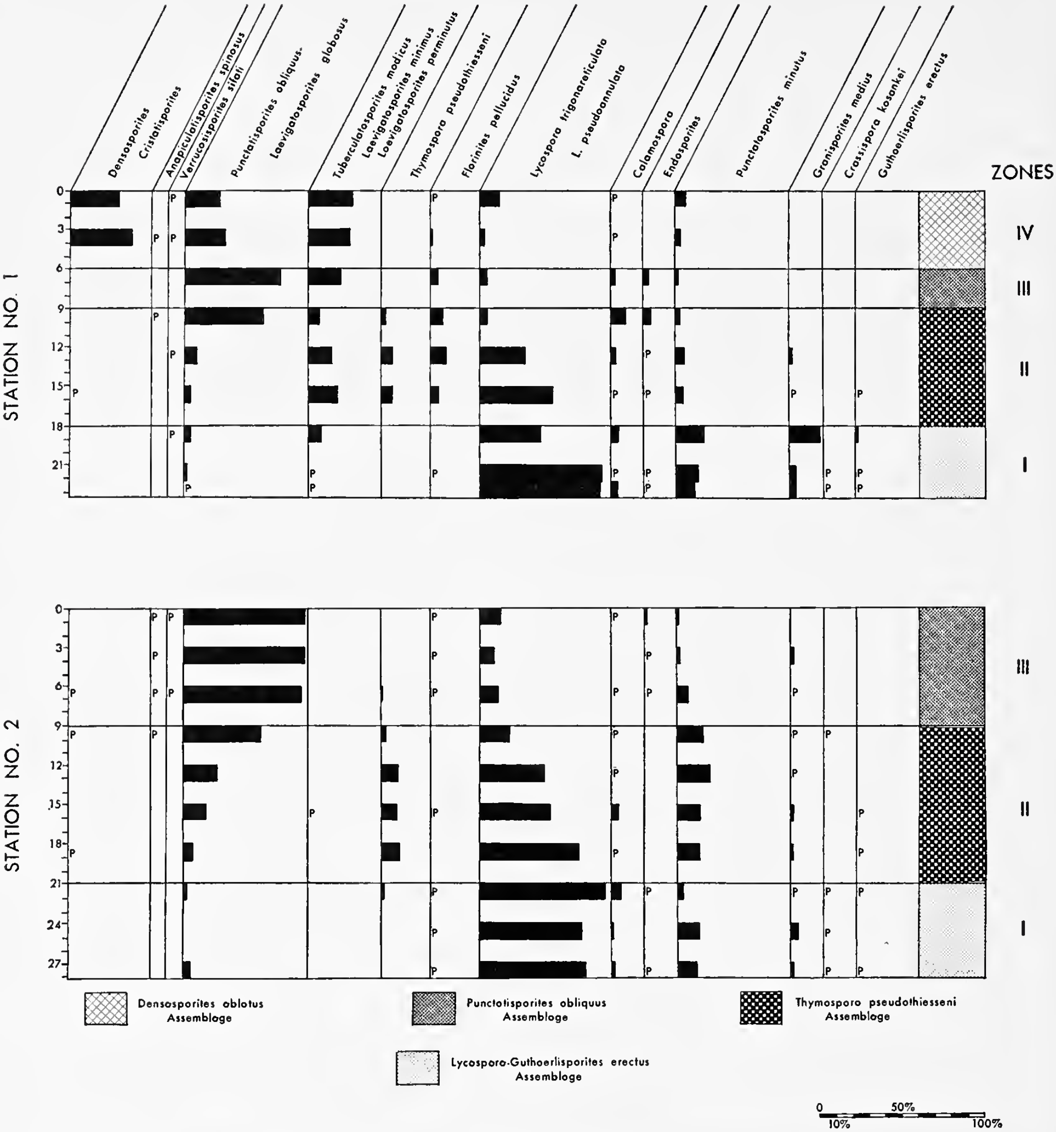
Remarks. This specimen is distinguished by its smaller size, slender elliptical outline, and thick distal folds.

DESCRIPTION OF SPORE AND POLLEN ASSEMBLAGES

The diagnostic characteristics of the five spore and pollen assemblages occurring in the Lower Kittanning coal seam are given in the succeeding numbered paragraphs. Following these are more detailed descriptions and discussions of the assemblages.

1. *Densosporites oblatus* assemblage. Total of all densospores in samples containing this assemblage ranges from 15 % to 47 %. The densospore species include *Densosporites oblatus*, *D. reynoldsburgensis*, *D. spackmanii*, and *Cristatisporites verrucosus.*
2. *Punctatisporites obliquus* assemblage. Range of *Punctatisporites obliquus–Laevigatosporites globosus* in incremental samples from 19 % to 90 %. Combined densospore species never exceed 13 % in any sample.
3. *Thymospora pseudothiessenii* assemblage. Range of *Thymospora pseudothiesseni* in incremental samples from 3·5 % to 24 %. *Florinites pellucidus* always occurs in its greatest amounts in the assemblage zones.
4. *Lycospora-Guthoerlisporites erectus* assemblage. *Lycospora* ranges in incremental samples from 30 % to 74 %. *Guthoerlisporites erectus* occurs in every assemblage zone. *Punctatosporites minutus*, *Granisporites medius*, and *Crassispora kosankei* occur here in greater amounts. There is the greatest diversity of saccate species in the assemblage zones.
5. *Lycospora* assemblage. *Lycospora* ranges from 40 % to 65 % in incremental samples. *Guthoerlisporites erectus* is totally lacking.

Bar histogram profiles of the more common species, with the delineated assemblage zones, are presented for most of the investigated localities in text-figs. 3–7.



TEXT-FIG. 3. Distribution of spores and pollen in the Lower Kittanning coal at Stations 1 and 2.

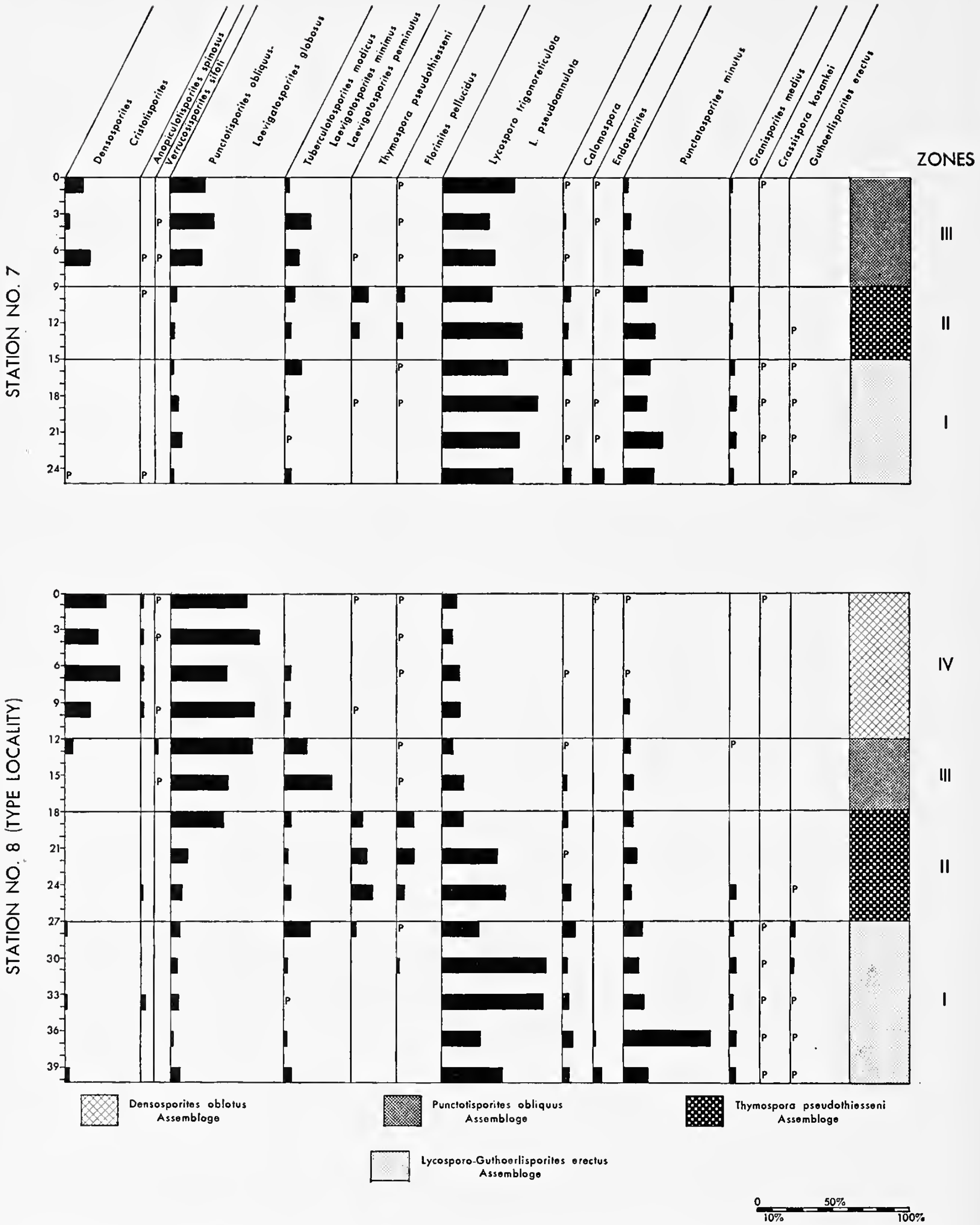
The average percentages of species in each assemblage are given in text-fig. 8. Each of the zones is defined solely on the basis of the spore and pollen assemblage occurring in it. Because the increase and decrease of species in the profiles are for the most part gradual, the boundaries of assemblage zones were drawn arbitrarily at the top of the uppermost sample containing the particular assemblage. Because of the sampling interval, it was decided to obtain more than one sample for any particular zone, except where the diagnostic species occurred in numbers well above the required minimum.

Densosporites oblatus *assemblage*

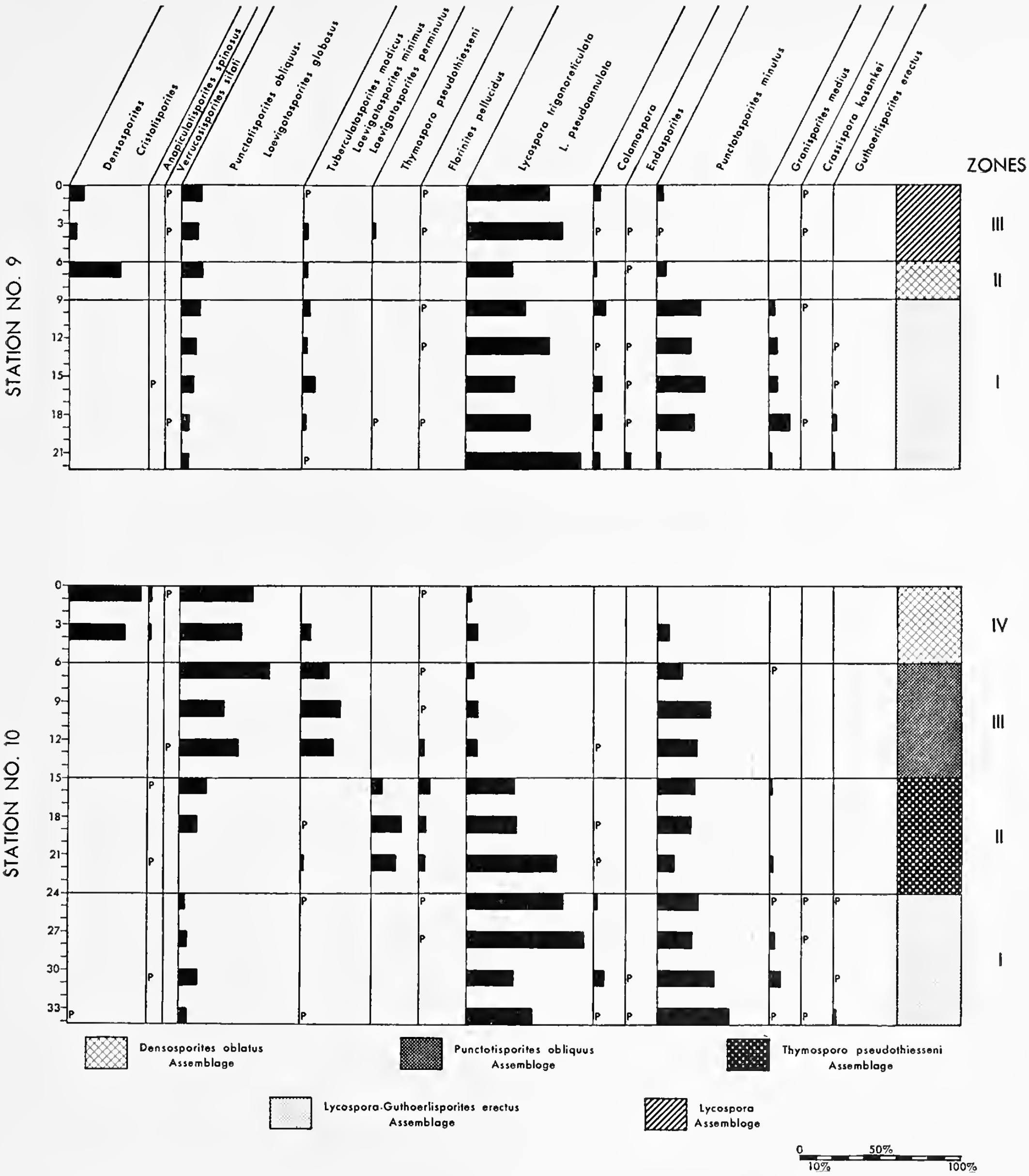
This assemblage is characterized by the relatively high percentage of densospores (*Densosporites*, *Cristatisporites*) which range in their respective assemblage zones from

TEXT-FIG. 4. Distribution of spores and pollen in the Lower Kittanning coal at Stations 5 and 6.

20·5 % in Zone III at Station 13 to 41·5 % in Zone IV at Station 10. With one exception, the lowest occurrence in any sample in a zone is 17 %. *Punctatisporites obliquus–Laevigatosporites globosus* is the most abundant spore species in the assemblage, although the densospores are collectively most abundant at approximately half the localities. *Densosporites oblatus* sp. nov. accounts for more than half the number of densospores present. Other species included in this group include *Densosporites reynoldsburgensis*, *D. spackmanii* sp. nov., and *Cristatisporites verrucosus* comb. nov. Other species which more frequently occurred in this assemblage include



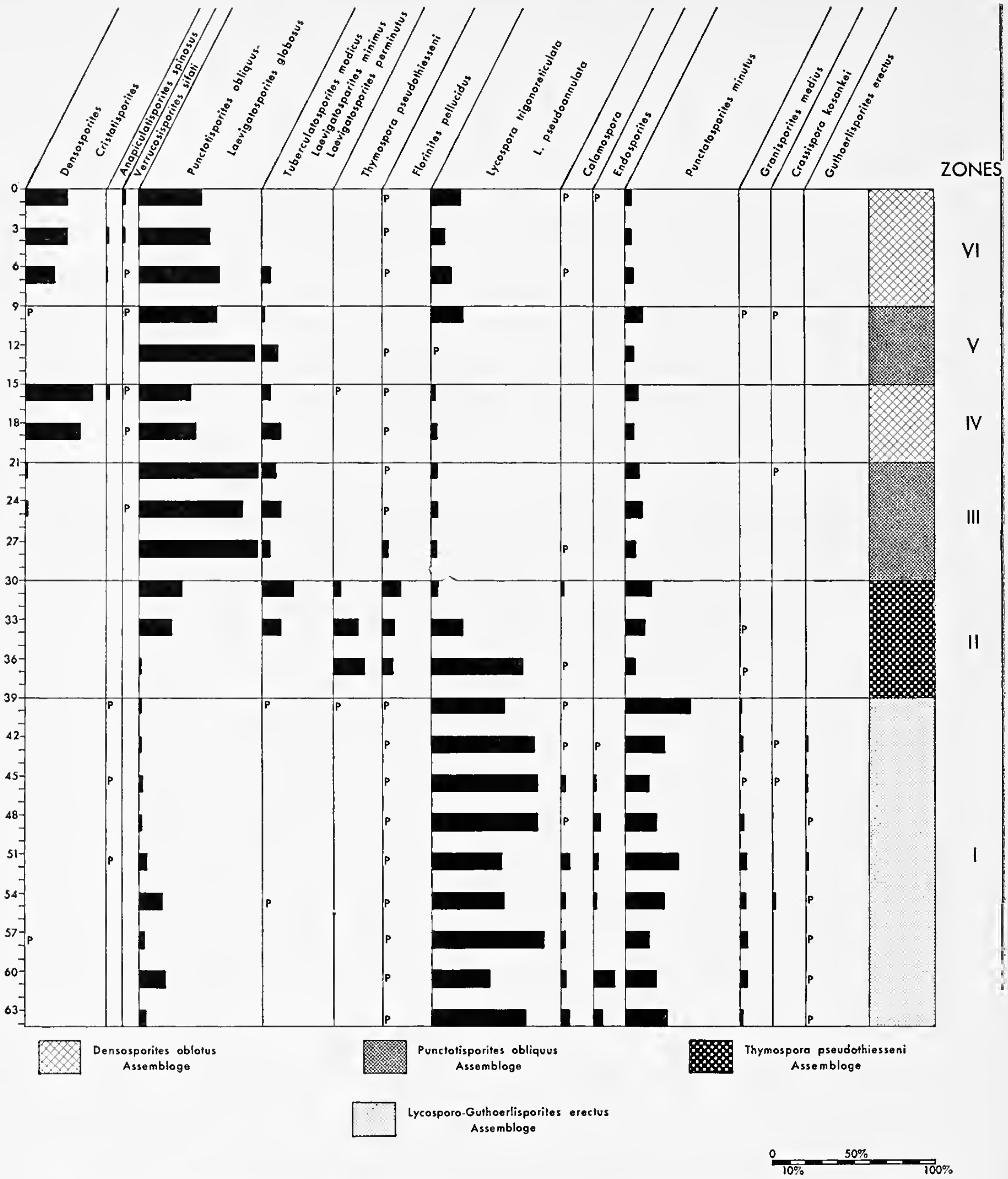
TEXT-FIG. 5. Distribution of spores and pollen in the Lower Kittanning coal at Stations 7 and 8.



