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DEVONIAN CORALS AND BRACHIOPODS FROM THE BRENDON HILLS, WEST SOMERSET

by B. D. WEBBY

ABSTRACT. The coral and brachiopod faunas of the Middle–Upper Devonian Ilfracombe Beds in the Brendon Hills, west Somerset, have been examined. The corals are restricted to two limestone horizons in the Ilfracombe Beds, the Rodhuish Limestone and the Roadwater Limestone; the brachiopods are sparse and more uniformly distributed throughout the succession. The rugose corals, *Heteroplrentis percevali* sp. nov., *Thamniophyllum caespitosum* (Goldfuss), *Acanthophyllum (Neostriangophyllum) concavum* (Walther) and *Mesophyllum (Arcohyllum) sandtillense* sp. nov.; a tabulate coral, *Thamnopora polyforata* (Schlotheim); and two brachiopods, *Spinocyrtia ascendens* (Priestersbach) and *Thomasaria gibbosa* Vandercammen, are described. The coral and brachiopod faunas suggest that the bulk of the Ilfracombe Beds is Givetian; the Upper Hangman Grits and the lower part of the Ilfracombe Beds (the Avill Group) are Lower–Middle Givetian; the Cutcombe Slate and Rodhuish Limestone are Middle–Upper Givetian; and the Roadwater Limestone is Upper Givetian. The Givetian–Frasnian boundary probably lies within the Leighland Beds, towards the top of the Ilfracombe Beds. In the light of the present study, Wedekind's Middle Devonian rugose coral zonal scheme is seen to be in need of considerable modification.

THE Devonian corals and brachiopods of the Ilfracombe Beds of west Somerset have received comparatively little attention in the past, possibly owing to the poor state of preservation of the brachiopods, and to the recrystallization of the corals. Perceval (1866, p. 185) listed twelve coral species from a locality near Sandhill Farm, Withycombe, and also mentioned that spiriferids were common, while Etheridge (1867, p. 593) gave a comparable list for the same locality (= his Hill Farm locality) and, in addition, identified corals from Golsoncott (p. 594) and from limestone bands at Wheddon Cross and Luckwell (p. 586). Lang and Smith (1935), in their redescription of *Disphyllum aequiseptatum* (Milne-Edwards and Haime), figured material collected by Perceval from Sandhill Farm, and indicated that *Disphyllum* {*Phacellophyllum*} *trigemme* (Quenstedt) occurs abundantly in the Ilfracombe Beds (Upper Givetian–Lower Frasnian) at Withycombe. Another important fauna, including brachiopods, corals, trilobites, and lamelli-branches, was described by Whidborne (*in* Hicks 1897, p. 441) from the slates at Treborough. Hicks ascribed this slate sequence to the Morte Slates, a mistaken correlation, as already emphasized by Ussher (1908). It can be clearly demonstrated that the slates at Treborough occur stratigraphically immediately above and below the Roadwater Limestone, and therefore appertain to part of the Ilfracombe Beds succession rather than to the Morte Slates as Hicks suggested.

Owing to the recrystallization of the corals, only relic structural elements have been retained. As a result, the original structures are readily observable in thin-sections prepared thicker than usual, but further grinding and polishing results in the total loss of the structures. Cellulose peels were also used but failed to give consistent results. The most satisfactory methods for studying the west Somerset material were to use polished sections for those corals differentially stained by percolating solutions from the New Red Sandstone, and thick thin-sections or cellulose peels for the other material.

STRATIGRAPHICAL PALAEOLOGY

The detailed stratigraphical succession for the Brendon Hills is shown in text-fig. 1, and has been summarized by Webby (1962*b*). The lowest unit, the Upper Hangman Grits, has yielded only plant fragments, and lamellibranchs from near the top of the formation. The overlying Hangman–Ilfracombe contact is quite sharp, consisting of a change from the predominant quartzitic sandstones of the Upper Hangman Grits to the alternating slates and thinly bedded siltstones of the Mansley Beds (lowest formation of the Avill Group), a distinctive lithology which seems to be identical with that of the Wild Pear Beds near Combe Martin, north Devon. This lithological correlation is supported by the fact that on the north Devon coast the Wild Pear Beds are underlain

MORTE SLATES	Upper Morte Slates		FRASNIAN	
	Brendon Hill Beds			
	Sticklepath Slate			
ILFRACOMBE BEDS	Leighland Beds with the Leigh Barton Limestone		U.	
	Roadwater Limestone			
	Cutcombe Slate with the Rodhuish Limestone			
	Avill Group	Oaktrow Sandstone	M.	GIVETIAN
		Harwood Beds		
		Walland Sandstone	L.	
		Mansley Beds		
HANGMAN GRITS	Upper Hangman Grits		? — ?	
			COUVINIAN	

TEXT-FIG. 1. The Devonian stratigraphical divisions in the Brendon Hills.

by the Hangman Grits and overlain by the Lester Series (Evans 1922), the last being equivalent to the middle and upper parts of the Avill Group (Walland Sandstone, Harwood Beds, and Oaktrow Sandstone) in the Brendon Hills. However, there is an important difference in the respective sequences of north Devon and west Somerset, because near Combe Martin the upper part of the Hangman Grits contains beds with *Stringocephalus* cf. *burtini* (Defrance), while in west Somerset it appears to be absent. Possibly the lamellibranch horizon in the Upper Hangman Grits is at the equivalent stratigraphical horizon in the Brendon Hills.

No brachiopod faunas have been found in the Mansley Beds and the Walland Sandstone, but the succeeding formations, the Harwood Beds and the Oaktrow Sandstone,

have yielded brachiopods, lamellibranchs, gastropods, and Polyzoa, and the Oaktrow Sandstone has also yielded *Decadocrius oaktrovensis* Webby. The brachiopods from the Oaktrow Sandstone are: *Schuchertella* sp., *Cupularostrum?* sp., *Spinocyrtia ascendens* (Spriestersbach), '*Spirifer*' sp., *Thomasaria gibbosa* Vandercammen, *Athyris?* sp., *Cyrtina* sp., *Centrouella* sp., and *Cranaena* sp. The occurrence of *Spinocyrtia ascendens* in the Oaktrow Sandstone, and also the Harwood Beds, is of considerable interest, for this species seems to be a useful index-fossil of the Givetian in Germany. It is almost certainly identical with many, if not most, of the forms hitherto referred to *Spirifer mediotextus* Archiac and Verneuil both in Belgium and Germany. *S. mediotextus* is given as the index-fossil for the Gic Zone of the Belgian Givetian type-succession, on the south side of the Dinant Basin (Lecompte and Waterlot 1957, p. 241). *Thomasaria gibbosa* has an Upper Givetian to Frasnian range in Belgium (Webby 1962a, p. 538). By considering the overlapping time-ranges of *Spinocyrtia ascendens* and *T. gibbosa*, it might be suggested that the Oaktrow Sandstone was Upper Givetian. However, as will be seen below, the coral evidence from the stratigraphically higher limestones suggests that the limestones are Upper Givetian; hence it seems likely that the Oaktrow Sandstone, and probably also the Harwood Beds, are Middle Givetian.