TEXT-FIG. 6. Distribution of spores and pollen in the Lower Kittanning coal at Stations 9 and 10.

Anapiculatisporites spinosus, *Verrucosisporites sifati*, *Ahrensisporites vagus* sp. nov., *Acanthotriletes echinatoides*, *Punctatisporites globulosus* sp. nov., and *P. ellipticus* sp. nov.

The analytical data on the *Densosporites oblatus* assemblage show a relatively small number of species counted and a small number observed per sample. The species ranged from as little as 12 to as many as 22, whereas a range of from 20 to 28 was

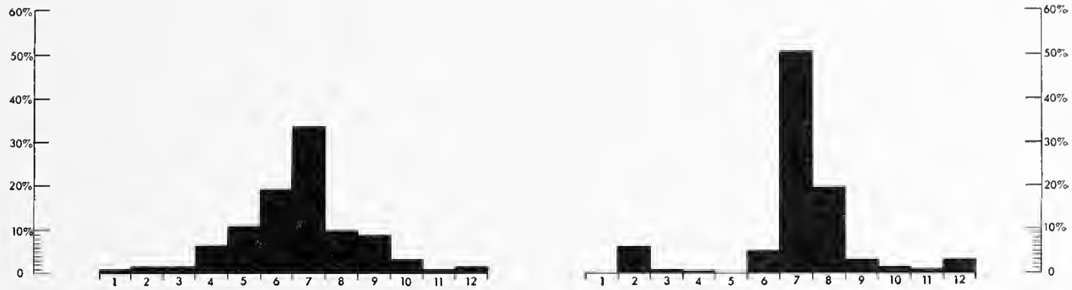


TEXT-FIG. 7. Distribution of spores and pollen in the Lower Kittanning coal at Station 12.

observed for the entire population. As many as 38 species were observed in the uppermost zone at Station 4, but this proved to be an exception. The high incidence of mineral matter and occurrence of species not found in other zones containing the *Densosporites oblatus* assemblage suggest their having been contributed from outside the immediate environment.

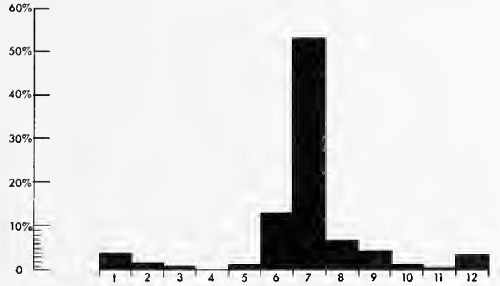
Densosporites oblatus Assemblage

Punctatisporites obliquus Assemblage



Thymospora pseudothiesseni Assemblage

Lycospora-Guthoerlisporites erectus Assemblage



Lycospora Assemblage

1. Densosporites oblatus, D. reynoldsburgensis, Cristatisporites verrucosus
2. Granisporites medius
3. Laevigatosporites desmoinensis, L. medius, L. vulgaris
4. Florinites pellucidus
5. Thymospora pseudothiesseni
6. Punctatisporites obliquus-Laevigatosporites globosus
7. Lycospora trigonoreticulata, L. pseudoannulata
8. Punctatosporites minutus
9. Tuberculatosporites modicus, Laevigatosporites minimus, L. perminutus
10. Triquitrites exiguus, T. bransonii, T. cheilus
11. Vesicaspora wilsonii
12. Calamospora multiplicata, C. pseudotriangulara

TEXT-FIG. 8. Average percentages of species in the spore and pollen assemblages. Numbers under histograms refer to listed species.

The rather small number of species comprising the *Densosporites oblatus* assemblage agrees with the data recorded by Smith (1962, pp. 448–9), who reported a low incidence of species in those portions of the seam rich in *Densosporites*. As a result, he concluded (p. 461) that the vegetation was composed of very few species. It seems reasonable to hypothesize an environment represented by relatively few plant species, either forming dense stands or 'overproducing' microspores to a great extent.

Zones containing the *Densosporites oblatus* assemblage occur at eight of the fifteen localities. They always occur in the upper portions of the seam when present, most frequently occupying the position in contact with the overlying Lower Kittanning shale. Where the assemblage occupies the uppermost zone, the overlying facies is marine or restricted-marine.

Punctatisporites obliquus *assemblage*

This assemblage is similar to the preceding one, but differs markedly in the reduced occurrence to near-absence of densospores. *P. obliquus–L. globosus* is usually most abundant. At a few localities the lack of densospores is compensated by the large numbers of *Lycospora* and/or small monolete species. *P. obliquus–L. globosus* ranges from a minimum of 24·2 % in Zone II at Station 7 to 77·3 % in Zone III at Station 2. Ten of the thirteen zones containing this assemblage, however, range from 34·5 % to 59 %. Densospores reach above 5 % in only two of the zones. At Station 7, they reach to 13 %, a maximum occurrence which is attended by large numbers of *Lycospora*. Species which are more frequently encountered in this assemblage include *Laevigatosporites perminutus*, *L. minimus*, *Tuberculatosporites modicus*, *Punctatisporites obesus*, *P. sphaerorigidus* sp. nov., *Endosporites zonalis*, *Acanthotriletes echinatoides*, *Ahrensisporites vagus* sp. nov., and *Verrucosisporites sinensis*.

The number of species per 200 spores counted ranges from 16 to 28, while the total number of species observed per sample ranges from 24 to 40. The total number of species per sample always increased in the lower portions of the assemblage zones.

The *Punctatisporites obliquus* assemblage occurs at 12 of the 15 localities. It most usually underlies zones containing the *Densosporites oblatus* assemblage or occurs as the uppermost zone of the seam. In either case, it underlies the Lower Kittanning shale where it contains a marine or restricted-marine facies.

Thymospora pseudothiesseni *assemblage*

This assemblage is defined by the presence of *Thymospora pseudothiesseni*, which ranges from 3·5 % to 19 % in its assemblage zones. Although the percentage is not high, this species is virtually absent in samples containing other assemblages, reaching in rare instances, only to as high as 2 %. Concomitant with the increase in *T. pseudothiesseni* is the relatively sudden jump in *Florinites pellucidus*, which ranges to 19·5 %. At only two localities, Stations 2 and 4, does this species not rise appreciably. Although it was found in almost every sample of the seam, only seldom did it increase above 2 % in other assemblages. It is within zones containing the *T. pseudothiesseni* assemblage that *P. obliquus–L. globosus* becomes replaced in the lower portions in being the most abundant representative. On the average this assemblage is less dominated numerically by a single species than are the other assemblages. Many of the species frequently encountered in lesser proportions in other assemblages consequently are more frequent here. *Vesicaspora wilsonii* is found in most zones of the seam, but occurs more frequently here, as do species of *Calamospora*, *Laevigatosporites*, and *Triquitrites*. Other species which are regular members of the *Thymospora pseudothiesseni* assemblage are *T. obscura*, *Schopfites dimorphus*, *S. colchesterensis*, *Cirratriradites annulatus*, *Triquitrites* *exiguus*, *Mooreisporites inusitatus*, *Laevigatosporites vulgaris*, *L. perminutus*, *L. minimus*, and *Tuberculatosporites modicus*. The latter three species occur in lesser proportions than in the previously described assemblages. Densospores are present in a few samples.

The number of counted species increases from 19 to 27, while the total number increases from 22 to 51. Most samples contain between 30 and 35 species.

The relatively larger numbers of *Florinites pellucidus*, combined with an increase in number of species per sample and lesser domination by a single species, suggests an environment such as an open herbaceous marsh, which would contain relatively a greater number of spores from surrounding plant communities. Chaloner (1958 *b*) proposed an 'upland' source for *Florinites*-producing plants, primarily on the results arrived at by Neves (1958). If a rather constant supply of *Florinites* pollen is introduced into the coal swamp from marginal sources, as is evidenced by its low but constant occurrence in almost all samples of the seam, a swamp environment (open marsh) without significant *in situ* spore production by the very nature of its inability to mask (i.e. compare with *Lycospora–Guthoerlisporites erectus* assemblage) would permit the increase in expression of this genus. The high number of species may have been brought in mostly when the environment was covered by the water table, as in floods.

Zones containing this assemblage are present at 12 of the 15 localities. It most frequently occurs in zones in the middle portion of the seam. The assemblage is best developed, i.e. highest percentage of *T. pseudothiesseni* and *F. pellucidus*, usually where the seam underlies ancient 'marine' sediments.

Lycospora–Guthoerlisporites erectus *assemblage*

This assemblage is characterized by the high percentage of *Lycospora* and low but consistent presence of *Guthoerlisporites*. *Lycospora* is represented by *L. trigonoreticulata* and *L. pseudoannulata* which together range over 45 % in twelve of the fourteen zones the assemblage occurs in. The genus is accompanied in almost every sample of the assemblage by *Guthoerlisporites erectus* sp. nov. Although the species does not occur in appreciable quantity, its near omnipresence serves to distinguish the assemblage. It was only very rarely found in other assemblage zones, and only in the lowermost portions which are directly above the *Lycospora–Guthoerlisporites erectus*. It was not found in any sample from Station 13, where the *Lycospora–Guthoerlisporites erectus* assemblage was not observed. It is in samples of this assemblage that *Punctatosporites minutus* becomes most abundant; in some samples, it replaces *Lycospora* in predominance. It reaches to 56 % of the population in a sample from Zone I at Station 8.

A higher number of species were found to occur regularly in this assemblage, including *Granisporites medius*, *Crassispora kosankei*, *Endosporites globiformis*, species of *Calamospora*, *Florinites similis*, *Spackmanites ellipticus* gen. et sp. nov., *S. facierugosus* comb. nov., *Mooreisporites inusitatus*, *Vestispora levigata*, *V. fenestrata*, and *V. profunda*. Other species which are not as widely distributed but still occur most frequently here are *Aculeispores aculeus*, *Cadiospora magna*, *Complexisporites polymorphus*, *C. chalonerii* sp. nov., *Alisporites symmetricus* sp. nov., *Florinites diversiformis*, *F. occultus* sp. nov., *Potonieisporites elegans* emend. *Pityosporites kittanningensis* sp. nov., *Guthoerlisporites delicatus* comb. nov., *Wilsonites kosankei*, and *Apiculatisporis globulus*. Of all these species, *G. medius* is the most abundant, ranging to 19·5 % in Zone I at Station 6.

This assemblage is characterized by a low number of counted species (16 to 24), but in contradistinction to the *Densosporites oblatus* assemblage, a rather high number of total species per sample (29 to 38). The low count is obviously due to the great preponderance of lycosporids. Most other species were well below 3 %. That the lycosporid species were produced by arborescent and presumably anemophilous lycopods may have masked the production of other smaller trees or herbaceous plants in the community. The over-all low percentage of gymnospermous pollen, represented, however, by a number of distinctive genera, suggests either long-distance transportation from outside the area of the coal swamp environments, or even *in situ* deposition during the very early stages of peat accumulation. Most of these species are confined to the lowermost samples of the seam.

This assemblage is present at 14 of the 15 studied localities.

Lycospora *assemblage*

This assemblage is very similar to the last, differing primarily in its total lack of *Guthoerlisporites erectus*. *Lycospora trigonoreticulata* and *L. pseudoannulata* range from 46 to 59·2 %, with *Punctatosporites minutus* never exceeding 14 % in any zone. The saccate gymnospermous species are notably missing, and *Endosporites globiformis* was observed in the assemblage only at Station 9. *Granisporites medius* occurs in larger numbers than in some other assemblages, but reaches only 3 %. *Punctatisporites obliquus–Laevigatosporites globosus* was recorded at approximately 12 %. The densospores are better represented than in many of the preceding assemblages, extending to 7 % at Station 9.

The *Lycospora* assemblage contains a low number of counted species (14 to 22), and a total number of 25 to 35 per sample. The low number of species counted is similar to that in the *Lycospora–Guthoerlisporites erectus* assemblage, which is due here also to the high occurrence of *Lycospora* species. The additional low number of species per sample, however, is in contrast.

The *Lycospora* assemblage occurs at 3 of the 15 localities and always occurs in the uppermost zone. It was found only where the seam underlies the non-marine facies of the overlying shale unit.

DISCUSSION

The most typical sequence in which the spore and pollen assemblages of the Lower Kittanning seam occur from the bottom to top is: (1) *Lycospora–Guthoerlisporites erectus* assemblage; (2) *Thymospora pseudothiesseni* assemblage; (3) *Punctatisporites obliquus* assemblage; (4) *Densosporites oblatus* assemblage. This sequence may be terminated at the top by the *Punctatisporites obliquus* assemblage. This sequence (1–4 or 1–3) is typical of those localities where the marine and restricted-marine facies lie directly over the seam. It is interrupted, and in one case considerably upset (e.g. Station 9) at the fresh-water localities. There, the *Lycospora* assemblage occurs in the uppermost zone. The vertical variation in abundance of species is less pronounced, and consequently fewer assemblages are represented. Even those assemblages more typical of other localities which are present (e.g. *Thymospora pseudothiesseni* and *Punctatisporites obliquus* assemblages) here appear to be less well-developed, presumably due in large part to the preponderance and masking effect of *Lycospora*.

CONCLUSIONS

The spatial arrangement of spore and pollen assemblage zones in the Lower Kittanning seam suggests a genetic relationship with the environmental conditions in which the overlying sediments were deposited (text-fig. 1). Their distribution can be compared in part with the Recent pollen deposits of southwestern Florida, only on the basis, however, of their relationship to marine sediments lying directly on buried portions, and distribution of assemblages according to salinity, water table level, and drainage factors (see Spackman, Dolsen, and Riegel 1966; Habib, Riegel, and Spackman 1966). Although both geo-botanical models cannot be considered completely analogous, they offer similar evidence for migration of peat environments and their contained spore and pollen assemblages in response to a transgressing sea.

The salinity factor, resulting from proximity to the sea, seems plausible in attempting to explain the distribution of assemblage zones in the seam. The arborescent lepidodendrids, from which *Lycospora* was disseminated, were presumably less-brackish paralic swamp dwellers which migrated towards the margins of the peat accumulating basin in step with the encroaching more-saline marine waters. Other factors which are also best manifested in selective zones of a coastal swamp are of equal importance, however. The position of the water table, relatively higher towards the centre of a basin, may have had a marked effect on the distribution of the plant communities from which the *Densosporites oblatus* and *Punctatisporites obliquus* assemblages were formed. The margins of the basin would be better drained and hence better able to support the retreating lepidodendrids.

The large number of species and more or less sudden jump in frequency of *Florinites pellucidus* in the *Thymospora pseudothiesseni* assemblage, suggest periods of widespread high water conditions in an open marsh environment. A modern day analogue of this hypothesis can be found in the surface peat deposits of southern Florida, where a relatively large number of pine pollen is present in an environment represented by many marsh plants (Spackman *et al.* 1966, fig. 16). The pollen deposits of this frequently flooded marsh environment are characterized by a large number of plant species.

As the effect of marine transgression became more intensive, the floral environments became more competitive, with an overall decrease in number of species. Here, the number of densospore-producing plants increased, as the water table rose and the area became more brackish. The apparently anomalous presence of the *Densosporites oblatus* assemblage in Zone II at Station 9, and increase in number of densospores at Station 7, may reflect the presence of a tongue of the marine embayment, or more brackish estuary extending northward. In the modern swamps of the Everglades region of southern Florida, the salinity tolerant red mangrove (*Rhizophora mangle* L.) extends up the banks of the lower reaches of the Shark River into areas containing less-brackish waters (Spackman and Dolsen 1962).