The presence of two distinct coralliferous limestones has been established, the lower named the Rodhuish Limestone, and the upper the Roadwater Limestone. The Rodhuish Limestone is restricted to the area around Rodhuish, and passes laterally into the Cutcombe Slate. The Roadwater Limestone is more or less persistent from Sandhill Farm, Withycombe, southwards to Roadwater, and thence westwards to Wheddon Cross. The rugose and tabulate corals are restricted to these two limestone formations. The following corals have been collected from the Rodhuish Limestone: *Heliophyllum halli* Milne-Edwards and Haime, *Disphyllum aequiseptatum* (Milne-Edwards and Haime), *Thamnophyllum caespitosum* (Goldfuss), '*Cystiphyllum*' *secundum* (Goldfuss), *Thamnopora* aff. *crouigera* (d'Orbigny) and *T. reticulata* (de Blainville). It should be noted that Schlüter (1889) described the type-species *Mesophyllum defectum* from one of the Goldfuss syntypes of '*Cystiphyllum*' *vesiculosum*, and Stumm (1949) designated it as lectotype, thereby making it *Mesophyllum vesiculosum*. Dr. R. Birenheide has indicated (pers. comm.) that the specimen selected by Schlüter is a compound form figured by Goldfuss in plate 17, fig. 5e, and that certain of the other Goldfuss syntypes should be grouped with '*C.*' *secundum* (Goldfuss). The west Somerset specimens are accordingly assigned to '*C.*' *secundum*.

The Cutcombe Slate and Rodhuish Limestone have yielded only a few poorly preserved, indeterminate brachiopods. Only *Cyrtospirifer* sp. has been identified from the Rodhuish Limestone. At Treborough the brachiopods and corals described by Whidborne (*in* Hicks 1897) were collected from the slates below the limestone band (and, therefore, from the topmost beds of the Cutcombe Slate). A revision of their material has demonstrated that much less confident palaeontological assignments than those given by Whidborne are probable. The new assessment does not support a Lower Devonian age as Hicks formerly suggested (1897, p. 444).

An abundant and varied coral fauna has been obtained from the Roadwater Limestone, and a small, comparatively unimportant, brachiopod fauna. The faunal list is as follows: *Syringaxon* sp., *Heterophrentis percevali* sp. nov., *Heliophyllum halli* Milne-Edwards and Haime, *Disphyllum aequiseptatum* (Milne-Edwards and Haime),

Phillipsastrea sp., *Thamnophyllum caespitosum* (Goldfuss), *Endophyllum abditum* Milne-Edwards and Haime, *Acanthophyllum* (*Neostrophophyllum*) *concauum* (Walther), *Digonophyllum* (*Digonophyllum*) *bilaterale*? (Champernowne), *Mesophyllum* (*Arcophyllum*) *sandhillense* sp. nov., '*Cystiphyllum*' *secundum* (Goldfuss), *Thamnopora cervicornis* (de Blainville), *T. reticulata* (de Blainville), *T. polyforata* (Schlotheim), *Alveolites suborbicularis* Lamarck, *Thecostegites* sp., *Cyrtina heteroclita* (Defrance), *Schizophoria* sp., rhynchonellid and productid species. The commonest corals are *Thamnophyllum caespitosum* and *Thamnopora cervicornis*, while *Disphyllum aequiseptatum*, *Heliophyllum halli*, and '*Cystiphyllum*' *secundum* are also important. Other species are not abundant.

No determinable faunas have been recovered from the overlying Leighland Beds. In the Leigh Barton Limestone, near the top of the Leighland Beds, *Cyrtospirifer* sp. and other indeterminate brachiopods have been obtained, but nothing that assists in determining the age of the beds.

The Morte Slates contain few fossils, which are invariably poorly preserved or distorted. *Cyrtospirifer* sp. has been collected from the Sticklepath Slate, in the lower part of the Morte Slates, and Whidborne has identified a trilobite, brachiopods, and lamellibranchs in the Upper Morte Slates from Oakhampton Quarry, near Wiveliscombe, to the south of the Brendon Hills (Hicks 1897, p. 443).

Age of the Rodhuish and Roadwater Limestones. In the absence of more precise zonal fossils it has become necessary to rely mainly on the rugose and tabulate corals for determining the age of the Devonian limestones in the Brendon Hills. Perhaps the most certain determination of the age of the limestones is obtained from a study of the whole aspect of the coral fauna within the limestones. The Roadwater Limestone altogether includes 16 different coral species, of which 11 are rugose and 5 tabulate corals. A number of the rugose corals are typical Middle Devonian species, for instance *Heliophyllum halli* and '*Cystiphyllum*' *secundum*, while species of *Heterophrentis*, *Endophyllum*, *Digonophyllum* (*Digonophyllum*), and *Mesophyllum* (*Arcophyllum*) are restricted to the Middle Devonian elsewhere in Europe and North America. The presence of *Acanthophyllum* (*Neostrophophyllum*) *concauum* is interesting since it appears to be restricted to the Upper Givetian of the Bergisches Land, the uppermost Eifelian and Givetian in the Eifel (Birenheide 1961, p. 125) and the Upper Givetian in Moravia (Ketternová 1932, p. 45). The species of *Phillipsastrea* collected from the Roadwater Limestone is possibly *P. hennahi* (Lonsdale), the same form as is found in the limestones of the Ilfracombe Beds at Doddington, on the northern flank of the Quantock Hills. *Phillipsastrea* is regarded as a typical Frasnian form by Smith (1945, p. 37), whereas both Taylor (1951, p. 192) and Middleton (1959, p. 156) recorded it in the upper Middle Devonian of south Devon, and Middleton from as low as his upper Sp Zone of the middle Middle Devonian. Presumably, the occurrence of this genus indicates an horizon high in the Middle Devonian, for it is not a characteristic Middle Devonian form in Europe. The association of this typically Frasnian form with the predominant Middle Devonian rugose coral element in the Roadwater Limestone strongly suggests that the horizon is situated not far below the Givetian–Frasnian boundary, viz. in the Upper Givetian.

The tabulate corals of the Roadwater Limestone include three species of *Thamnopora*: *T. cervicornis*, *T. polyforata*, and *T. reticulata*. The time-ranges for numerous species of *Thamnopora* in the Middle and Upper Devonian of the Dinant Basin, given by Lecompte

(1939, p. 198), shows that *T. cervicornis* ranges through the whole of the Givetian in the Dinant succession, *T. polyforata* (= *dubia*) ranges from topmost Givetian (Gid) to Frasnian, and *T. reticulata* ranges from Couvinian (Co2) to Frasnian. On the basis of the overlapping time-ranges of *T. cervicornis* and *T. polyforata*, the Roadwater Limestone may be tentatively correlated with the Gid Zone, or the Upper Givetian. In addition, the occurrence of *Thecostegites* points to a position close to the Givetian-Frasnian boundary, because the type species *Thecostegites bouchardi* (Michelin), which it resembles, is recorded from the Frasnian at Ferques and in the Dinant Basin (Milne-Edwards and Haime 1851; Lecompte 1939).

The Rodhuish Limestone contains no typical Upper Devonian forms. *Thamnophyllum caespitosum* and *Thamnopora reticulata* may occur in the Frasnian, but they are just as common in the Givetian. All the other species, particularly *Heliophyllum halli* and '*Cystiphyllum*' *secundum*, are typically Middle Devonian forms. Although the Rodhuish Limestone does not contain *Thamnopora cervicornis*, it does yield a form closely similar to *T. cronigera*, which in the Dinant succession ranges through the Middle Givetian (Gib to Gic). From its relationship to the Oaktrow Sandstone below and the Roadwater Limestone above, and from its coral content, the Rodhuish Limestone may be regarded as Middle or Upper Givetian in age.

The total evidence adduced from the coral faunas of the Ilfracombe Beds in the Brendon Hills thus indicates that the Rodhuish Limestone is Middle-Upper Givetian, and the Roadwater Limestone is Upper Givetian. The Givetian-Frasnian boundary lies above the Roadwater Limestone but the precise position remains in doubt. Until a good fauna is obtained from the Leighland Beds, or its equivalent stratigraphical horizon in another area, nothing can be said with certainty on its precise position, which may lie within the Leighland Beds (text-fig. 1), or it might be a little higher, perhaps at the contact between the Ilfracombe Beds and the Morte Slates.

For convenience the Morte Slates may be considered to be Frasnian, though as yet no indubitable Frasnian fossils have been found.

Correlation of the Rodhuish and Roadwater Limestones, and the Wedekind Zonal Scheme. On the north Devon coast, Evans (1922) identified a number of different limestone bands within the Ilfracombe Beds, placing the Givetian-Frasnian boundary between the Red Limestone Series and the David's Hole Beds. He referred to well-preserved corals—identified by Stanley Smith as *Endophyllum* (*Spongophyllum*) *bowerbanki* Milne-Edwards and Haime, *Cyathophyllum caespitosum* and *Pachypora cervicornis*—in the Jenny Start Beds, which underlie the Red Limestone Series, and are, therefore, included in the Givetian. Holwill (1961) re-examined the coastal section and concluded that there are only three limestones, which are repeated by folding and faulting; the oldest, the Jenny Start Limestone, is correlated with the Givetian, followed by the Combe Martin Beach Limestone and the David's Stone Limestone, both of which are thought to be Lower Frasnian.

More recently, Holwill (1963) has indicated that the Combe Martin Beach Limestone contains the corals *Barrandeophyllum*, *Syringaxon*, *Metriophyllum*, *Alveolites*, and *Thamnopora*, while the overlying David's Stone Limestone includes *Syringaxon*, *Barrandeophyllum*, and *Thamnopora*. He considered the species of *Metriophyllum* to be close to *M. bouchardi* from the Frasnian of the Boulonnais. As yet *Barrandeophyllum* and

Metriophyllum have not been confirmed in the limestones of the Brendon Hills. If they characterize a limestone horizon higher than the Roadwater Limestone, then there must be important facies changes between north Devon and west Somerset.

Correlations with south Devon are even more uncertain. The only recent work on corals is by Taylor (1951) and Middleton (1959), who have adhered closely to Wedekind's zonal scheme as their basis for dating the Middle Devonian limestones. The scheme was established by Wedekind (1923, 1924, 1925, 1937) from his studies of rugose corals in the Eifel, and used subsequently outside Germany with modifications by Soshkina (1936) in Russia, and Taylor (1951) and Middleton (1959) in south Devon.

The recent work of Birenheide (1961) placing *Grypophyllum* as a subgenus of *Acanthophyllum* is indicative of the close relationship between the acanthophyllids and grypophyllids. Furthermore, *Ptenophyllum* (*Ptenophyllum*), *Ptenophyllum* (*Astrophyllum*) and *Ptenophyllum* (*Rhopalophyllum*), *Leptoinophyllum* and *Stenophyllum* (*partim.*) are considered as synonyms of *Acanthophyllum*, and *Neostriophyllum* as a subgenus, like *Grypophyllum*. According to the Wedekind zonal scheme, acanthophyllids (*sensu stricto*) are restricted to the lower Middle Devonian (*Digonophyllum* Zone to *Dohmophyllum* Zone inclusive); *Leptoinophyllum* is abundant in the *Leptoinophyllum* Zone and the grypophyllids are abundant in the *Stenophyllum* and *Sparganophyllum* Zones of the middle Middle Devonian; and *Neostriophyllum* occurs in the *Dialytophyllum* Zone of the upper Middle Devonian. All the cited forms are closely related and are now included in the one genus, *Acanthophyllum*. Thus, the acanthophyllids (*sensu lato*) extend from the base of the lower Middle Devonian to the upper Middle Devonian and, accordingly, are not useful zonal indicators, except in a more general sense than that intended by Wedekind.

The digonophyllids, according to the Wedekind scheme, are restricted to the lower part of the lower Middle Devonian, whereas Ketternová (1932) recorded three species of *Digonophyllum* (*Digonophyllum*) from the Givetian limestones of Čelechovice, in Moravia, and *Digonophyllum* (*Digonophyllum*) *bilaterale?* is present in the Upper Givetian Roadwater Limestone in the Brendon Hills. Middleton (1959, p. 140) suggested that digonophyllids may be found even as high as the upper Middle Devonian, and the west Somerset occurrence strongly endorses this view.

Another modification of the zonal scheme seems necessary, as the keriophyllids were regarded as restricted to the lower Middle Devonian. There is much difference of opinion on the interpretation of the genera *Heliophyllum* and *Keriophyllum*. Wedekind (1923) and Haller (1935) have not recognized *Heliophyllum* for their German forms; Stumm (1949, p. 21) regarded *Keriophyllum* as congeneric with *Heliophyllum*; Hill (*in* Moore 1956, p. F278) recognized both *Heliophyllum* and *Keriophyllum*, the chief difference between them being the yard-arm carinae of the former, and the zigzag carinae of the latter; and Middleton (1959, p. 155) regarded *Keriophyllum* as a subgenus of *Heliophyllum*. Birenheide (1962) has indicated that most of Wedekind's and Haller's species of *Keriophyllum* should be assigned to *Cyathophyllum* (*Cyathophyllum*) Goldfuss and *Cyathophyllum* (*Peripaedium*) Ehrenberg, and only '*K.*' *dahlemense* Haller should be assigned to the genus *Heliophyllum*. The validity of the *Keriophyllum* Zone thus becomes open to question, unless *Heliophyllum dahlemense*, which characterizes the Dahlemer *Keriophyllum* Zone, is excluded. The range of *Heliophyllum* in Europe appears

to be at least from the lower Middle Devonian (as indicated by *H. dahlmense* in the Eifel) to upper Middle Devonian (as suggested by *H. halli* in the Brendon Hills).

Wedekind (1925, 1934) indicated that lythophyllids are abundant in the middle Middle Devonian and absent from the upper Middle Devonian. An exception to this is seen in the presence of '*Cystiphyllum*' *secundum* (= *Lythophyllum septatum* Wedekind and *L. corneolum* Wedekind and Vollbrecht) in the upper Middle Devonian Rodhuish and Roadwater Limestones of west Somerset.