That the influence of the subsiding basin was little felt in the initial stages of peat accumulation is attested by the extensive distribution of the *Lycospora–Guthoerlisporites erectus* and to a lesser degree *Thymospora pseudothiesseni* assemblages in the lower zones of the seam. Factors introduced with the advent of the marine embayment are recorded as having begun to affect the coal-swamp complex during the time of the *Thymospora pseudothiesseni* assemblage, although it would have become intensive in the next higher zones. It is quite possible, of course, that the basin was actively subsiding during the initial stages also, but without presenting evidence into the spore–pollen record.

Immediately prior to, or at the very beginning of, peat formation in the swamp environment, the area was clothed with a gymnospermous (i.e. *Alisporites, Pityosporites, Complexisporites, Wilsonites, Guthoerlisporites*, and *Potonieisporites*) and endosporitid–lycopod forest. The gymnospermous genera may instead represent the allochthonous elements of extra-swamp ('highland') plant communities; restricted occurrence to the lowermost portions of the seam appears to obviate this alternative, however.

In Great Britain, Smith (1963, 1964) found no apparent relationship between coal seams containing *Densosporites*-rich assemblages and the facies of the overlying shales. He suggested instead, that the sequence of assemblages culminating in one containing abundant *Densosporites* represent a succession of hydrological units in a stable environment, and that the *Densosporites*-rich assemblage may have formed partially under subaerial conditions. This is difficult to envisage for the Lower Kittanning seam, where in places marine beds rest directly on the coal.

BIOSTRATIGRAPHICAL IMPLICATIONS

The detailed description of spore and pollen assemblages in the coal seams of western Pennsylvania may well lead to a more meaningful biostratigraphical zonation of the Pennsylvanian rocks of the eastern United States, on the basis of paleoecological interpretations. Similarly conducted palynological investigations of several other coal horizons (e.g. Brookville and Lower Clarion seams by Frederiksen 1961; Upper Freeport and Redstone seams, unpublished work by the author) have demonstrated the occurrence of spore and pollen assemblages and/or assemblage sequences unique to each seam. As a result, two broad categories of assemblages could be established, according to the position of the seams in marine and non-marine stratigraphical sections.

This type of palynological investigation also brings to light the significance of the less abundant but nevertheless persistent spore–pollen species, which are of importance for the determination of more accurate stratigraphical ranges.

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A NON-MARINE OSTRACOD FAUNA FROM THE COAL MEASURES OF DURHAM AND NORTHUMBERLAND

by JOHN E. POLLARD

ABSTRACT. The occurrence and ostracod fauna of the Hopkins Band, Lower *Anthraconaia modiolaris* Zone, of the Lower Coal Measures of Northumberland and Durham are described. In this Band the ostracod *Geisina arcuata* is associated with five species of *Carbonita*, newly recorded, and variants of the non-marine lamellibranchs *Anthracosia regularis*, *Carbonicola oslancis*, *Naiadites productus*, and *Anthraconaia modiolaris*. A vertical sequence of six faunal phases is recognized in this Band and is compared with that previously recorded from an equivalent stratigraphical horizon in the Yorkshire Coal Measures.

Vertical changes in the number of ostracod species and number of moults present in the Hopkins Band are recorded and explained in terms of the changing conditions in the environment of deposition. Certain ecological requirements of the ostracods are suggested.

In the systematic description of the fauna a lectotype for *Geisina arcuata* and a new species *Carbonita claripunctata* are proposed. The species *Carbonita humilis*, *C. evelinae*, *C. pungens*, and *C. inflata* are briefly described and their morphology and stratigraphical distribution discussed.

Lectotypes for *Carbonita agnes*, *C. evelinae*, *C. humilis*, *C. inflata*, *C. pungens*, and *C. rankiniana* are designated by F. W. Anderson in a postscript.

DESPITE the profusion of non-marine ostracods at many horizons within the British Coal Measures, these fossils have received little attention since the latter half of the nineteenth century. The earliest descriptions of Coal Measures ostracods were by Bean (1836) from Northumberland and Durham, and Murchison (1839) from North Staffordshire, but the majority of known species have been described and named by Jones (1870), and Jones and Kirkby (1867, 1879, 1886*a*, 1886*b*, and 1890). The Carboniferous ostracod faunas of Scotland were revised by Latham (1932) in the light of the then current American work (i.e. Ulrich and Bassler 1906, 1908; Harlton 1927, 1928; Knight 1928; and Roundy 1926), but since then little has been published on British Coal Measure species, except for occasional lists and records given in the publications of the Geological Survey.

In the Coal Measures there is a fairly sharp distinction between marine and non-marine associations of ostracods. Ostracods are relatively rare in marine and *Lingula* bands in which only *Hollinella bassleri*, *Paraparchites*, and *Cypridina* occur with any frequency. Ramsbottom (1952) recorded a unique fauna from the Cefn Coed Marine Band of South Wales which included the genera *Amphissites*, *Cornigella*, *Cypridina*, *Kirkbya*, *Knightina* and *Roundyella*, as well as *Hollinella*. All these genera are common in the American Pennsylvanian. Although non-marine assemblages of ostracods are of much commoner occurrence than marine ones, and occur in greater profusion, the number of genera represented is smaller. *Geisina* and *Carbonita* are the only common genera, and it is with these that this paper is concerned.

The ostracods that have been recorded by various authors from horizons in the Northumberland and Durham Coal Measures are shown in text-fig. 1. Apart from one specimen of *Hollinella bassleri*, recorded by Armstrong and Price (1953) from the

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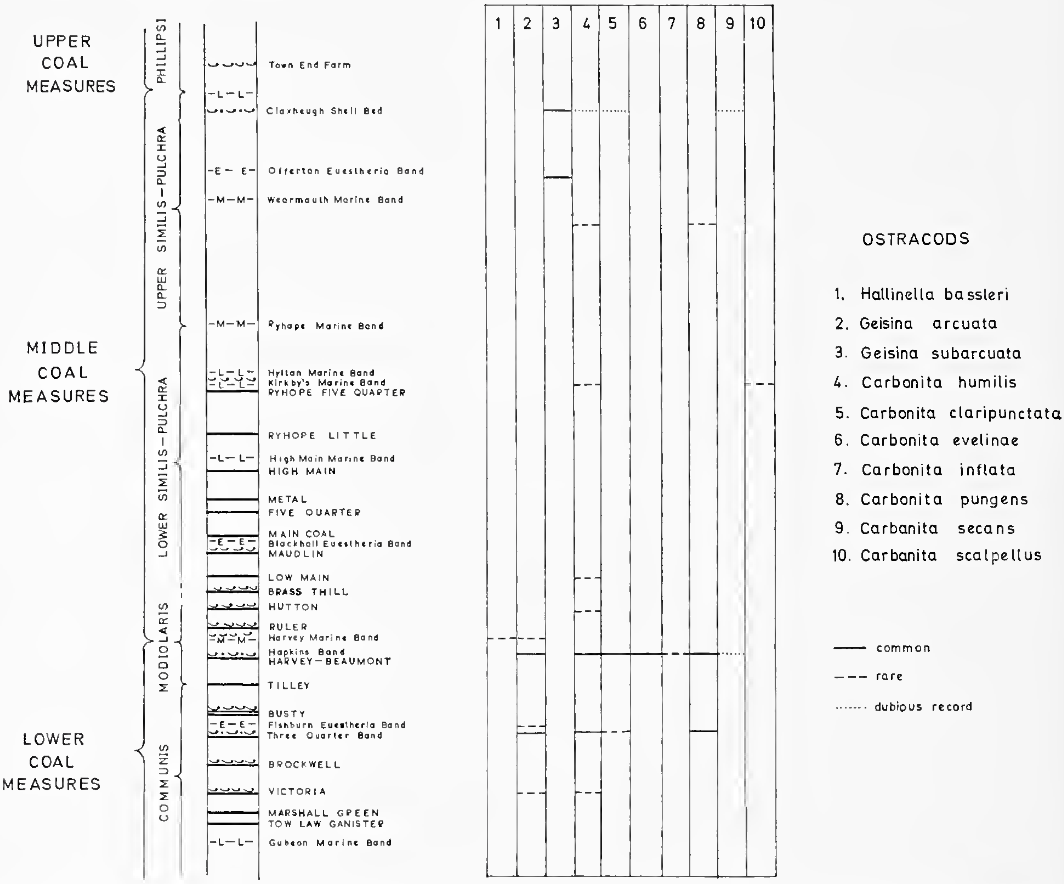
mid-*modiolaris* or Harvey Marine Band, all the others are species of the non-marine genera *Geisina* and *Carbonita*. Most of these records are of a few specimens of one or two species found at isolated localities and horizons, but that of the Hopkins Band in the Lower *A. modiolaris* Zone is of a rich fauna which occurs at the same horizon throughout much of the coalfield. The purpose of this paper is to describe the ostracod fauna of this Band in detail, and to relate its major vertical changes to the changing conditions in its depositional environment.



TEXT-FIG. 1. Ostracod species recorded from the Coal Measures of Northumberland and Durham.

THE OCCURRENCE AND FAUNA OF THE HOPKINS BAND

Definition. The Hopkins Band, or Hopkins Shell Bed, was first described by Hopkins (1927) as 'The Ostracod Band' above the Beaumont or Harvey Seam of the Northumberland and Durham Coalfield, and was named after him by Carruthers (1930, p. 69). A complete definition was given by Hopkins (1928, p. 6):

> This Band is unique in the coalfield as wherever it is found it shows a constant threefold division.
>
> (3) An upper division composed of *Carbonicola* and *Naiadites*.

(2) A middle division composed of *Spirorbis* and a few Carbonicolae, and
(1) A basal division composed entirely of ostracods.

It is not the presence of the ostracod '*Beyrichia*' *arcuata* (Bean) that makes it distinctive but the assemblage and order of deposition of the ostracods, annelids and mussels.

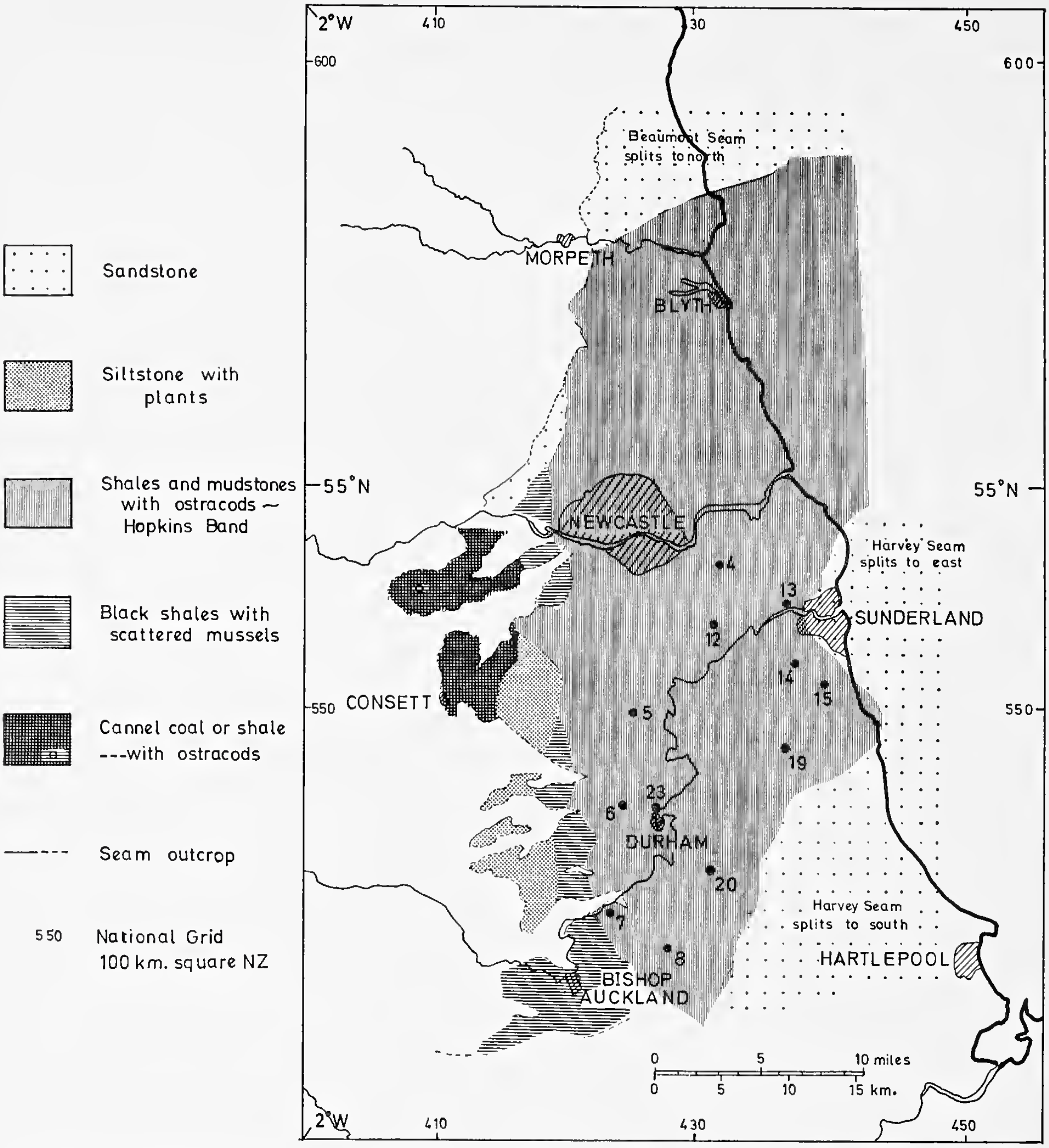
A complete account of subsequent reference to this Band was given by Hopkins (1960) in the Lexique Stratigraphique International.

Other ostracod–mussel associations at a corresponding stratigraphical horizon in the *modiolaris* Zone were later described from many other British Coalfields; for instance, from Scotland (Leitch, Absalom, and Henderson 1937), from Lancashire and Yorkshire (Wright 1931; Eagar 1961), from North Wales (Wood 1937), and from North Staffordshire (Melville 1946). The importance of the Hopkins Band is that it was the first band of its type to be described, is the best known, and is probably the type horizon for the common Coal Measure ostracod *Geisina arcuata* (Bean).

Occurrence and stratigraphy. Text-fig. 2 shows the geographical distribution of the different sediment types associated with the Hopkins Band in the roof strata of the Harvey–Beaumont Seam, as mapped from borehole information and underground evidence. The Band can be traced northwards from Ferryhill in County Durham to Blyth in Northumberland, and eastwards in County Durham from Burnopfield to Sunderland, covering an area of approximately 450 square miles. Throughout this area the stratigraphy of the Band is consistently as shown in text-fig. 3, although the thickness of the fossiliferous strata may vary from 6 in. to 3 ft. 6 in. Magraw, Clarke, and Smith (1963, p. 162) recorded an association of ostracods and mussels in shales above the Harvey Seam in Offshore Bore No. 1, four and a half miles east of Blackhall Colliery but the stratigraphy is not typical of the Hopkins Band.