The Wedekind zonal scheme must be modified to accommodate all the exceptions before it can become an effective tool in European Middle Devonian stratigraphical studies, or else its use must be restricted to Germany. The zonal scheme could not be applied to rugose corals in limestones of the Brendon Hills. Instead, age determination of the limestones has been founded on complete faunal analysis of the rugose and tabulate corals.

SYSTEMATIC DESCRIPTIONS

Numbers of specimens catalogued in the Geology Department Collection, Bristol University, are prefixed BU; those from the British Museum (Natural History) by BM; and those from the Geological Survey Museum by GSM.

Phylum COELENTERATA

Order RUGOSA

Suborder STREPTELASMATINA Wedekind 1927

Superfamily ZAPHRENTICAE Milne-Edwards and Haime 1850

Family STREPTELASMATIDAE Nicholson, *in* Nicholson and Lydekker 1889

Genus HETEROPHRENTIS Billings 1875

Type species. H. spatiosa Billings 1875.

Diagnosis. Solitary, large, ceratoid to trochoid; cardinal fossula on convex side; septal stereozone narrow; major septa with very sparse axial lobes, slightly withdrawn from the axis; tabulae complete or incomplete, flat-topped to axially depressed domes, depressed at the fossula.

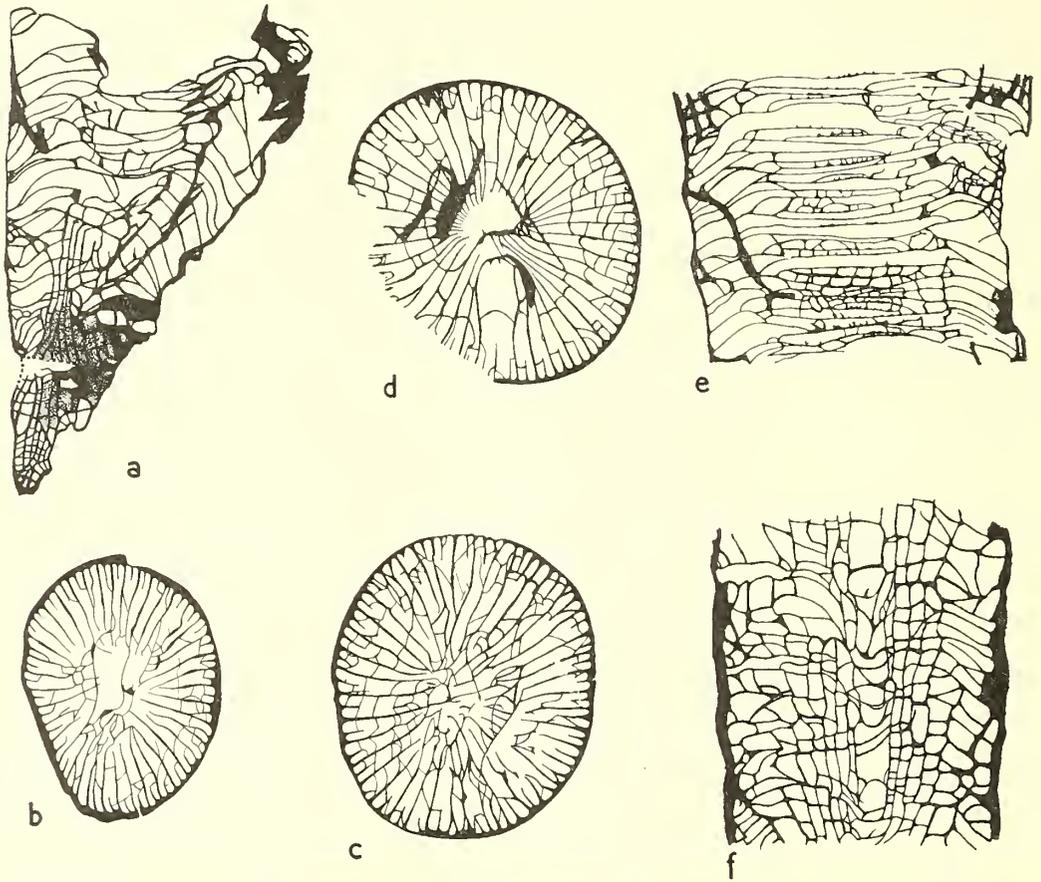
Heterophrentis percevali sp. nov.

Text-fig. 2a-f

Diagnosis. *Heterophrentis* with major septa extending two-thirds the distance to the axis, minor septa usually short and contratingent; 38-44 major septa in the epebic stage; cardinal fossula commonly indistinct.

Description. Simple trochoid to ceratoid coral, slightly curved, attaining a length of 14 cm., and a diameter of 35 mm. Calice moderately deep, more than 10 mm., with fairly steeply inclined sides. Wall less than 1 mm. thick. Major septa long and thin, apart from peripheral dilatation, extending to two-thirds the distance from periphery to axis, or slightly more, in the epebic stage; number—38 to 44 in sections of between 22 and 28 mm. average diameter. Minor septa short, about one-fifth the length of the major, and often contratingent. Cardinal fossula clearly observed in two specimens (paratypes

BU 18092 and 18224); in others it is indistinct. Tabulae make up a series of complete and incomplete floors, flat or gently sagging in the axial region, arched in the periaxial region, and sloping downwards towards the periphery. A longitudinal section at right angles to the cardinal fossula shows the tabulae bent downwards across it. No dissepiments.



TEXT-FIG. 2. *Heterophrentis percevali* sp. nov. *a*, Holotype, BU 18090, longitudinal section. *b*, *c*, Paratype, BU 18091, transverse sections at different levels, 17 mm. apart. *d*, Paratype, BU 18224, transverse section showing cardinal fossula. *e*, Paratype, BU 18224, longitudinal section. *f*, Paratype, BU 18092, longitudinal section in the periaxial region showing tabulae bent downwards across the cardinal fossula. All the figured specimens are from the Roadwater Limestone, *a-e* from Sandhill Farm and *f* from between Wheddon Cross and Luckwell Bridge. All enlargements $\times 1.5$.

Remarks. Champernowne (1884) described a number of Devonian corals from south Devon, several of which clearly belong to the Streptelasmataidae. He assigned two specimens to *Zaphrentis* sp., one of which (plate 23, fig. 1*a-b*; BM R23461) is similar to *Heterophrentis percevali*, but differs in having thicker major septa, while the other (plate 21, fig. 7), a specimen which cannot be traced, is smaller and has fewer major septa. Another specimen (GSM 75731) from Woolborough, south Devon, is also similar,

and may be conspecific. It has an average diameter of 30 mm., long major septa, numbering 44, and short minor septa, differing only in the possession of a thicker wall, slightly more than 1 mm. in thickness.

Le Maître (1934, p. 146) described *Streptelasma armoricanum* from the Lower-Middle Devonian strata of the Ancenis Basin, France, which may be a species of *Heterophrentis*. From her description and figures (plate 5, figs. 1, 2—the latter being orientated upside down), it is apparent that there are a number of similarities to the west Somerset specimens. The simple corals are of large dimensions, with a diameter of 17 to 30 mm., and carry a thick wall of stereozone from 1 to 5 mm. in thickness. The major septa are stated to number 44 to 50 in the sections studied, but only 37 major septa are visible in the specimen figured in transverse section. Dissepiments are stated to occur between major septa, although they are lacking in the figured longitudinal section. The traces giving the appearance of dissepiments in the transverse section are probably intercepted portions of the downward turned tabulae in the periaxial region. No well-defined fossula is apparent. The main differences between *Streptelasma armoricanum* and *H. percevali*, based on Le Maître's description, are the thicker wall, the greater number of major septa (44–50), and the presence of dissepiments in the former.

In comparison with North American species of *Heterophrentis*, *H. percevali* bears the closest resemblance to *H. ferronensis* Stumm (1962, p. 235, pl. 1, figs. 1–7; pl. 2, figs. 1–6). The main differences are that in most specimens of *H. percevali* the cardinal fossula is indistinct, there are fewer major and minor septa, the walls are uniformly thin and, at least in one specimen (BU 18224), the coral attains a much greater length. Greater differences are exhibited by other North American species, such as those described by Stewart (1938). The range of the North American forms is from Lower to Middle Devonian, being most common in horizons of the lower Middle Devonian.

Derivation of name. In honour of S. G. Perceval, for his thorough collecting and for his invaluable faunal list (1866, p. 185) from the coralliferous limestone at Sandhill Farm, Withycombe.

Holotype. BU 18090. *Paratypes.* BU 18091–2, 18224–5; BM R16184, R16211–12; GSM 86215.

Occurrence. Present in the Roadwater Limestone north of Rodhuish, and between Wheddon Cross and Luckwell Bridge, west Somerset. It may also occur in south Devon.

Family PHILLIPSASTRAEIDAE C. F. Roemer 1883

Genus THAMNOPHYLLUM Penecke 1894

Type species. *T. stachei* Penecke 1894.

Diagnosis. Dendroid or phaceloid, corallites united by dissepimental tissue at axils of branches; septa withdrawn from axis and dilated in dissepimentarium; dissepiments consisting of an outer row of flat plates and an inner row of horse-shoe plates, often replaced by stereoplasmic thickening; tabulae complete or incomplete, flat or slightly bowed.

Thamnophyllum caespitosum (Goldfuss)

Text-fig. 3a–d

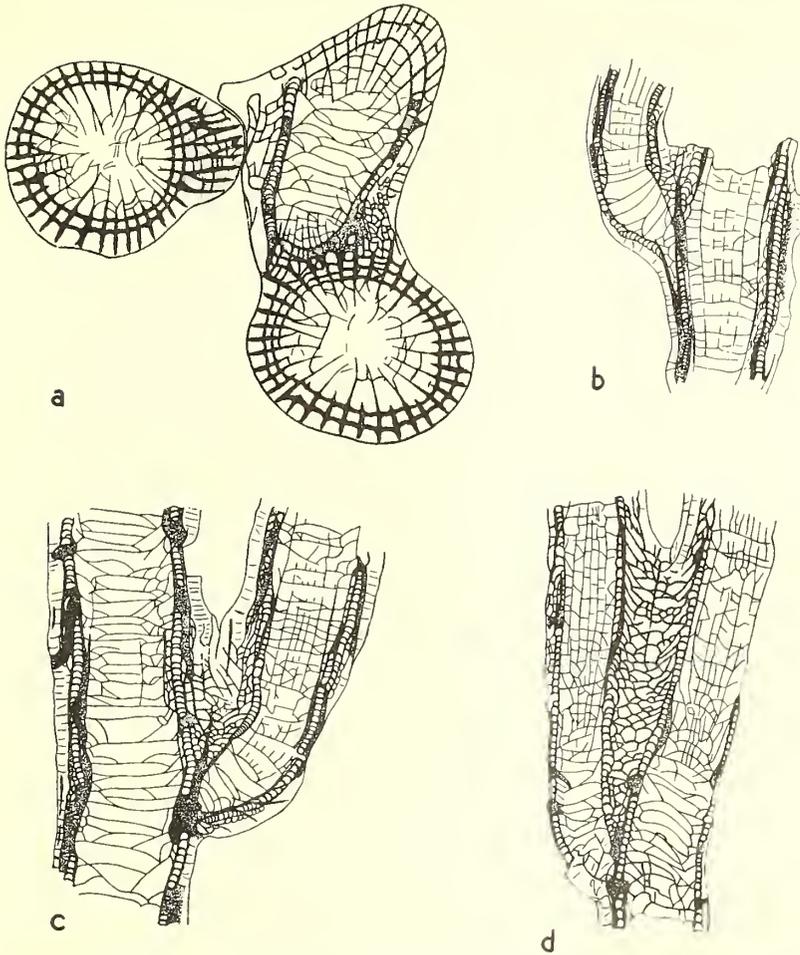
1826 *Lithodendron caespitosum* Goldfuss, p. 44, pl. 13, fig. 4.

1935 *Disphyllum* {*Phacellophyllum*} *caespitosum* Lang and Smith, p. 573, pl. 35, figs. 1, 2; text-figs. 28, 29.

- 1949 *Macgeea* (*Thamnophyllum*) *caespitosa* Schouppé, p. 138, pl. 9, fig. 3; pl. 11, figs. 40–43 (*cum syn.*).
 1949 *Phacellophyllum caespitosum* Stumm, p. 36, pl. 17, figs. 11–13.
 1951 *Disphyllum* {*Phacellophyllum*} *caespitosum* Taylor, p. 186, pl. 3, fig. 3a, b; non fig. 4a, b.
 1956 *Thamnophyllum caespitosum* Rózkowska, p. 308, text-figs. 30–32.
 1957 *Thamnophyllum caespitosum* Rózkowska, p. 89, text-fig. 8.
 1958 *Macgeea* (*Thamnophyllum*) *caespitosum* Schouppé, p. 227, text-figs. 7–9.
 1962 *Thamnophyllum cf. caespitosum* Assereto, p. 11.