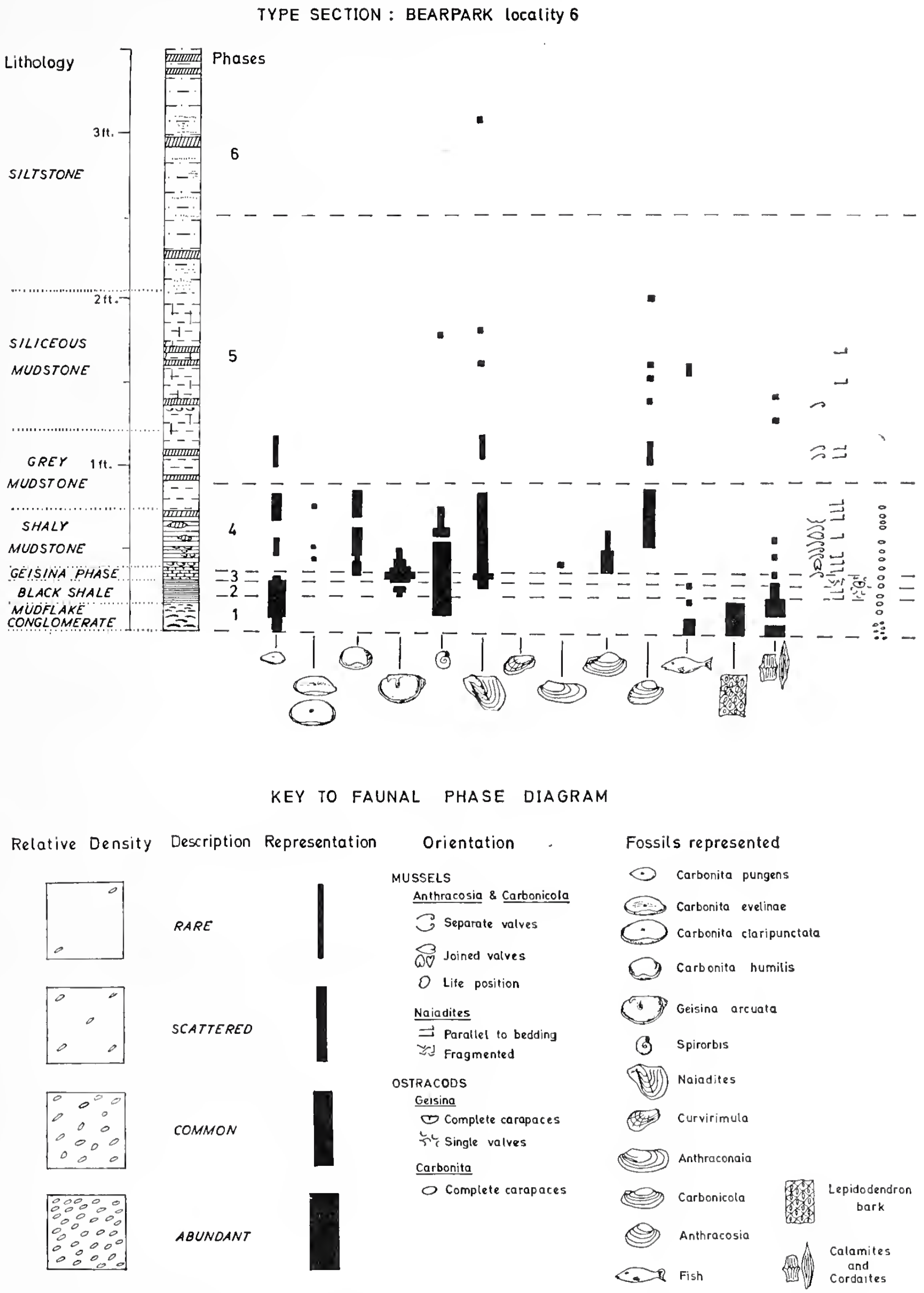
The normal stratigraphic sequence of the Hopkins Band shows that the Harvey–Beaumont seam is overlain either by a bed of ankeritic mudflake conglomerate between a quarter and six inches in thickness, or else by a black carbonaceous shale. A black shale with between 5% and 8% of organic carbon, rich in macroscopic plant remains, ostracods, and *Naiadites* succeeds the conglomerate or its lateral equivalent. At the top of this shale is a densely packed coquina of ostracods, *Naiadites*, and *Spirorbis*, which I have called the *Geisina* Phase. This is equivalent to the Hopkins (1928) division 1 of the Band. Above the *Geisina* Phase, the lithology changes abruptly (text-fig. 3) to a laminated grey shaly-mudstone with less than 1% organic carbon. At this level the population density of the ostracod fauna declines and the non-marine lamellibranch *Carbonicola* appears. This is Hopkins division 2. Clay ironstone nodules and bands appear in the upper part of the grey mudstone, and the lamellibranchs *Anthracosia* and *Naiadites* replace *Carbonicola*, as in Hopkins division 3. A fine siltstone succeeds the mudstone and the fauna then disappears.

Faunal composition. The fossils recorded from the Hopkins Band prior to the present study have been listed by Hopkins (1960). The present work reveals a more extensive fauna than was previously known, and a more detailed faunal sequence, as shown in text-fig. 3. Five species of the ostracod genus *Carbonita*, namely *C. humilis* (Jones and Kirkby), *C. evelinae* (Jones), *C. pungens* (Jones and Kirkby), *C. inflata* (Jones and Kirkby), and *C. claripunctata* sp. nov., are recorded from this band for the first time in association with *Geisina arcuata* (Bean).



TEXT-FIG. 2. Distribution of the sediment types in the immediate roof-strata of the Beaumont–Harvey Seam of the Northumberland and Durham Coalfield. (The large black spots and adjacent numbers refer to the localities mentioned in the text and in Table 5.)

Most of the non-marine lamellibranchs recorded by Hopkins have been found and the overall mussel fauna is of the *oslancis–regularis* type (Calver 1956), which is typical of horizons below the mid-*modiolaris* Marine Band. *Naiadites* is represented by variants of the *N. triangularis–productus* group and carinate forms of *N. carinatus–flexuosus*. The specimens of *Carbonicola* are mainly variants of *C. oslancis* with a low height–length ratio, but smaller, more orbicular forms close to *C. venusta* are fairly common. The



TEXT-FIG. 3. Faunal phases of the Hopkins Band at the type-locality, Bearpark Colliery, County Durham.

upper part of the Band is dominated by *Anthracosia regularis* with rare variants towards *A.* cf. *aquilina* and *A.* cf. *ovum*. Rare specimens of *Anthraconaia* also occur and these are mainly *A. modiolaris* or forms close to *A. robertsoni* and *A. williamsoni*.

Fish remains are confined to the lowest black shale, where scales and spines of palaeoniscids, crossopterygians and acanthodians, including *Megalichthys*, *Elonichthys*, *Strepsodus*, *Rhadinichthys*, and *Acrolepis*, have been found. The tubicolous annelid *Spirorbis pusillus* Martin occurs throughout the Band, being attached to both mussels and plant remains at different levels. The plants are represented by lycopods and *Calamites* in the black shale at the base, and allochthonous fragments of *Calamites*, *Cordaites*, and rare pteridosperms in the siltstone at the top of the Band.

TABLE 1. *Faunal phases of the Hopkins Band*

Hopkins Divisions (1927)		*Faunal phases*	*Lithology*
	6	Scattered *Naiadites* and plant fragments with attached *Spirorbis*	Siltstone and siliceous mudstone
	5	*Anthracosia* common, *Naiadites* without attached *Spirorbis*, *Carbonita pungens* and *C. humilis* rare	Siliceous mudstone and pale grey mudstone with ironstone
(3) (2)	4	*Carbonicola* common, *Anthracosia* and *Anthraconaia* rare, *Naiadites* and *Spirorbis* common, *Carbonita pungens* and *C. humilis* common, *Geisina* rare.	Dark grey shale and mudstone with mussels.
(1)	3	*Geisina*, *Spirorbis* and fragmented *Naiadites* abundant	'*Geisina* Phase'; Black shale laminae
	2	*Geisina* common, *Naiadites* and *Spirorbis* scattered, *Carbonita pungens* common	Black carbonaceous shale
	1	*Carbonita pungens* common, fish scales and plants	Black shale and mudstone conglomerate

Faunal phases. By detailed analysis of the relative density of the various fossils on bedding planes throughout the vertical thickness of the Hopkins Band at twelve localities, it has been possible to recognize a vertical sequence of six faunal phases. Text-fig. 3 shows the faunal distribution and faunal phases at the type-locality of the Band. Each of these phases, numbered 1 to 6, is characterized by changes in the dominance of the fossils present, as represented in Table 1.

The ostracod *Geisina arcuata* has so far only been found in phases 2, 3, and 4 and only occurs in real abundance in the *Geisina* Phase, i.e. phase 3. In these phases *G. arcuata* is associated with *Naiadites*, *Spirorbis*, *Carbonita* and plant fragments, but rarely occurs with *Carbonicola*, and has never been found with *Anthracosia* (text-fig. 3). The species *Carbonita pungens* and *C. humilis* have a longer vertical range than *Geisina arcuata*, occurring from phase 1 to phase 5, and are thus associated at different levels with all elements of the fauna.

A similar sequence of faunal phases was described by Eagar (1961) from the shales above the Flockton Thin and Flockton Thick Coals near Wakefield in Yorkshire (Table 2).

Although *Geisina* is listed in three of Eagar's phases, he did not record the presence of associated species of *Carbonita*. Dr. Eagar has kindly permitted me to examine his material and as in the Hopkins Band, *Carbonita humilis* and *C. pungens* occur throughout the sequence. In the Flockton succession, *Geisina arcuata* is again restricted to the more carbonaceous shale, but in phase 2 occurs in association with abundant specimens of *Anthraconaia*, a situation not paralleled in the Hopkins Band. The association of abundant specimens of *Carbonicola* and rare *Anthraconaia*, with *G. arcuata* in Eagar's phase 3, has a parallel in the lower part of phase 4 of the Hopkins Band in some localities, where *Geisina* persists a little above the *Geisina* Phase. As in the Hopkins Band *Geisina* is not known to occur with *Anthracosia*. Therefore, in both the Hopkins Band and the Flockton shales *Geisina* and *Carbonita* show distinct, but consistent, differences of range, population density, and faunal association.

TABLE 2. *Faunal phases of Flockton Shales, Lower* A. modiolaris *Zone, L. Coal Measures, Cold Bath Opencast Site, Sheffield, Yorks.* (*from Eagar* 1961)

	Fauna	*Lithology*
5	*Naiadites* only, relatively sparse	Pale grey mudstone
4	*Anthracosia* abundant. Relatively high H/L ratio. *Naiadites*, *Anthraconaia* occasional	Grey, typically ferruginous mudstone with little carbonaceous matter.
3	*Carbonicola* abundant. Relatively low H/L ratio. *Naiadites*, *Anthraconaia* occasional. *Geisina* (*Jonesina*) very abundant	Dark fine grained richly carbonaceous shale marked by prolific quantities of ostracods, mainly of *Geisina* group.
2	*Anthraconaia* abundant with less common *Naiadites*. *Geisina* (*Jonesina*) very abundant	Macroscopic pyrite may occur, notably towards the base
1	*Naiadites* and *Geisina* (*Jonesina*) very abundant	
0	Fish scales abundant	

DISTRIBUTION AND PALAEOECOLOGY OF THE OSTRACOD FAUNA

Vertical distribution. In order to study the vertical distribution of the ostracod fauna of the Hopkins Band, ostracods were extracted from two series of shale samples obtained throughout the vertical thickness of the Band at Bearpark Colliery, Co. Durham. The heights of the samples above the Harvey Seam and numbers of the various ostracods extracted are shown in Table 3.

There is a distinct vertical change in the species of ostracods present in the Hopkins Band, and this is independent evidence for the validity of the faunal phases outlined in the previous section of this paper. *Geisina arcuata* is restricted vertically, as previously mentioned, and only occurs abundantly in the *Geisina* Phase, where it is the dominant species. *Carbonita humilis* occurs throughout the vertical sequence, with fairly constant population density. The small 'darwinuloid' form *C. pungens* is most abundant in the three inches of conglomerate and shale immediately above the coal, but it persists vertically, as shown in text-fig. 3. At higher levels, however, it cannot be extracted by the hydrogen-peroxide sludge technique that was used, because the fragile disarticulated valves are easily destroyed. A most interesting antipathetic relationship between the species *Carbonita evelinae* and *C. claripunctata* is suggested by this study (see Table 3). *Carbonita evelinae* is restricted to the grey shaly mudstone above the *Geisina* Phase (3¾–4½ in.), while *C. claripunctata* is absent from this mudstone, but is present in the *Geisina* Phase and in the black shale below.

TABLE 3. *Vertical distribution of ostracods in the Hopkins Band, Lower* A. modiolaris *Zone, L. Coal Measures, at Bearpark Colliery, County Durham*

Numbers indicate the number of specimens extracted

Height above Harvey Seam (in inches)	*Species of ostracods* *Geisina arcuata*	*Carbonita humilis*	*Carbonita evelinae*	*Carbonita pungens*	*Carbonita claripunctata*
12–14		2	1		
9½–10					
8¼–9½		4			
7½–8¼		31	25		
6¾–7½		12	3		
6–6¾		35	6		
4½–5½	9	36	14		
3¾–4½ (*Geisina* Phase)	101	38		1	4
2–3		6			
1–2		29		12	2
0–1		6		25	2
Total number of ostracods extracted	110	199	49	38	8

In the grey mudstone between 7½ and 8¼ in. above the Harvey Seam, *C. evelinae* shows an increase in abundance in both series of samples, and rivals *C. humilis* as being the dominant member of the ostracod population (Table 3). A petrographic study of the enclosing mudstone shows a reduction in the amount of the coarser detrital constituents and the first appearance of framboidal pyrite, suggesting a decrease in the rate of sedimentation. Such a change in the rate of sedimentation could account for the relative abundance of ostracods at this level.

By measuring the height and length of the ostracod carapaces extracted from the series of samples at Bearpark, the number of moult stages or instars of the various species present at different levels was obtained. The lowest two inches of the black shale contain at least two moults of *Carbonita pungens* and *C. humilis* respectively, and three or more of *C. claripunctata*. In the *Geisina* Phase, all the ostracods extracted were adults. The mudstone above the *Geisina* Phase contains persistently two moults of *C. humilis*, while *C. evelinae* is present generally as the adult and rarely as the preceding instar as well.

The absence of early moults from the *Geisina* Phase was confirmed from all localities studied, not only Bearpark (e.g. the size-frequency distribution of *G. arcuata* at Eppleton, text-fig. 5), and could be due to removal by current sorting, or preservation, or extraction failure. Petrographic examination of the *Geisina* Phase sediments shows that at some levels complete and fragmented ostracod carapaces are restricted to lenticular pockets or laminae within the sediments. This observation, when considered with their low clay mineral and high silt content, suggests that these sediments may have undergone mild winnowing by currents at the time of deposition. A thin band of carbonaceous shale with ostracods, very similar to the *Geisina* Phase, occurs above the Eighteen Inch Seam in the *A. modiolaris* Zone of the Cumberland Coalfield (Taylor and Calver 1961, p. 9). At least the three largest moults of both *Geisina arcuata* and *Carbonita humilis* are randomly distributed throughout the two inches of shale of this band. This shale is poorer in detrital silt, and richer in clay mineral material, than the *Geisina* Phase sediments, and probably accumulated more slowly under less turbulent conditions of sedimentation. This comparison further supports the suggestion that selective removal, or fragmentation, of the early instars by mild current action, rather than preservation failure, accounts for the absence of the young ostracod instars from the *Geisina* Phase of the Hopkins Band.

Lateral variation in the Geisina *Phase*. Samples of the *Geisina* Phase were examined in detail from eleven localities in the coalfield, besides Bearpark, to determine if any lateral changes in the ostracod fauna occurred (Table 4). No major lateral changes were found, apart from the rare occurrence of *Carbonita inflata* at two localities near Sunderland.

TABLE 4. *Ostracods extracted from the* Geisina *Band of the Hopkins Band at various localities in County Durham*

Numbers in parentheses refer to localities in text-fig. 2, numbers without parentheses indicate the number of specimens extracted

	Ostracods extracted						
Localities	*Geisina arcuata*	*Carbonita humilis* *Male*	*Female*	*C. claripunctata*	*C. evelinae*	*C. inflata*	*Total*
Follonsby (4)	99	3	2	2			106
Pelton (5)	177	36	62	2	6		283
Bearpark (6)	57	15	23	6	2		103
Whitworth (7)	24	5	13	1	6		49
Ferryhill (8)	97	6	7				110
Washington (12)	65	4	7	3	1		80
Hylton (13)	24	5	18	1	3	7	58
Silksworth (14)	122	77	79	3	4		285
Ryhope (15)	120	18	23	4	1		166
Durham Main (18)	34	1	9	1	1		46
Eppleton (19)	212	34	111	11	1	5	374
Bowburn (20)	32	6	12	1			51
Total	1063	210	366	35	25	12	1711
Approximate % of fauna	60	35		3			98

When all the 1711 ostracods extracted from the twelve localities are considered together the approximate proportions of species present in the *Geisina* Phase can be deduced. Approximately 60% of the ostracods are referable to *Geisina arcuata*, about

35% to *Carbonita humilis*, about 3% to *C. evelinae* and *C. claripunctata* together, and about 2% to *C. pungens*. *Carbonita inflata* is very rare and only of local occurrence.

As shown in Table 4, sexual dimorphism in *Carbonita humilis* was recognized at most localities, although the ratios of the dimorphs extracted varied considerably. Dimorphism was not recognized in any other species of *Carbonita*. The greatest population densities of ostracods in the *Geisina* Phase were found in the centre of the coalfield, at the localities Pelton, Follonsby, Eppleton, Silksworth, and Ryhope, where the Phase is between 1 and 1½ in. in thickness. In the localities towards the south and south-western part of the coalfield, at Durham Main, Bowburn, Ferryhill, and Whitworth Opencast Site, the shales of the *Geisina* Phase thin to between ¼ and ½ in. with an associated reduction in the population density of the ostracod fauna.

Palaeoecology of Geisina *and* Carbonita. The vertical changes in the ostracod fauna of the Hopkins Band are believed to be related to changing conditions in the environment of deposition of the sediments. In these sediments *Geisina arcuata* is associated with *Naiadites*, *Spirorbis*, *Carbonita*, and plant fragments, and is restricted to the carbonaceous shale with between 2% and 8% organic carbon. These facts suggest that in its ecology this ostracod was associated with plant matter, and a pseudoplanktonic fauna. Eagar (1961) and Heath (1961) reached similar conclusions regarding the ecology of this species. The genus *Carbonita*, however, does not show any particular vertical restriction or geochemical correlation and occurs with both pseudoplanktonic and benthonic faunas. These facts and the similarity of shell shape may indicate that in its ecology this genus is similar to the living *Cypridopsis* (Scott and Summerson 1943; Kesling 1951).