Description. Corallum is large, compound, and typically phaceloid. Corallites cylindrical, frequently showing lateral branching, occasionally with two or three branches arising from one level. Diameter of corallites varies from 4 to 13 mm., the average being close to 6 mm. Occasionally the corallum is sub-dendroid, with corallite-diameters greater than the average for the species, and large sediment-filled spaces between the corallites. Lateral buds develop at right angles to the mother corallite, and show little tendency to curve upwards into a similar alignment to that of the mother corallite (text-fig. 3a). Dissepimental tissue between the mother and daughter corallites (plocoid structure of Lang and Smith 1935) is reduced or absent. Most commonly the corallum is phaceloid, with corallite-diameters about the average for the species, and narrow sediment-filled spaces between corallites. Lateral buds curve sharply almost into parallelism with the mother corallite, and at the point of division are united by dissepimental tissue (text-fig. 3b, c). Occasionally the corallites are more tightly packed, and there are only thin sediment-filled spaces between corallites. The corallite-diameters are about, or less than, the average for the species. Lateral buds curve even more sharply into line with the mother corallite, and they are united by dissepimental tissue for upwards of 25 mm. from the point of furcation (text-fig. 3d). The extreme of close packing is seen in a few cerioid to sub-cerioid forms (BU 10088, 18226; BM R16167). It is not yet clear whether these forms are linked throughout growth, or merely represent a level at which a large number of daughter corallites develop. In different specimens the number of major septa varies from 14 to 24, but is usually 18 to 19. Major septa usually extend inwards to 1 mm. from the axis, and they are attenuated within the tabularium. Minor septa are about half the length of the major. Both major and minor septa are dilated in the dissepimentarium, which includes an outer row of flat dissepiments, and an inner row of horseshoe dissepiments. Sometimes the inner and outer rows are not continuous along the length of the corallite, and appear to be replaced by stereoplasmic thickening. Tabularium occupies about half the diameter of the corallite. Two types of tabulae are present, inner flat or slightly domed tabulae, and outer smaller, axially inclined, arched tabulae on the margin of the tabularium.

Remarks. This species was formerly the type species of *Phacellophyllum*, but it has been assigned to *Thamnophyllum* by Schouppé (1949) and Rózkowska (1956, 1957). They studied the variability of the amount of stereoplasmic thickening in different species of *Thamnophyllum*, and considered that *T. caespitosum* fell within this range of variability. The main differences from the type species, *T. stachei* Penecke (Lang and Smith 1935, p. 581), are the longer major septa, the lesser stereoplasmic thickening, and the different mode of budding, characters which cannot be regarded as diagnostic of a different genus. Therefore, *Phacellophyllum* should be regarded as a synonym of *Thamnophyllum*.



TEXT-FIG. 3. *Thanmophyllum caespitosum* (Goldfuss). *a*, BU 18105, transverse section of two corallites, one with a lateral bud. *b*, BU 18108, longitudinal section of a corallite with a lateral bud. *c*, BU 18106, longitudinal section of a corallite with a lateral bud. *d*, BU 18107, longitudinal section of corallite with a lateral bud in a tightly packed corallum. All figured specimens are from the Roadwater Limestone at Sandhill Farm, except for *a*, which is from the Rodhuish Limestone at Higher Rodhuish Farm. All enlargements $\times 2.5$.

Occurrence. Widespread and common in the Middle and lower Upper Devonian of Europe. It is present in the Ilfracombe Beds of north Devon and west Somerset, and in south Devon. In the Brendon Hills it is common in both Rodhuish and Roadwater Limestones.

Suborder COLUMNARIINA Rominger 1876
 Family PTENOPHYLLIDAE Wedekind 1923
 Genus ACANTHOPHYLLUM Dybowski 1873

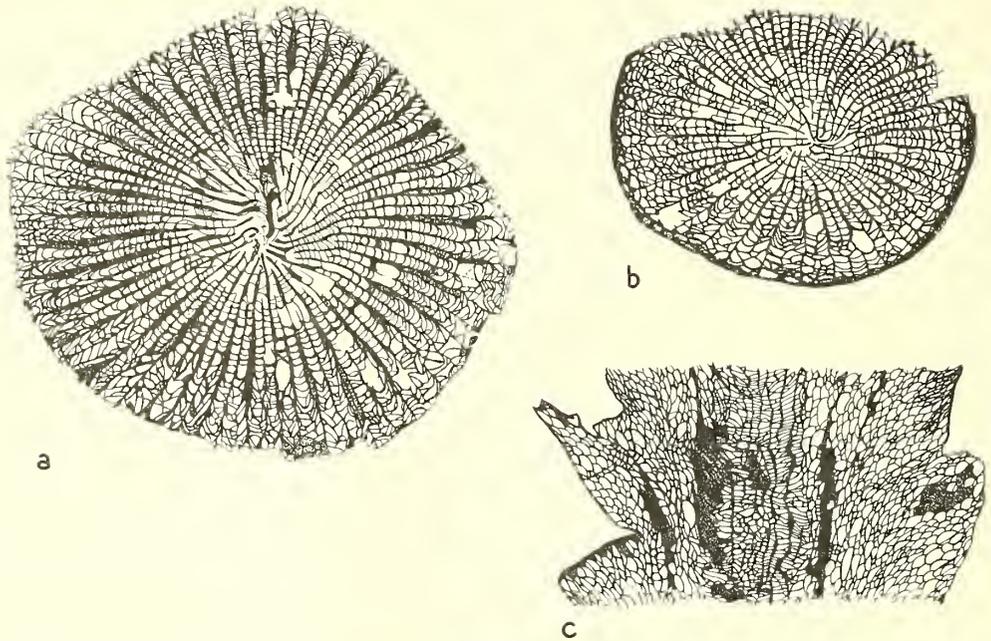
Type species. *Cyathophyllum heterophyllum* Milne-Edwards and Haime.

Diagnosis. See Birenheide (1961, p. 81).

Subgenus *NEOSTRINGOPHYLLUM* Wedekind 1922

Type species. Neostringophyllum ultinum Wedekind 1922.

Diagnosis. See Birenheide (1961, p. 124).



TEXT-FIG. 4. *Acanthophyllum (Neostringophyllum) concavum* (Walther). *a*, BM R16533, transverse section, Roadwater Limestone at Sandhill Farm. *b*, BU 18222, transverse section, limestones of the Ilfracombe Beds at Lower Aisholt, Quantock Hills. *c*, BU 18223, longitudinal section, locality as for *b*. All enlargements $\times 1.5$.

Acanthophyllum (Neostringophyllum) concavum (Walther)

Text-fig. 4a-c

- 1886 *Endophyllum acanthicum* Frech, p. 87, pl. 6, fig. 1 only.
 1922 *Cyathophyllum heterophyllum* Paeckelmann, p. 68.
 1925 *Neostringophyllum* sp. Wedekind, pl. 11, figs. 66-69; non pl. 16, figs. 93, 94.
 1928 *Neostringophyllum concavum* Walther, p. 114, text-fig. 8.
 1928 *Neostringophyllum simplex* Walther, p. 113, text-fig. 7.
 1928 *Neostringophyllum planum* Walther, p. 113, text-fig. 6.
 1932 *Sparganophyllum delicatum* Ketternová, p. 45, text-figs. 28, 29.
 1961 *Acanthophyllum (Neostringophyllum) concavum* Birenheide, p. 125, pl. 7, figs. 23, 24.