Several workers have suggested distinct palaeosalinity differences between these two genera. Jones, Kirby, and Young (1899), Scott and Summerson (1943), and Scott (1944), all suggested that *Carbonita* flourished mainly in freshwater lakes or lagoons. In the Ruhr Coal Measures, however, *Geisina* is considered to occur only in brackish or marine shales (Kremp and Grebe 1955; Ernst, Krejci-Graf, and Werner 1958; Ernst, Michelau, and Tasch 1960; Knauf 1963; and Böger 1964). The gradual predominance and final survival of *Carbonita* over *Geisina* in ostracod bands from the Lower to the Upper Coal Measures is thought by Calver (1966) to be due to the gradual reduction of marine influence on the Coal Measure environments.

The solution of the apparent enigma of these two genera occurring together is probably that salinity was not the sole ecological factor determining their distribution. Such related factors as types of bottom substrate, available food supply, and depth, may have been equally important.

In terms of detailed palaeoecology, *Geisina arcuata* appears to have been a browser on floating or deposited plant matter and to have had a wide salinity tolerance, perhaps being euryhaline. Some species of *Carbonita*, namely *C. humilis* and *C. pungens*, may have been ubiquitous bottom crawlers or near bottom swimmers (cf. *Cypridopsis*, Kesling 1951), while others show distinct substrate preferences, *C. claripunctata* to a carbon rich substrate and *C. evelinae* to a carbon poor substrate. *Carbonita* appears to have been oligohaline, tolerant of fresh to slightly brackish water, as it has not so far been found associated with what are normally regarded as marine faunas in the Coal Measures.

Palaeoecology and vertical distribution of the ostracods. This section is an attempt to reconstruct the changing conditions of the depositional environment from a consideration of changes in the sediments and associated faunas.

After the initial inundation of the swamp that later formed the Harvey–Beaumont Seam, quiet lagoonal conditions were presumably established over the area of the coalfield now occupied by the Hopkins Band (text-fig. 2). The sediment coming into this lagoon contained large and small plant fragments, together with silt and fine clay, which, after deposition, were compacted to form a carbonaceous shale with between 5% and 8% of organic carbon and up to 10% free silica. Such a lagoonal environment would have had a richly carbonaceous floor thickly populated by swarms of *Carbonita pungens*, scattered *C. humilis* and *C. claripunctata*, and small groups of *Geisina arcuata* clustered around decaying plant fragments.

Petrographic and geochemical examination of the sediments of the *Geisina* Phase shows these to be poor in detrital silt and fine clay, but are largely composed of organic carbon, pyrite, and calcareous shell material. This widespread Phase seems to represent a coquina of *Geisina*, *Carbonita*, *Naiadites*, *Spirorbis*, and plant matter, which accumulated under conditions of reduced inorganic detrital sedimentation, but mild turbulence.

The abrupt change in lithology at the top of the *Geisina* Phase suggests a change in the source and type of sediment being supplied to the environment. The faintly laminated shaly-mudstone that succeeds the *Geisina* Phase consists largely of clay minerals, less than 1% organic carbon, and less than 5% free silica. On this muddy substrate, a benthonic fauna of the lamellibranchs *Carbonicola* and *Anthracosia* and the ostracod *Carbonita* flourished. *Geisina arcuata* died out with the failure of the detrital plant matter, but a new species of *Carbonita*, *C. evelinae*, appeared and soon rivalled *C. humilis* as the dominant ostracod.

At a higher level in the mudstone there is a gradual increase in the detrital silt content, and the mudstone passes into a siltstone. This increase in silt in the water was probably the major factor responsible for the elimination of the Hopkins Band fauna. The benthonic lamellibranchs *Carbonicola* and *Anthracosia* first became scattered or grouped (Broadhurst 1964) and then disappeared, to be survived only by *Naiadites*, which probably had a pseudoplanktonic mode of life. *Carbonita* disappeared with the benthonic lamellibranchs.

The environment of deposition of the sediments and fossils of the Hopkins Band, described above, represents the basal lagoonal phase of a typical Coal Measure cyclothem. These fossiliferous sediments are nowhere more than 6 ft. thick and are succeeded by 40–50 ft. of deltaic sandstone that forms the main 'regression phase' (Payton and Thomas 1959) of the cyclothem. The ecological changes suggested above are those normal in such a lagoonal environment undergoing gradual sedimentary infilling with the approach of the deltaic phase of the cyclothem.

Acknowledgements. I would like to thank Dr. W. Hopkins for help and encouragement during the course of this work, Dr. F. W. Anderson for advice on ostracod taxonomy, Dr. F. M. Broadhurst and Dr. J. W. Stanley for offering many helpful suggestions, and Professor K. C. Dunham and his technical staff for the use of the facilities of the Department of Geology, University of Durham. I am grateful to the officers of the National Coal Board, Northumberland and Durham Divisions, for giving access to underground and opencast workings and borehole records; the Assistant Director and Mr. M. A. Calver of the Geological Survey Office, Leeds, for giving access to material in their collections; and to the Assistant Keeper and Dr. R. H. Bate of the British Museum (Natural History), Dr. W. I. Rolfe of the Hunterian Museum, Glasgow, and Dr. R. M. C. Eagar of the Manchester Museum, for the loan of ostracod material. The work was carried out during the tenure of a D.S.I.R. Research Studentship, which is gratefully acknowledged.

SYSTEMATIC DESCRIPTIONS

As well as the new ostracod species proposed in this study, the other species recorded are briefly redescribed, since this is the first study involving large numbers of these ostracods from the British Coal Measures. The lectotype of *Geisina arcuata* is in the collections of the British Museum (Natural History) and is described here. The species of *Carbonita* are compared with lectotype material in the British Museum as designated by F. W. Anderson in a postscript to this paper. All numbers of specimens quoted are British Museum (Natural History) registration numbers.

Subclass OSTRACODA Latreille 1806
Order PALAEOCOPIDA Henningsmoen 1953
Suborder KLOEDENELLOCOPINA Scott 1961
Superfamily KLOEDENELLACEAE Ulrich and Bassler 1908
Family GEISINIDAE Sohn 1961
Genus GEISINA Johnson 1936

Geisina arcuata (Bean) 1836

Text-fig. 4 *a–f*

1836 *Cypris arcuata* Bean, p. 377, fig. 55.
1886*b* *Beyrichia arcuata* (Bean); Jones and Kirkby, p. 438, pl. 12, figs. 12–14.
non 1889 *Beyrichia arcuata* (Bean); Jones, p. 381, pl. 17, fig. 7*a–c*.
1908 *Jonesina arcuata* (Bean); Ulrich and Bassler, p. 324, pl. 44, figs. 17–19.
non 1927 *Jonesina arcuata* (Bean); Harlton, p. 205, pl. 32, fig. 6*a–c*.
1928 *Jonesina arcuata* (Bean); Knight, pp. 243–6, pl. 31, fig. 6*a–c*; pl. 33, fig. 6.
1932 *Sansabella arcuata* (Bean); Latham, p. 366, fig. 12.
1943 *Jonesina arcuata* (Bean); Scott and Summerson, p. 672, pl. 1, figs. 12–15, 19, 21.
1946 *Geisina arcuata* (Bean); Cooper, p. 110, name only.
1949 *Limnoprimitia arcuata* (Bean); Kummerow, p. 49, fig. 1.
1952 *Jonesina arcuata* (Bean); Marple, p. 936, pl. 135, figs. 4–8.
1953 *Limnoprimitia arcuata* (Bean); Kummerow, p. 15, pl. 1, fig. 7.
1955 *Jonesina arcuata arcuata* (Bean); Kremp and Grebe, pp. 159–62, pl. 1, figs. 8–10.
1957 *Jonesina arcuata* (Bean); Vangerow, p. 468, pl. 20, figs. 27–30.

Type specimens. Lectotype, In 43596, specimen 12; complete carapace, adult female, designated here. *Paratype*, In 43596, specimens 1–7, 10, 18–23 (Ex Bean Collection, purchased Kirkby 1888).

Dimensions. Lectotype: length, 1·28 mm.; height, 0·81 mm.; width, 0·62 mm.

Type locality. Newcastle area (see discussion).

Type horizon. Coal Measures, probably Hopkins Band, Lower *A. modiolaris* Zone, Lower Coal Measures (see discussion).

Description. Carapace sub-ovate to sub-rectangular in lateral view. Dorsal margin straight, hinge line slightly depressed in posterior half; ventral margin convex. Ends rounded, the anterior more than the posterior. Anterior cardinal angle obtuse, posterior cardinal angle 90° or less. Greatest height median; greatest width median in the male, posterior of middle in the female, giving a strongly sub-ovate dorsal outline.

Anterior sulcus S1 weak, wide, and shallow, or absent. Posterior to S1 there is an indistinct node that fades towards the dorsum. Median sulcus S2 prominent, slightly anterior of middle, extending from dorsal margin to central area, straight sided, deepest and widest in the dorso-central area. Posterior to S2, the shell swells dorsally above the hinge line in a raised area.

Right valve the larger, overlapping the left at the ventral and end margins. On the exterior of the right valve are two swellings, one on the central anterior border and the other at the posterior cardinal angle. Anterior swelling is a low pointed bulb which imparts pointed appearance to the anterior end of the right valve. Posterior swelling is a rectangular bulb which curls posteriorly and gives the distinctly right-angled appearance to the postero-dorsal corner. Ventral edge of the right valve is thickened and projects below the left valve on overlap. Left valve smaller, lacks the swellings of the right, but is distinctly rimmed.

Hinge line straight, about two-thirds length of dorsal margin, with flexure of right valve over the left at both cardinal angles. Surface ornament a reticulate pattern of polygonal pits over the lateral surface of both valves.

Internal features. The internal features could not be seen on the articulated carapace of the lectotype, so they are described from both complete and fragmentary valves of this species from the Hopkins Band of Durham and the Flockton Shales of Yorkshire.

Hinge structure is of true *Geisina* type (Johnson 1936, p. 22). There is a narrow shallow groove in the dorsal contact margin of the right valve into which the dorsal edge of the left valve fits. In the anterior half of the hinge of the right valve the groove is wide, and its lower edge is reflexed ventrally into a sloping flange, so that the anterior half of the hinge of the left valve is reflexed upwards to overlap the flange of the right valve, as described by Johnson (text-fig. 4*e*).

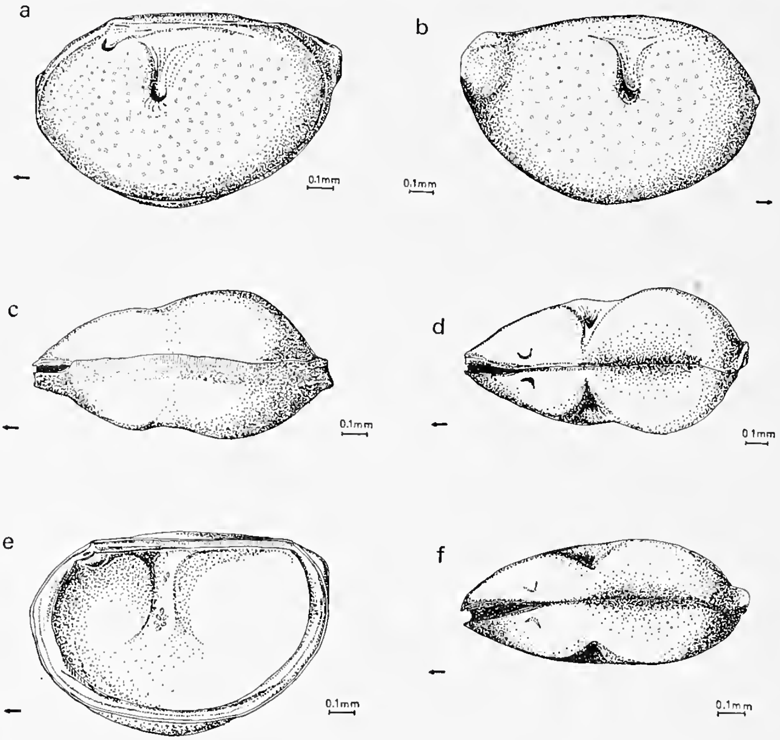
A wide thickened rim runs internally around the contact margin of both valves. This rim may be the remains of the duplicature, stated by Sohn (1961, p. 182) to be present in this genus. In the thickened rim of the right valve there is a ridge and groove to accommodate the overlapped edge of the left valve.

The median sulcus S2 swells and thickens slightly internally to form a ridge that fades in the central area. Rarely, faint markings suggesting two groups of muscle scars can be seen on this ridge.

Other features from a study of specimens from the Geisina *Phase*. Dimorphism can be clearly recognized in any population of this ostracod. It is of typical kloedenellid type (Scott and Wainwright 1961), being shown by the inflation of the posterior part of the carapace of the female, giving distinctly different dorsal outlines to the dimorphs (text-fig. 4*d*, *f*). Johnson (1936) describes differences in lateral shape as well as posterior inflation between the dimorphs of the type species *Geisina gregaria*, but no such differences are discernible in *G. arcuata*.

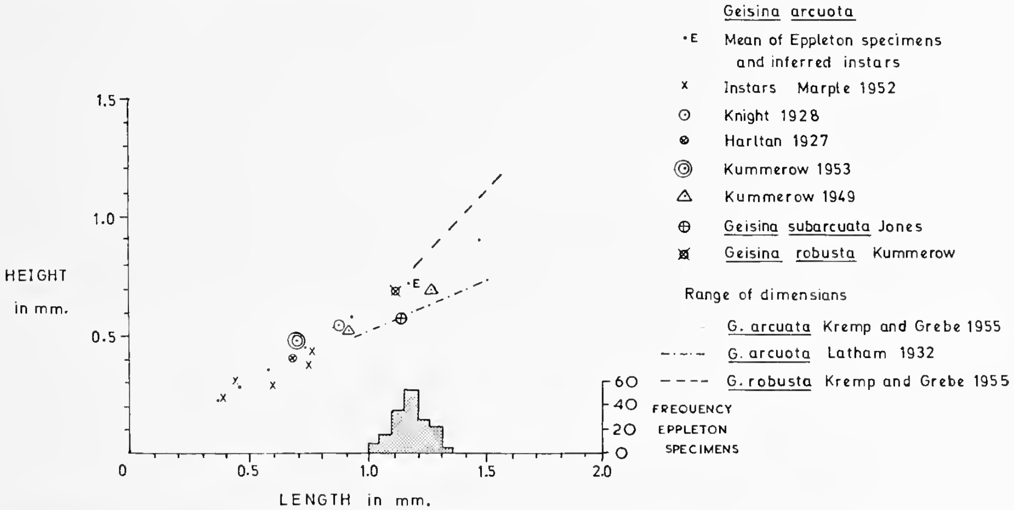
In a sample of 180 well-preserved specimens of this species from Eppleton, near Sunderland, 80 % fall within a range of size dimensions: length, 1·10–1·30 mm.; height, 0·60–0·80 mm. The mean sizes are: length, 1·17 mm.; height, 0·72 mm., slightly smaller than the lectotype. When this range of size dimensions is plotted graphically (text-fig. 5), it confirms that only one instar is present. The dimensions given by other workers for synonymous or allied species of *G. arcuata* are plotted in text-fig. 5 and suggest that in many cases they are earlier moults than those represented in the *Geisina* Phase.

Discussion. Morphologically this species is fairly close to the American type species *G. gregaria*, and although lacking its postero–dorsal spine, has a rectangular bulb in a similar position. *G. arcuata* is distinguished from *G. subarcuata* Jones, the only other species of this genus recorded from the British Coal Measures, by the smaller size of the adult, the deeper median sulcus S2, and the presence of the exterior bulbs on the right valve. In many characters this species closely approaches various of the American species of *Geisina* listed by Echolls and Creath (1959), previously described by other workers.



TEXT-FIG. 4. *Geisina arcuata* (Bean). *a–d*, Lectotype, In 43596, specimen 12. *a*, exterior view of left valve; *b*, exterior view of right valve; *c*, ventral view of entire carapace; *d*, dorsal view of entire carapace showing posterior inflation of the female; *e*, interior of the right valve showing grooved hinge and thickened marginal rim, specimen from Flockton Shale of Yorkshire; *f*, dorsal view of complete male carapace from Hopkins Band at Eppleton Colliery, County Durham.

Because of the confused taxonomic history of this species, as revealed by the synonymy, it is necessary to discuss the choice of type material and the generic relationships. The original description by Bean (1836) was brief and in general terms, and the original figure very poor. The type locality and horizon were likewise vague, being 'the coal formation near Newcastle'. The specimen proposed here as the lectotype, however, from the British Museum collection, bears the label '*Cypris arcuata* mihi' in Bean's handwriting. This proposed lectotype comes from a piece of shale lithologically and faunally identical with the *Geisina* Phase of the Hopkins Band in the Newcastle area. The historical record (*History of Northumberland*, 1930, **8,** p. 25) shows that the Beaumont Seam was being worked about 1836 along the north bank of the Tyne west of Newcastle, and so it is here suggested that a fragment of the roof shale of this seam, rich in *G. arcuata*, was sent by an interested amateur, 'Mr. Alder' (Bean 1836, p. 377), to the well-known Yorkshire naturalist, William Bean. Therefore, it is believed that the specimens of this species described in this paper come from the type horizon and approximately the type locality of *G. arcuata* (Bean).



TEXT-FIG. 5. Height and length dimensions of *Geisina arcuata* (Bean) and related species.

Jones and Kirkby (1886*b*) gave the first detailed description of this species as *Beyrichia arcuata* (Bean), and recorded its occurrence from the Coal Measures of the Midlands, Manchester, Lanark, and County Durham (Ryhope and Claxheugh). Material from these localities is preserved in the Kirkby Collection in the British Museum (Natural History), and apart from the Lanarkshire specimens, from Carluke, they appear to be *G. subarcuata*, as their localities in the Middle Coal Measures would suggest. The species was placed in the genus *Jonesina* by Ulrich and Bassler (1908) when they erected this genus on the type species *Beyrichia fastigiata* Jones and Kirkby without description of, or reference to, a type specimen. However, when Johnson (1936) erected the new genus *Geisina* for a Nebraskan Pennsylvanian form, he borrowed the only known material of '*Beyrichia*' *fastigiata* identified by Jones and Kirkby, in the British Museum collections, and distinguished between *Geisina* and *Jonesina*. Although Johnson (1936) described only one species, *Geisina gregaria* (Ulrich and Bassler), *Jonesina arcuata* was referred here by Cooper (1946), but only as a passing mention without examination of any material.

The specimens *Jonesina* '*Beyrichia*' *fastigiata* in the British Museum (numbered I 1774 and In 32494–6) have been re-examined and compared with *G. arcuata*. The genus *Jonesina* is considered to be valid and cannot be dismissed as suggested by Sohn (1961, p. 413), and differs from *Geisina* in the valves being strongly and deeply bisulcate, the median sulcus S2 being deep and terminating in a pit, the hinge not being depressed in the posterior half, and the hinge structure only showing overlap at the cardinal angles. These characters correspond to those given as distinctive of *Jonesina* in an apparently little-known revision of the generic diagnosis by Cooper (1941, pp. 55, 56).

Post-war German work on Ruhr Coal Measure ostracods has shown an ignorance of both American literature and the existence of type material of *G. arcuata* in British collections. Kummerow (1949, 1953) proposed and described a new genus, *Limnoprimitia*, for *G. arcuata*, but Kremp and Grebe (1955, p. 161) dismissed the genus as invalid because of the poor state of preservation of the original material. On the advice of Dr. B. Kellett, however, Kremp and Grebe (loc. cit.) considered both *Limnoprimitia* and *Geisina* to be synonymous with *Jonesina* and so have retained the species as *Jonesina arcuata*. Their further subdivision of the species into *J. arcuata arcuata* and *J. arcuata cingulata* seems to be due to their confusion of the latter variety with the species *Geisina subarcuata* (Jones).

Stratigraphical distribution. Published records of *G. arcuata* in Britain range from the Lower Carboniferous to the Upper Coal Measures, but most probably this species is really restricted to the Lower Coal Measures. The Scottish Lower Carboniferous forms may well belong to *Sansabella*, *Jonesina*, or other Mississippian genera, while the higher Coal Measure forms are generally close to *G. subarcuata*. Authors such as Wright (1931), and Edwards and Stubblefield (1947) are probably correct in referring the range of the species to the *C. communis* and Lower *A. modiolaris* Zones of the Coal Measures, that is, to horizons below the Clay Cross Marine Band.

A similar stratigraphical range for this species exists in the European coalfields. Pruvost (1930) stated that it is an excellent zonal indicator of Westphalian A, while Kremp and Grebe (1955) recorded it as occurring in Namurian C and Westphalian A, but not above the Katharina (= Clay Cross) Marine Band.

Echolls and Creath (1959) recorded that the range of *G. arcuata* in the United States is Lower and Middle Pennsylvanian, from the Morrowan to the Desmoinesian stages. This is broadly equivalent to the European Westphalian. However, Scott and Summerson (1943) described '*Jonesina*' *arcuata* occurring in abundance with species of *Carbonita* and *Anthraconaia modiolaris* in the Hance Formation of Tennessee. They correlated this horizon with the Upper Westphalian A stage of the European Coal Measures.

The general picture therefore seems to suggest that despite its wide distribution from central and eastern United States, and across Europe as far as the Russian coalfields, *Geisina arcuata* (Bean) has a limited stratigraphical range, from Namurian C to the top of Westphalian A. It is at its greatest abundance in Upper Westphalian A, which is equivalent to the Lower *A. modiolaris* Zone of the British Coal Measures in which the ostracod fauna from the Hopkins Band of County Durham occurs.

Order PODOCOPIDA Müller 1894
Suborder PODOCOPINA Sars 1866
Superfamily CYPRIDACEA Baird 1845
Family CYPRIDIDAE Baird 1845

(Placed here by Cooper 1946, family uncertain Swain 1961)

Genus CARBONITA [CARBONIA] Jones 1870

(Preoccupied by *Carbonia* Robineau-Desvoidy 1863 = *Carbonita* Strand (1926; 1928, pp. 40, 41)

Type species. Carbonita [*Carbonia*] *agnes* Jones 1870.

Generic diagnosis. Carapace sub-ovate, ovate–oblong, or elongate. Greatest height usually in the posterior third; greatest thickness median to posterior. Dorsal margin slightly to broadly convex; ventral margin straight to slightly convex. Ends unequal, broadly rounded to acutely pointed. Hinge in the middle third of the dorsal margin, straight and simple with the left valve usually raised above the right along the hinge line, closely adpressed or with a narrow groove. Right valve the larger, overlapping the left on the ventral margin and narrowly overlapping or over-reaching left on the end margins. Surface smooth to coarsely reticulate. Ornament may consist of longitudinal striae or concentric reticulation, but may vary with preservation. Muscle scar circular, sunk into the shell, anterior or antero-ventral of the mid-point. Major muscle scar encloses a variable pattern of secondary scars. Shell usually thickened internally postero-ventrally of the muscle scar, in a low ridge that may leave a pronounced furrow on internal moulds.

Carbonita humilis (Jones and Kirkby) 1879

Text-fig. 6

	1879	*Carbonia fabulina* var. *humilis* Jones and Kirkby, p. 31, pl. 2, figs. 11–14.
	1884	*Carbonia fabulina* var. *humilis* Jones and Kirkby, p. 388, pl. 2, fig. 9.
	1911	*Carbonia fabulina* (Jones and Kirkby) in part; Pruvost, pp. 68–70, pl. 2, figs. 1–8.
	1930	*Cytherella foveolata* Wright, p. 49, pl. 1, fig. 2*a*–*b*.
Non	1955	*Carbonita humilis* (Jones and Kirkby); Kremp and Grebe, p. 151, pl. 16, fig. 1.
	1955	*Whipplella rhenana* (Kummerow); Kremp and Grebe, pp. 155–7, pl. 16, figs. 5, 6.
	1955	*Whipplella cenisa* Kremp and Grebe, pp. 152–5, pl. 16, figs. 3, 4.

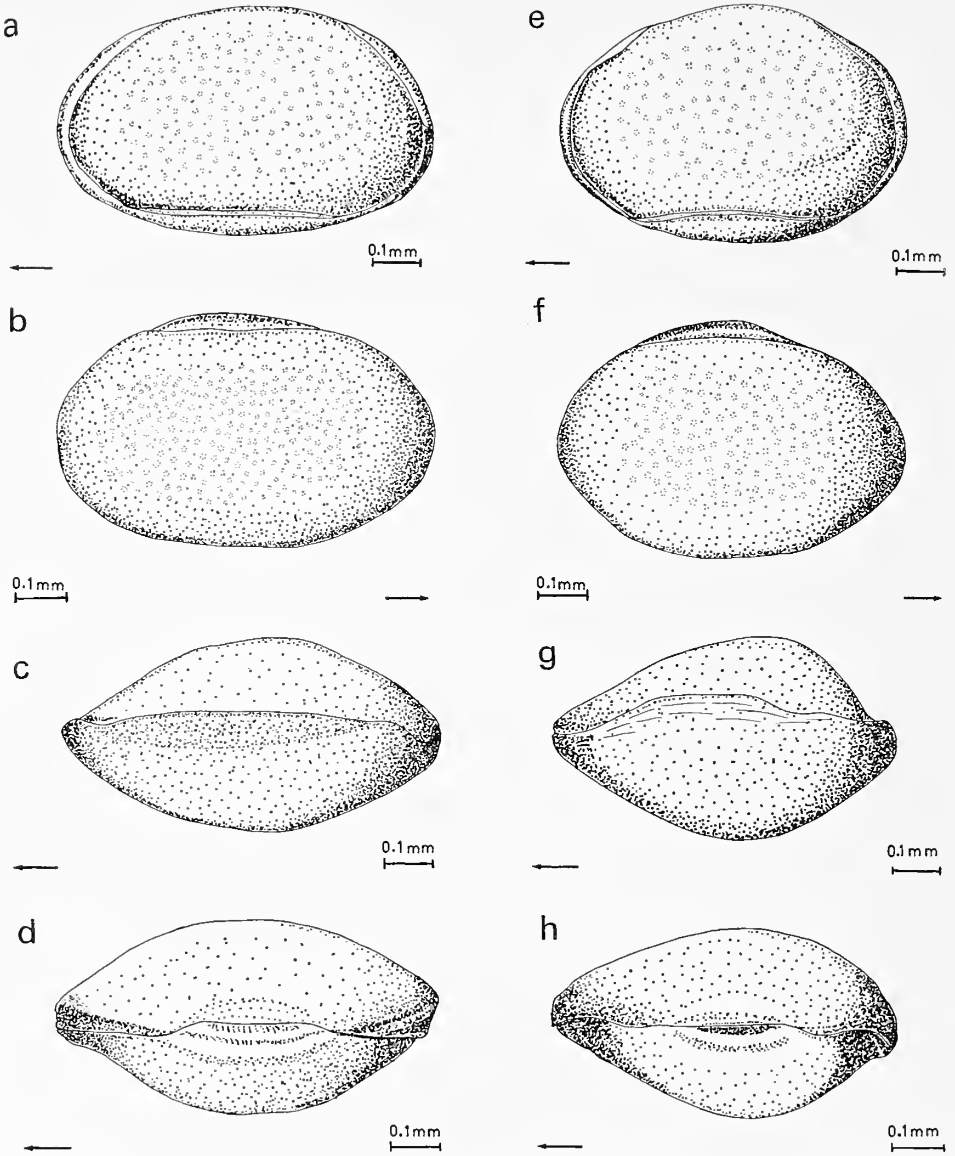
Lectotype. A figure; Jones and Kirkby 1879, pl. 2, fig. 14. Chosen by Anderson (see Postscript); type material not found.

Specimens described. Female, IO 2980, Hopkins Band, Bearpark Colliery, Co. Durham. Male, IO 2981, Hopkins Band, Ryhope Colliery, Co. Durham.

Dimensions. In mm.

		Length	*Height*	*Width*
Female	IO 2980	0·74	0·48	0·43
Male	IO 2981	0·81	0·48	0·41

Description. Female. Carapace tumid, sub-ovate, dorsal margin gently convex, ventral margin straight to slightly convex. Ends rounded, posterior more obtuse. Greatest height just posterior of the middle, while the greatest width is well posterior of middle. Ridge of thickening externally at antero–ventral corner of the left valve. Hinge short, straight, in central third of dorsal margin, left valve raised above the right along the hinge with a narrow groove between the valves. Valves unequal, right overlaps the left



TEXT-FIG. 6. *Carbonita humilis* (Jones and Kirkby). *a–d*, specimen IO 2981, complete male carapace. *e–h*, specimen IO 2980, complete female carapace. *a*, exterior left valve; *b*, exterior right valve; *c*, ventral view; *d*, dorsal view; *e*, exterior left valve; *f*, exterior right valve; *g*, ventral view; *h*, dorsal view.

on ventral and both end margins. Ventral overlap wide, end overlap narrow but distinct. Shell surface distinctly pitted with small polygonal pits. Internally valves are bordered with a narrow rim and they possess a typical muscle scar and slightly thickened ridge postero-ventral of the muscle scar.

Male. As female except lateral shape elongate–ovate, maximum height and thickness median, not posterior of middle. Height to length ratios: male about 60%, female 70%.

Discussion. In the original description of *Carbonia fabulina* var. *humilis* Jones and Kirkby (1879, p. 31) emphasized that this variety differed from *C. fabulina* (sensu stricto) in the flatter dorsal margin and the rounded ends being more nearly alike. These characteristics fit the male of the species as described above, and the original figures (pl. 2, figs. 11, 12) are of the male. The lectotype, however (pl. 2, fig. 14), is relatively higher than the others, sub-ovate with a blunter posterior, and although an internal mould it is probably a female. It thus seems that although only the male was originally described by Jones and Kirkby (1879), both forms were recognized and figured.

In the later description of *C. fabulina humilis* from the Nova Scotia Coal Measures, Jones and Kirkby (1884) stated that this form is further distinguished from *C. fabulina* (sensu stricto) by the thicker shell, the distinct pitting, and stronger amount of overlap. These differences appear to be persistent, so the 'var. *humilis*' of Jones and Kirkby has been elevated to specific rank by recent workers (Kremp and Grebe 1955; Copeland 1957; Anderson (in press). This present study of the population of *C. humilis* in the Hopkins Band confirms that it is a species in its own right.

Although Jones and Kirkby originally recorded *C. fabulina* var. *humilis* from both the Lower and Upper Carboniferous, this distinctly pitted form with strong marginal overlap seems typical of the Coal Measures, while *C. fabulina* (sensu stricto) may be restricted to the Lower Carboniferous. This stratigraphical distinction has been proposed by Dr. F. W. Anderson (pers. comm.), and so the lectotype figure he has chosen is from the Coal Measures at Pirnie Colliery, Fife.

Cytherella foveolata Wright, described and figured by Wright (1930) is undoubtedly *C. humilis* in an inverted orientation (cf. text-fig. 6 with Wright 1930, pl. 1, fig. 2*a*, *b*). This conclusion is confirmed by Dr. Anderson's examination of Wright's specimens, and material from this horizon in the collections of the Geology Department of Manchester University, examined by me.

The form described and figured by Kremp and Grebe (1955, p. 151, pl. 16, fig. 1) is not considered synonymous with *C. humilis* as described here. However, the forms they describe and figure as *Whipplella cenisa* and *W. rhenana* are probably the male and female dimorphs of *C. humilis* respectively. The lateral outlines, overlap, hinge, and dimension ratios are all similar to those of the respective dimorphs described here. The American genus *Whipplella* Holland 1934 was erected for forms like *C. fabulina* (sensu lato) but with a stronger marginal overlap. The overlap can be so variable in this form that *Whipplella* and *Carbonita* are here considered to be synonymous, in agreement with Cooper (1946, p. 67).

Stratigraphical distribution. The species *C. humilis* is common throughout the Coal Measures, although its acme is probably in the *A. modiolaris* Zone at about the horizon of the Hopkins Band. It is the dominant species of *Carbonita* in the Bottom Three Quarter Seam ostracod band in the *C. communis* Zone of Durham (text-fig. 1), and is abundant in the Upper *A. similis–A. pulchra* Zone faunas from both Ryhope Colliery, Durham, and the 'Foveolata Zone' of Wright (1931) from the Manchester area. There are frequent references to the occurrence of this form in the *A. phillipsi* Zone faunas of the Ardwick Series of Manchester (Jones and Kirkby 1890) and the Newcastle Beds of North Staffordshire (Melville 1946).

Carbonita evelinae (Jones) 1870

Text-fig. 7

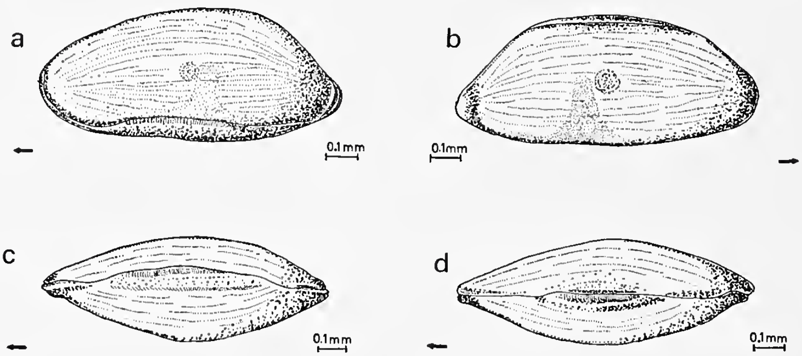
1870 *Carbonia evelinae* Jones, p. 218, pl. 9, fig. 4.
1870 *Carbonia agnes* var. *rugulosa* Jones, p. 218, pl. 9, fig. 8.
1870 *Carbonia agnes* var. *subrugulosa* Jones, p. 218, pl. 9, fig. 7.
1866 *Carbonia wardiana* Jones and Kirkby, p. 265, pl. 9, fig. 10*a*, *b*.
1943 *Hilboldtina evelinae* (Jones); Scott and Summerson, p. 870.
1957 *Hilboldtina evelinae* (Jones); Copeland, p. 28, pl. 1, figs. 5–7.