Description. Large solitary coral, subcylindrical. Epitheca thin. Greatest length observed is 9 cm., and the average diameter 35 mm., though one specimen (BM R16533) reaches a diameter of 45 mm. Between 68 and 74 septa, consisting of alternate major and minor. Major septa extend to the axis and have slightly twisted and swollen ends; they attenuate near the periphery, dilate across the inner part of the dissepimentarium, become slightly less dilated in the outer part of the tabularium, and then swell at their axial ends. Minor

septa are thinner and extend to about two-thirds of the length of the major. Tabularium occupies one-third of the diameter of the coral. In longitudinal section the dissepimentarium and tabularium are quite distinct. Herringbone and lateral dissepiments occur in the outer part of the dissepimentarium, but mostly the former type, while dissepiments of normal type occupy the inner part of the dissepimentarium. Dissepiments small, globose, inclined at a moderate angle to the periphery, though becoming steeply inclined towards the tabularium, and also slightly more elongated. Floor of tabularium gently concave with numerous closely spaced, flat, gently concave or gently convex tabellae; an average of about three tabellae to the millimetre.

Remarks. The specimens from Sandhill Farm, Withycombe, and Lower Aisholt, Quantock Hills, agree closely with the description of *Acanthophyllum* (*Neostrophophyllum*) *concauum* given by Birenheide (1961, p. 125). *Neostrophophyllum plamm* Walther (1928, p. 113) is also considered synonymous with *A. (N.) concauum*, only differing in a smaller diameter (20–22 mm.) from the west Somerset specimens.

Occurrence. *Acanthophyllum* (*Neostrophophyllum*) *concauum* has its type-locality in the Upper Givetian Schwelmer Kalk of the Bergisches Land, and it also occurs in the Junkerberg Schichten, Fleringer Schichten, and Dreimühlen Schichten of the Upper Eifelian and Lower Givetian in the Eifel (Birenheide 1961). It is also found in the Upper Givetian Čelechovice limestones of Moravia (Ketternová 1932, p. 45). In west Somerset four specimens have been collected from Sandhill Farm, Withycombe, from the Roadwater Limestone (BM R16533, R16196, R16218; GSM 75710), and two specimens from limestones at Lower Aisholt, Quantock Hills (BU 18222–3).

Suborder CYSTIPHYLLINA Nicholson, *in* Nicholson and Lydekker 1889
 Family DIGONOPHYLLIDAE Wedekind 1923
 Genus MESOPHYLLUM Schlüter 1889

Type species. *Cyathophyllum vesiculosum* Goldfuss 1826.

Diagnosis. See Hill (*in* Moore 1956, p. F318).

Subgenus ARCOPHYLLUM Markov 1926

Type species. *A. typus* Markov 1926.

Diagnosis. See Hill (*in* Moore 1956, p. F318).

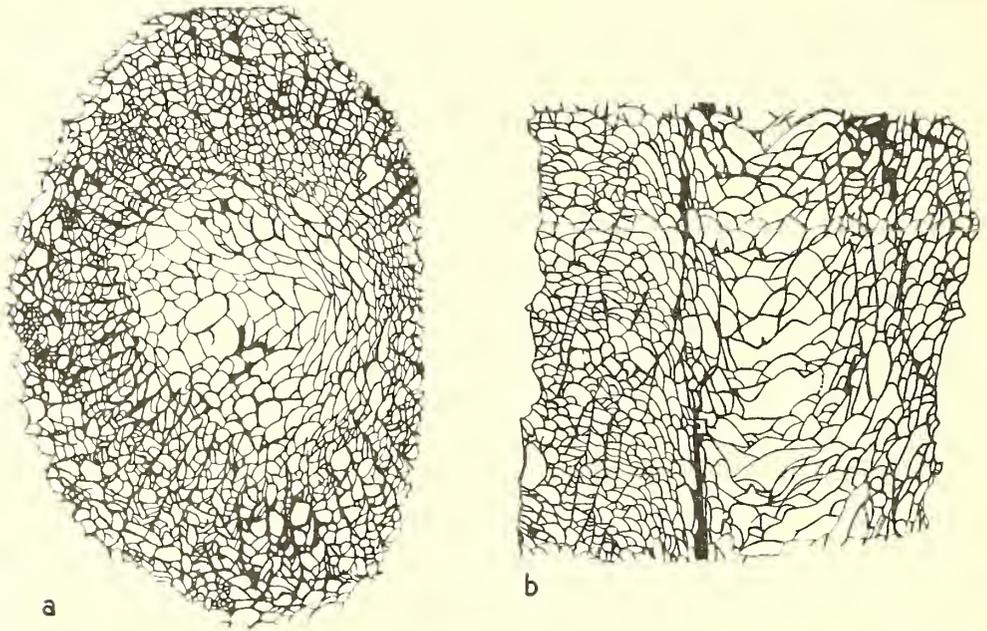
Mesophyllum (*Arcophyllum*) *sandhillense* sp. nov.

Text-fig. 5a, b

Diagnosis. Large *Mesophyllum* (*Arcophyllum*) with a bell-shaped calice; tabularium occupies one-third, or slightly more, of the diameter. Septa withdrawn from the axis and periphery, and mainly restricted to the inner part of the dissepimentarium; minor septa short or absent; approximately fifty major septa. Tabellae large. Carinae developed but not obvious in transverse section.

Description. Corallum is large, single, and subcylindrical; paratype 7 cm. long, and

expands in this length from 36 to 45 mm. Calice is bell-shaped, 15 to 18 mm. deep. Holotype is oval in transverse section, 45 mm. minimum diameter, 70 mm. maximum diameter (an average of 57 mm.). The outer surface is seen in a small part of the paratype where there are vague annulations. Major septa estimated at about fifty, variable in length; some extend almost across the dissepimentarium, others short and restricted to the middle or inner part of the dissepimentarium. Minor septa irregular in distribution; they may alternate between major septa or may be absent. There is a narrow peripheral zone of lonsdaleoid dissepiments. Tabularium occupies one-third, or slightly more, of



TEXT-FIG. 5. *Mesophyllum (Arcophyllum) sandhillense* sp. nov. *a*, Holotype, BM R16085, transverse section. *b*, Paratype, BM R16087, longitudinal section of the upper part of the corallum. The type specimens are from the Roadwater Limestone at Sandhill Farm. Both enlargements $\times 1.25$.

the diameter. In longitudinal section of the paratype, the dissepimentarium is seen to vary in width; in the lower part the tabularium is markedly asymmetrical, being situated to one side, and the dissepimentarium is broad on one side and virtually absent from the other; towards the middle of the corallum there is still a pronounced asymmetry, but a narrow band of dissepimental tissue has appeared opposite the broad zone; and in the upper part this dissepimental band broadens until it is approximately the same width on both sides of the tabularium (text-fig. 5*b*). The tabularium remains about the same width throughout the length of the corallum, 15 to 18 mm. diameter. Dissepiments, as seen in longitudinal section, are variable in size, somewhat globose, steeply inclined near the inner margin, gradually flattening out towards the periphery. Carinae prominent, steeply inclined to the periphery, more or less straight, sometimes bifurcating. Tabellae large, mostly gently convex, forming a series of concave floors.