Lectotype. In 56370, specimen 9; chosen by Anderson (see Postscript).

Specimen described. IO 2985, Hopkins Band, above *Geisina* Phase, Bearpark Colliery, Co. Durham.

Dimensions. Length, 0·94 mm.; height, 0·42 mm.; width, 0·30 mm.; H/L ratio, 44·7 %.

Description. Carapace elongate, sub-ovate. Dorsal margin slightly arched; ventral margin straight to slightly convex. Anterior end obtuse, lower than posterior; posterior end more acutely pointed, high and with a steep postero–dorsal slope. Greatest height median; greatest width posterior of middle giving an elongate–ovate dorsal outline. Hinge straight, less than half the length, left valve raised along hinge line but no groove between the valves.



TEXT-FIG. 7. *Carbonita evelinae* (Jones). *a–d*, specimen IO 2985, complete carapace. *a*, exterior left valve; *b*, exterior right valve; *c*, ventral view; *d*, dorsal view.

Valves almost equal, right valve narrowly overreaches left on the free ends and overlaps it along ventral margin. Shell surface ornamented by fine longitudinal striae or ridges that converge towards the ends. These striae may be weakly developed or absent. Internally the shell has a circular muscle scar and ridge of thickening posterior to it. The muscle scar may contain a number of polygonal secondary scars.

Discussion. Dimorphism has not been detected in specimens of this species from the Hopkins Band.

The lectotype of *C. evelinae* in the British Museum (Natural History) is badly crushed, with strong longitudinal striae, a muscle spot, and pattern of cracks very close to those on Jones's original figure (Jones 1870, pl. 9, figs. 4*a*, *b*). Because of the crushed state of this specimen, I agree with Dr. F. W. Anderson (in press) that the shape distinction between *C. evelinae*, *C. agnes rugulosa*, and *C. agnes subrugulosa* drawn by Jones is not valid. All these three forms are probably one species, *C. evelinae*, similar in shape to *C. agnes* but differing in the surface ornament. Likewise, the species *C. wardiana* Jones and Kirkby, of which type material is in the Kirkby Collection in the British Museum (I 1695), is considered synonymous with *C. evelinae*. The Hopkins Band specimens described here are a little closer in lateral outline to *C. wardiana* than to *C. evelinae* (sensu stricto) but the variable nature of this character does not warrant specific distinction.

The genus *Hilboldtina* Scott and Summerson 1943 was erected for elongate forms of *Carbonita* with striated surface ornament from the Pennsylvanian of North America. This genus is here considered synonymous with *Carbonita*, since surface ornament is not a character of generic value, and the other characters mentioned in the original diagnosis of *Hilboldtina* are present in most species of *Carbonita* as described here.

Stratigraphical distribution. The lectotype of this species is from the Upper Coal Measures, *phillipsi* Zone, of the South Wales Coalfield. The form *C. wardiana* was first recorded from a similar horizon in North Staffordshire. The presence of this species in the Hopkins Band in the *modiolaris* Zone of Co. Durham is the first published record of its occurrence outside the Upper Coal Measures, although similar specimens may be seen in the Geological Survey collections from the Upper *A. modiolaris* Zone of the Cumberland Coalfield.

It seems probable that although this species is predominantly an Upper Coal Measure form, it occurs rarely throughout the Coal Measures. Similar elongate striated specimens of *Carbonita* are reported by Scott and Summerson (1943) from the Pennsylvanian of Tennessee and by Copeland (1957) from the Upper Carboniferous of Nova Scotia.

Carbonita inflata (Jones and Kirkby) 1879

Text-fig. 8

1879 *Carbonia fabulina* var. *inflata* Jones and Kirkby, p. 31, pl. 2, figs. 15–99.
1933 *Bythocypris tumidus* Upson, p. 24, pl. 2, fig. 11*a–c*.
1934 *Whipplella cuneiformis* Holland, p. 344, pl. 25, fig. 5*a–c*.
1935 *Carbonita*? *tumida* Kellett, p. 160, pl. 16, fig. 9*a–c*.
1946 *Carbonita inflata* (Jones and Kirkby); Cooper, p. 66, pl. 8, figs. 40–42.
1957 *Carbonita inflata* (Jones and Kirkby); Copeland, p. 26, pl. 1, figs. 12–14, pl. 2, figs. 18, 19.

Lectotype. I 1745; chosen by Anderson (see Postscript).

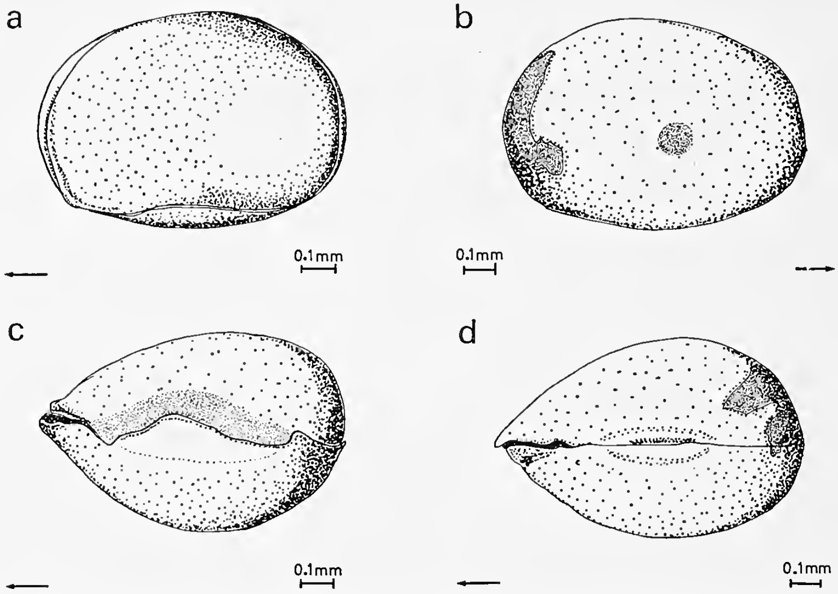
Specimen described. IO 2986, Hopkins Band, Hylton Colliery, Sunderland, Co. Durham.

Dimensions. Length, 0·97 mm.; height, 0·68 mm.; width, 0·63 mm.; ratio H/L, 70 %; width/height, 92·5 %.

Description. Carapace tumid, sub-ovate. Dorsal margin convex; ventral margin straight to slightly concave. Ends rounded, anterior more obtuse than the posterior, which is distinctly tumid. Greatest height and width posterior and dimensions almost equal (W/H ratio: $> 90\%$). Dorsal outline subcuneiform or broad sub-ovate.

Hinge short, in middle third of dorsal margin, depressed in a distinct but shallow groove. Left valve hardly raised above right along the hinge line. Valves unequal, right valve overlaps left around free margin. Overlap most pronounced on anterior margin and anterior end of ventral margin. Ventral overlap narrow and ventral margin is flattened along area of overlap. Externally the left valve possesses a low thickened ridge antero–ventrally. Shell coarsely pitted, and is generally thick with rimmed margins internally. Muscle scar circular antero–ventral of mid-point.

Discussion. This species is rare in the Hopkins Band and was only found at two localities, Hylton and Eppleton. No details of moults or dimorphism are known. The specimens described are very similar to the original description and figures of Jones and Kirkby, and to the lectotype in the British Museum (Natural History). The coarsely pitted thick shell, tumid carapace, with posterior width nearly equal to height, and short depressed hinge, are all sufficiently persistent characters to make the var. *inflata* of Jones and Kirkby a species in its own right.



TEXT-FIG. 8. *Carbonita inflata* (Jones and Kirkby). *a–d*, specimen IO 2986, complete carapace. *a*, exterior left valve; *b*, exterior right valve; *c*, ventral view; *d*, dorsal view.

Cooper (1946) examined the type material of the various species named by Upson, Holland, and Kellett, given in the synonymy, and considered them to be conspecific with *C. inflata* Jones and Kirkby. My redescription of this species and comparison with the descriptions and figures of the various authors, confirms this synonymy. Many of the characters by which these authors distinguished their species from *C. inflata* are in fact present on perfectly preserved specimens of the latter species but were not included in the original description. The synonymity of this form with *Whipplella cuneiformis* Holland, the type species of *Whipplella*, is an additional reason for the rejection of this genus as suggested in the discussion of *C. humilis*.

Stratigraphical distribution. The lectotype comes from the Coal Measures at Pirnie Colliery in Fifeshire, but the precise level within the Coal Measures is not recorded.

Forms similar to those described here from the *A. modiolaris* Zone are included in *C. fabulina* (sensu lato) recorded from the Upper *similis-pulchra* Zone of Durham, but they have not been found in the Three Quarter Seam Band in the *C. communis* Zone. *C. inflata* is also a common form in the *A. phillipsii* Zone faunas of North Staffordshire and the Manchester area. It seems probable that this species occurs sporadically throughout the Coal Measures.

Cooper (1946) recorded this species from the Pennsylvanian of Illinois, and the synonymous forms of other authors come from the Pennsylvanian of Nebraska, Kansas, Pennsylvania, and West Virginia. This species is also a common one in the Upper Carboniferous faunas of Nova Scotia described by Copeland (1957).

Carbonita pungens (Jones and Kirkby) 1879

1867 *Cythere pungens* Jones and Kirkby, p. 222.
1879 *Carbonia pungens* Jones and Kirkby, p. 37, pl. 3, figs. 21–23.
1884 *Cythere* (*Darwinella*) *pungens* (Jones and Kirkby); Jones, pp. 319, 325.
1911 *Carbonia pungens* (Jones and Kirkby); Pruvost, pp. 71–72, pl. 12, figs. 13, 14.
1932 *Carbonia pungens* (Jones and Kirkby); Latham, p. 386.
1946 *Darwinula pungens* (Jones and Kirkby); Cooper, p. 78, pl. 10, figs. 39, 40.
1957 *Carbonita pungens* (Jones and Kirkby); Copeland, p. 26.

Lectotype. I 1731, no. 6; chosen by Anderson (see Postscript).

Specimens described. IO 2987*a–c*, black shale below the *Geisina* Phase, Bearpark Colliery, Co. Durham.

Dimensions. In mm.

	Length	*Height*	*Width*	*H/L ratio*
IO 2897*a*	0·53	0·26	0·22	49·2 %
IO 2897*b*	0·44	0·19	0·18	43·2 %
IO 2897*c*	0·57	0·29	0·19	50·8 %

Description. Carapace small, sub-cylindrical in shape, ends equal. Dorsal margin straight or flatly convex, sloping from posterior to anterior; ventral margin straight. Anterior end low and pointed; posterior end high, rounded, and somewhat tumid. Greatest height and width posterior, the height being less than half the length (H/L < 50%). Dorsal and ventral outlines sub-cuneiform, thickness about equal to height.

Hinge line straight, low, longer than half the length. Left valve not raised along hinge line and no groove. Valves almost equal, the right slightly larger and overlapping the left narrowly along the ventral margin. Maximum overlap in posterior half of ventral margin. Shell not preserved on Durham specimens; thin and smooth on type specimens. Muscle spot antero-ventral of mid-point, arrangement of secondary scars uncertain.

Discussion. Although the specimens described here are too badly preserved to be figured, their general features are close to the original description and figures of Jones and Kirkby (1879). These specimens are smaller than those of Jones and Kirkby but comparable with the dimensions given for this species by Latham (1932).

The generic relationship of this species has been in doubt since its earliest description, as the synonymy suggests. In 1884 Jones doubtfully referred it to *Darwinella* (= *Darwinula*, *Darwinella* preoccupied). Brady and Robertson, and several later authors, followed suit. Cooper (1946), describing American specimens he considered synonymous, removed this species from *Carbonita* and placed it in *Darwinula* on account of its hinge structure and the character of the overlap of the valves. The left valve is not raised above the right along the hinge as in most species of *Carbonita*, but the variation of this character within the genus suggests that the simple hinge of *C. pungens* is more a matter of structural simplicity in this thin shelled form than a fundamental generic distinction. Cooper also suggested that in *C. pungens* the maximum overlap of the valves is around the ends, not along the ventral margin as is the normal situation in *Carbonita*. However, the lectotype specimen shows the normal *Carbonita* overlap, not that described by Cooper.

C. pungens is certainly darwinuloid in shape but the distinctive *Darwinula* pattern of muscle scar has not been recorded. It is considered, therefore, best to retain this species in the genus *Carbonita*.

The frequent occurrence of bedding planes in Coal Measures shale crowded with myriads of *C. pungens* is comparable to the mode of occurrence of *Darwinula* proper in Mesozoic, Tertiary, and Recent non-marine sediments (Jones 1885; Kaufmann 1900; Harper and Sutton 1935; and Swain 1955). Mandelstam (1956) also recorded a similar occurrence, with up to forty variants of *Darwinula*, from the Upper Permian rocks of the Kuznetsk Coalfield of Russia. In mode of occurrence, therefore, if not in structure, *C. pungens* is very like *Darwinula*.

Stratigraphical distribution. The lectotype of this species comes from one of Jones and Kirkby's original localities, the Coal Measures at Methil in Fifeshire, but the same authors also recorded this form from freshwater limestones in the Carboniferous Limestone Series of Scotland. In the English Coal Measures, Jones and Kirkby (1890) recorded its abundance in the Upper Coal Measures of the Manchester area. Edwards and Stubblefield (1947) found it in the Upper *similis–pulchra* Zone of Nottinghamshire and Derbyshire. The present study has shown the abundance of *C. pungens* in both the *A. modiolaris* and *C. communis* Zones of Durham (text-fig. 1). These records, though sparse, suggest that this species ranges throughout the Coal Measures in Britain and occurs locally in the Lower Carboniferous of the Central Valley of Scotland.

This species has also been recorded from the Coal Measures of France by Pruvost (1911), the Pennsylvanian of Illinois by Cooper (1946), and the Upper Carboniferous of Nova Scotia by Copeland (1957).

Carbonita claripunctata sp. nov.

Text-fig. 9

1879	*Carbonia rankiniana* Jones and Kirkby, p. 34 (in part), pl. 3, figs. 3, 8.
1897	*Carbonia rankiniana* (Jones and Kirkby); Dawson, p. 396, fig. 10.
1932	*Carbonia rankiniana* (Jones and Kirkby); Latham, p. 385 (in part).
1955	*Carbonita agnes* (Jones); Kremp and Grebe, p. 148, pl. 16, fig. 2.

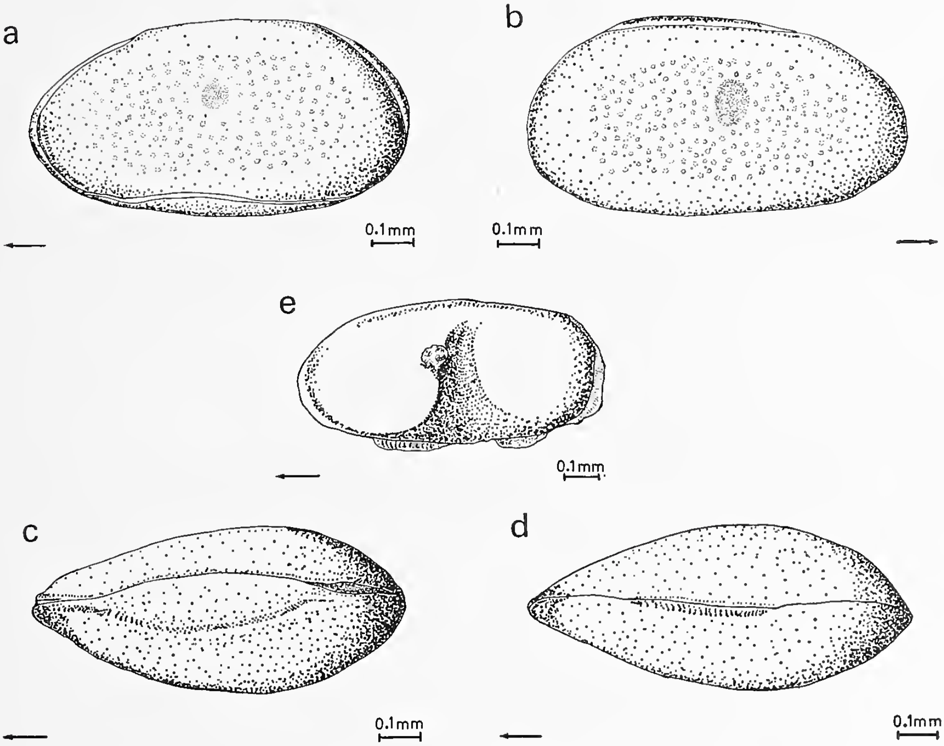
Derivation of name. *Clarus* (lat.)—distinct; *punctatus* (lat.)—pitted, punctate.

Holotype. Complete carapace, IO 2983. *Paratypes*. 4 complete carapaces, IO 2982 and IO 2984.

Occurrence. Holotype, IO 2983, *Geisina* Phase, Hopkins Band, Lower *A. modiolaris* Zone, Lower Coal Measures, Ryhope, Sunderland, Co. Durham. IO 2982, horizon as holotype, localities Washington and Follonsby, Co. Durham. IO 2984, shales above Flockton Thin Coal, Lower *A. modiolaris* Zone, Lower Coal Measures, Warncliffe Woodmoor Colliery, Doncaster, Yorkshire.

Dimensions. In mm.

	Length	*Height*	*Width*	*H/L ratio*
Holotype, IO 2983	1·04	0·55	0·43	52·8 %
IO 2982*a*	0·98	0·50	0·40	51·0 %
b	1·02	0·54	0·42	53·0 %
IO 2984*a*	1·07	0·57	0·47	53·2 %
b	1·06	0·55	0·46	52·7 %



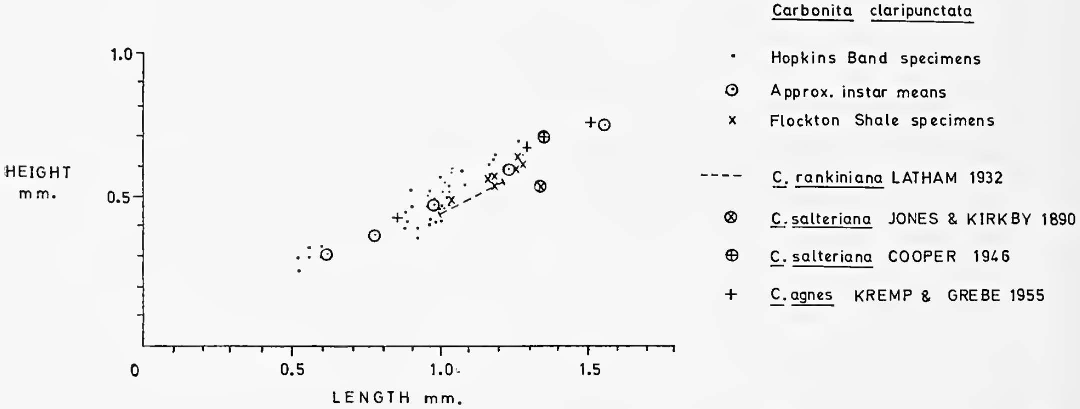
TEXT-FIG. 9. *Carbonita claripunctata* sp. nov. *a–d*, paratype, IO 2984*a*, complete carapace. *a*, exterior left valve; *b*, exterior right valve; *c*, ventral view; *d*, dorsal view; *e*, internal mould showing furrow and muscle scar cast, from the *Geisina* Phase of the Hopkins Band, Ryhope Colliery, County Durham.

Description. Carapace elongate, sub-ovate, slightly tumid posteriorly. Dorsal margin straight or slightly convex, sloping posterior to anterior; ventral margin gently convex. Posterior end high, broadly rounded; anterior end low, bluntly pointed, with a steep antero–dorsal slope. External anterior margin of left valve bears a low ridge of thickening inside the overlap of the right valve; a similar thickening is present on the postero-ventral margin of the left valve. Greatest height and width posterior, dorsal outline broadly sub-ovate.

Hinge line straight, or arched slightly in lateral view, about half the length of the dorsal margin and mainly posterior. Left valve raised very slightly above right along the hinge, and there is no groove. Right valve larger and overlaps the left narrowly on the ventral, anterior, and postero-dorsal margins. Shell surface coarsely pitted except over the muscle spot. These pits may tend to show a concentric pattern of arrangement. Muscle scar circular, antero-ventral of mid-point, with irregular secondary scars sometimes suggesting a rosette pattern. Internal ridge of shell thickening posterior to muscle scar well developed and leaving a characteristic furrow on internal moulds. A second fainter ridge is sometimes present anterior of the muscle scar.

Discussion. Dimorphism has not been detected in this species in the Hopkins Band, probably owing to the relatively small number of well-preserved specimens that were extracted.

In their original description of *Carbonia rankiniana*, Jones and Kirkby (1879) included both smooth and punctate forms from the Lower Carboniferous and Coal Measures of Scotland and the Coal Measures of England. The new species proposed here is similar in lateral outline to the form they figure as fig. 2 and, like the shell of fig. 8, is punctate. Their figured specimens came from the Coal Measures at Provenhall in Lanarkshire, and material from that locality in the John Young Collection at the Hunterian Museum, Glasgow, undoubtedly belongs to *C. claripunctata* sp. nov. The new species was included in Jones and Kirkby's original broad definition of *C. rankiniana*. It differs, however, from *C. rankiniana* (sensu stricto) in lateral outline, the greatest height being nearer the posterior end, and in having a punctate shell. *C. rankiniana*, as recently restricted by Anderson (in press), is a smooth shelled Lower Carboniferous species.



TEXT-FIG. 10. Height and length dimensions of *Carbonita claripunctata* sp. nov. and allied or synonymous species.

Carbonita claripunctata sp. nov. differs from the Upper Coal Measures species *C. salteriana*, and the synonymous *C. roederiana* in shape, punctate shell, the ventral thickening of the shell, and in the presence of a well-developed internal ridge posterior to the muscle scar.

The form described and figured by Kremp and Grebe (1955) as *C. agnes* Jones from the Coal Measures of the Ruhr is similar to this new species in lateral outline, overlap, hinge characters, surface ornament, and size dimensions (text-fig. 10). The type species, *C. agnes* Jones, although similar to *C. claripunctata* in size and surface ornament, differs in the arch of the dorsum and rounding of the ends. The German specimens should, therefore, more correctly be referred to *C. claripunctata* sp. nov. than to *C. agnes* Jones.

Stratigraphical distribution. Although the type material comes from the Lower *A. modiolaris* Zone of the Lower Coal Measures of Durham and Yorkshire, this species occurs in the Bottom Three Quarter ostracod band in the *C. communis* Zone of Durham. Scottish specimens are likewise from the Lower or Middle Coal Measures.

Kremp and Grebe (1955) recorded their synonymous form '*C. agnes*' as occurring sporadically throughout stages Westphalian A to Westphalian C in the Ruhr coalfield.

POSTSCRIPT

by F. W. Anderson

A complete revision of the genus *Carbonita* has been undertaken and is being prepared for publication. It was found necessary during the progress of this work to designate lectotypes for most of the species described by Jones (1870) and by Jones and Kirkby (1879).

In the foregoing paper Dr. Pollard has had occasion to refer to some of these species, and lectotypes are therefore here designated.

1. *Carbonita agnes* (Jones) 1870

Lectotype. In 43513, Adams Coll., Brit. Mus. (Nat. Hist.).

Horizon. Black Band Beds (*A. tenuis* Zone), Upper Coal Measures.

Locality. Cilfach Bargoed Colliery, Glamorgan, South Wales.

A holotype was not designated by Jones. The lectotype is from the type material and is the nearest to that figured by him (1870, pl. 9, fig. 6*a*).

2. *Carbonita evelinae* (Jones) 1870

Lectotype. In 56370, Adams Coll., Brit. Mus. (Nat. Hist).

Horizon. Black Band Beds (*A. tenuis* Zone), Upper Coal Measures.

Locality. Cilfach Bargoed Colliery, Glamorgan, South Wales.

Holotype not designated by Jones (1870), but the original of his fig. 4*a*, pl. 9, is easily recognized in the type material and is here chosen as the lectotype.

3. *Carbonita humilis* (Jones and Kirkby) 1879

Lectotype. The specimen figured by Jones and Kirkby, 1879, pl. 2, fig. 14.

Horizon. Earl David's Parrot Coal (*A. modiolaris* Zone), Coal Measures.

Locality. Pirnie Colliery, Leven, Fife, Scotland.

The species was originally figured by Jones and Kirkby as *Carbonia fabulina* var. *humilis*. Several specimens still exist in the type material in the Brit. Mus. (Nat. Hist.) Collection but none of these can be identified with any certainty as that figured by Jones and Kirkby.

4. *Carbonita inflata* (Jones and Kirkby) 1879

Lectotype. I 1745, Brit. Mus. (Nat. Hist.) Coll.

Horizon. A. modiolaris Zone, Coal Measures.

Locality. Pirnie Colliery, Leven, Fife, Scotland.

The lectotype is one of the specimens figured by Jones and Kirkby (1879, pl. 2, figs. 15–19) as *Carbonia fabulina* var. *inflata*, probably fig. 15.

5. *Carbonita pungens* (Jones and Kirkby) 1879

Lectotype. I 1731, T. R. Jones Coll., Brit. Mus. (Nat. Hist.).

Horizon. Coal Measures, probably Lower *A. similis–pulchra* Zone.

Locality. Methil, Fife, Scotland.

The lectotype is taken from the type material and is the nearest to that figured by Jones and Kirkby (1879) as pl. 3, fig. 21.

6. *Carbonita rankiniana* (Jones and Kirkby) 1879

Lectotype. I 1741, Brit. Mus. (Nat. Hist.) Coll.

Horizon. Calciferous Sandstone Series, Lower Carboniferous.

Locality. Coast west of Pittenweem, Fife, Scotland.

The lectotype is one of the specimens figured by Jones and Kirkby (1879, pl. 3, figs. 1, 6, 7) from Pittenweem. Those on the same plate, from the Coal Measures at Provenhall, Glasgow, i.e. figs. 2–5, 8, are thought to be specimens of *C. salteriana* (Jones).

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THE PALAEONTOLOGICAL ASSOCIATION

Extracts from the Annual Report of the Council for 1965–6

MEMBERSHIP. On 31 December 1965 there were 1,342 members (673 Ordinary, 114 Student, and 555 Institutional), a net increase of 73 members during the year.

FINANCE. Because of the continued growth of Ordinary and Institutional membership, income from subscriptions increased during the year by £232. Favourable interest rates helped to increase income from this source by £116, but the figure includes £22 relating to 1964. Donations from authors for specific papers and from oil companies have been very welcome and still form a substantial part of income. They show an increase of £188 over 1964. It is hoped this support will continue at the same generous level into 1966 when the Association has to meet further cost increases and new commitments.

The very large drop in income from sales (£542) is mainly attributed to the Association's agents selling stock valued at £930 which had been paid for in 1964; the income from sales in 1964 was therefore inflated at the expense of 1965.

The cost of publishing *Palaeontology* rose sharply, due to increasing the print off from 1,600 to 2,000 copies, to increasing the size by 56 pages (8 per cent) and 2 plates, and to an increase of charges by the printers.

When the surplus balance of £207, transferred to the Publications Reserve, is used to meet the remaining cost of Volume 8, the year's working will have almost exactly balanced.

'PALAEONTOLOGY'. The four parts of Volume 8 were published during 1965. They contained 44 papers and consisted of 767 pages and 111 plates.

MEETINGS. Four meetings took place during 1965–6. The Association is grateful to the Council of the Geological Society of London, Professor J. H. Taylor (King's College, London), and Professor F. H. T. Rhodes (University College, Swansea) for generously granting facilities for meetings, and to the Local Secretaries for their efficient services.

a. The *Eighth Annual General Meeting* was held in the Rooms of the Geological Society of London, Burlington House, London, W. 1 on Wednesday, 3 March 1965, at 5.00 p.m. The Annual Report of the Council for 1964–5 was adopted and the Council for 1965–6 was elected. Professor T. S. Westoll, F.R.S., delivered the *Eighth Annual Address* on 'Problems of the Arthrodiran Fishes'.

b. A *Field Demonstration Meeting* was held at Castleton, Derbyshire, on Saturday, 8 May 1965. The theme was 'Faunal facies variations within the Lower Carboniferous reefs of Derbyshire'. Dr. F. M. Broadhurst and Dr. I. M. Simpson acted as Leaders and Miss Joan I. Norcott was Local Secretary.

c. A *Discussion Meeting* on 'Accumulation of pelagic skeletal remains' was held at King's College, London on Wednesday, 27 October 1965 at 2.00 p.m. About eighty persons attended. Dr. J. E. Prentice was Local Secretary.

d. A *Joint Symposium Meeting* of the Geological Society and Palaeontological Association was held in the Department of Geology, University College, Swansea on Monday/Tuesday, 20/21 December 1965. The symposium meeting was focused on some aspects of the volume 'The Fossil Record' (to be published by the Geological Society). Papers were read and discussed at three half-day sessions and a Symposium Dinner was held in College House. Dr. V. G. Walmsley was Local Secretary.

SPECIAL GENERAL MEETING. Immediately before the Discussion Meeting at King's College, London, on Wednesday, 27 October 1965, a Special General Meeting was held at 1.45 p.m. to consider a change in Rule 2 of the Constitution. The following motion was proposed from the Chair and passed (*nem. con.*):

> That, effective from 1 January 1966, Rule 2 of the Constitution be amended to read as follows: 'There shall be Ordinary members, Institutional members, and Student members, and their annual subscriptions shall be Three Guineas, Seven Pounds, and Two Guineas respectively. Each subscriber shall be considered a member of the Association, but Institutional members shall not be eligible to take part in the Government of the Association.'

COUNCIL. The following were elected members of the Council of the Association for 1965–6 at the Annual General Meeting on 3 March 1965: *President*: Dr. L. R. Cox, F.R.S. *Vice-Presidents*: Dr. W. S. McKerrow, Professor F. H. T. Rhodes. *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, Professor P. M. Butler, Dr. W. J. Clarke, Dr. G. Y. Craig, Dr. T. D. Ford, Dr. B. M. Funnell, Dr. J. M. Hancock, Dr. G. A. L. Johnson, Dr. F. A. Middlemiss, Mr. M. Mitchell, Dr. W. D. I. Rolfe, Dr. A. J. Rowell, Professor Scott Simpson, Dr. L. B. Tarlo, Dr. H. Dighton Thomas.

BALANCE SHEET AND ACCOUNTS FOR THE YEAR ENDING 31 DECEMBER 1965

BALANCE SHEET

Liabilities	£	*s.*	*d.*	£	*s.*	*d.*
Publications Reserve Account Balance as per Annexed Account				6,290	2	3
Amounts received in Advance Subscriptions for 1966 . . .				401	0	6
Provision for Cost of Publication of *Palaeontology* Vol. 8 as per Income and Expenditure Account	7,147	19	8			
Less expenditure incurred to 1 December 1965 . . .	4,681	2	0	2,466	17	8
Sundry Creditors				11	4	4
Note: No amount has been included in these Accounts for Subscriptions unpaid at 31 December 1965				£9,169	4	9

Assets	£	*s.*	*d.*	£	*s.*	*d.*
Office equipment				20	15	0
Investments at cost:						
Equities Investment Fund for Charities—958 units	999	18	3			
5 per cent Defence Bonds	4,000	0	0	4,999	18	3
Sundry Debtors and Payments in Advance:						
Authors for offprints	173	9	10			
Palaeontology, Vol. 9	47	15	0	221	4	10
Cash at Bank—Deposit Account				2,807	8	7
Current Account				1,119	18	1
				£9,169	4	9

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 1965 and of its income and expenditure for the year ended on that date.

JOSHUA WORTLEY & CO.
Chartered Accountants.

Income and Expenditure Account
for the year ended 31 December 1965

Expenditure	£	*s.*	*d.*	£	*s.*	*d.*
To Provision for Cost of Publication of *Palaeontology*,						
Vol. 8, Part 1	1,827	13	10			
Part 2	1,820	5	10			
Part 3	1,750	0	0			
Part 4	1,750	0	0			
	7,147	19	8			
Add extra cost of Vol. 7, Part 4	9	17	1			
	7,157	16	9			
Less excess Provision for Vol. 7, Part 3 (not now required)	161	4	0	6,996	12	9
Administrative Expenses:						
Insurance	1	15	3			
Auditor's Fee	10	10	0			
Post and Stationery	162	9	1			
Assistance to Treasurer	100	0	0			
Duplicating and dispatching of circulars	109	1	4			
Cost of distributing publications	60	7	1			
Meetings, etc.	45	1	9	489	4	6
Depreciation of equipment				2	6	2
Excess of Income over Expenditure for the Year. Transferred to Publications Reserve Account				207	14	4
				£7,695	17	9

Income	£	*s.*	*d.*	£	*s.*	*d.*
By Subscriptions for 1965	5,052	3	11			
Subscriptions for 1964	103	2	7	5,155	6	6
Sales of Publications				1,243	0	10
Interest Received:						
5 per cent Defence Bonds	200	0	0			
Bank Deposit Account	120	16	9			
Equities Investment Fund for Charities	90	4	3	411	1	0
Specific Donations				96	10	0
General donations:						
Californian Oil Co.	157	10	0			
British Petroleum Co.	250	0	0			
Total Oil Co.	50	0	0			
Texaco	175	0	0			
Burmah Oil Co.	100	0	0	732	10	0
Miscellaneous Receipts				57	9	5
				£7,695	17	9

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THE PALAEONTOLOGICAL ASSOCIATION

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