Remarks. The type species of *Arcophyllum*, *A. typus* Markov, from the Middle Devonian of the Urals, resembles *Mesophyllum* (*Arcophyllum*) *sandhillense*, differing mainly in being much smaller, in having a narrower tabularium and fewer septa (Markov 1926, p. 54, pl. 3, figs. 3, 5, 7; Soshkina 1949, p. 60, pl. 16, fig. 2; pls. 18–21; pl. 23, fig. 3). *A. septatum* Bulvanker is also similar, but differs in having longer major septa, extending from the middle of the dissepimentarium to well within the tabularium (Bulvanker 1958, p. 63, pl. 25, fig. 2; pl. 26, fig. 1; pl. 27, fig. 1), and *A. markovi* Bulvanker differs in having a broad, flaring form and a funnel-shaped calice (Jakovlev 1947, p. 54, pl. 5, fig. 2). The German species *A. dachsbergi* (Vollbrecht) differs in having a much greater development of peripheral carinae, more complete septa, and smaller tabellae (Wedekind and Vollbrecht 1931, pl. 41, figs. 1, 4; pl. 42, figs. 1–6; pl. 44, fig. 9a), and *Hemicosmophyllum limbatum* Wedekind and Vollbrecht is similar, but the septa are fewer, the major septa are slightly longer, extending closer towards the axis, and the minor septa are absent or represented by a few septal crests (Wedekind and Vollbrecht 1931, pl. 45, figs. 6–12; 1932, pl. 12, figs. 1–8). The differences between *Arcophyllum* and *Hemicosmophyllum* are slight, and the only distinction is the somewhat greater continuity of minor septa in *Arcophyllum*. Hill (*in* Moore 1956) regarded *Hemicosmophyllum* as a subgenus of *Mesophyllum*, but it is desirable to regard it as a synonym of *Arcophyllum*, as there does not appear to be any fundamental difference between the two forms.

Holotype. BM R16085–6. *Paratype.* BM R16087.

Occurrence. Two specimens from the Roadwater Limestone at Sandhill Farm, Withycombe.

Order TABULATA
Family FAVOSITIDAE Dana 1846
Subfamily PACHYPORINAE Gerth 1921
Genus THAMNOPORA Steininger 1831

Type species. *T. madreporacea* Steininger 1831.

Diagnosis. See Lecompte (1939, p. 102).

Thamnopora polyforata (Schlotheim)

Text-fig. 6a, b

1820 *Milleporites polyforatus* Schlotheim, p. 365, *partim*.

1829 *Calamopora polymorpha* var. *gracilis*, *ramis gracilibus*, *elougatis* Goldfuss, p. 79, pl. 27, fig. 5.

1936 *Favosites dubius* Lecompte, p. 54, pl. 10, fig. 1 (*cum syn.*).

1939 *Thamnopora dubia* Lecompte, p. 120, pl. 18, figs. 7–12.

1945 *Thamnopora polyforata* Smith, p. 63, pl. 28, figs. 1, 2 (*cum syn.*).

? 1952 *Thamnopora polyforata* Smith, p. 301.

1953 *Thamnopora dubia* Kropfisch and Schouppé, p. 95, pl. figs. 2, 3 (*cum syn.*).

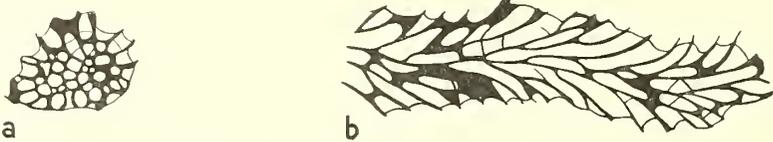
? 1954 *Thamnopora* cf. *polyforata* Hill, p. 31, pl. 1, figs. 7–9.

Description. Small ramous corallum with branches 5 to 7 mm. diameter. Corallites usually subcircular in transverse section, expanding markedly and curving outwards

from the axis to reach the surface obliquely. The walls only slightly thickened towards the axis, but distally the thickening increases considerably. Calices are alveolitoïd with projecting lip, usually 1 to 1.5 mm. diameter. Tabulae few and irregularly spaced. Mural pores indistinct in the specimens studied. Septal spines not seen.

Remarks. The specimens differ from Lecompte's diagnosis of the species (1939, p. 121) in only one respect, viz. in the absence of septal spines. They may be absent owing to the recrystallization and destruction of the elements, or they may not have developed in the specimens examined. Septal spines have not been recognized in the species by Smith (1945, p. 64), who noted that *T. polyforata*, while resembling species of *Striatopora*, is distinguished from these by the absence of septal spines.

Kropfitch and Schouppé (1953, p. 95) excluded *Thamnopora dubia* (de Blainville) from *T. polyforata* (Schlotheim) as described by Smith (1945), because of differences in the fibrous structure of the corallite walls, and the branch diameters. Smith stated that



TEXT-FIG. 6. *Thamnopora polyforata* (Schlotheim). *a*, BU 18115, transverse section. *b*, BU 18114 longitudinal section. Both figured specimens from the Roadwater Limestone at Sandhill Farm. Both enlargements $\times 2.5$.

under 'magnification the walls show fibrous structure, and fibres running at right angles to the wall, and also, although much less distinctly, a laminar structure parallel to the walls' (p. 64). Because of this laminar structure parallel to the walls, Kropfitch and Schouppé (1953, p. 96) considered that Smith's *T. polyforata* should be included in the genus or subgenus *Pachypora* Lindstrom. This proposal is unsatisfactory for, while the type species of *Pachypora* has laminae parallel to the walls, it has no prominent fibrous structure at right angles to the wall as described in *T. polyforata* by Smith (see Lecompte 1936, p. 27, pls. 4, 5, for excellent figures of the type-species *P. lamellicornis* Lindstrom). Furthermore, Smith indicated that 'Schlotheim's type . . . which consists of a single branch is in a somewhat better state of preservation than Goldfuss's, which comprises several branches'. Differences in the state of preservation may, indeed, account for the presence of the faint laminar structure parallel to the wall in Schlotheim's material and the absence of the same structure in Goldfuss's specimen. Lecompte (1936, p. 57), in his study of the Goldfuss material, indicated a branch diameter not exceeding 6 mm., and later (1939, p. 121), in his diagnosis of *T. dubia*, 'Polypier branchu à rameaux délicats de 6 à 8 mm. de diamètre'. Kropfitch and Schouppé have preferred the earlier interpretation of Lecompte, considering that the branch diameter is 6 mm., whereas Smith has indicated that the branches are typically about 7.5 mm. in diameter, in agreement with Lecompte's later viewpoint. Smith's inclusion of '*Favosites dubia* Edwards and Haime 1851' in his synonymy of *T. polyforata*, a species which was made a synonym of *T. boloniensis* by Lecompte (1939), is rightly questioned by Kropfitch and Schouppé. Altogether there seems to be too little evidence assembled by Kropfitch and Schouppé for separating *T. polyforata* and *T. dubia*, and they should be regarded as synonyms.

Occurrence. *T. polyforata* has been recorded from many localities in Europe, chiefly in Belgium and Germany, and a closely comparable form is reported from Australia. The species occurs in the Upper Givetian and Frasnian of the Dinant Basin (Lecompte 1939), in the Middle Devonian of Germany and Austria (Kropfitch and Schouppé 1953), and the Givetian or Frasnian of Western Australia (Hill 1954).

Phylum BRACHIOPODA (ARTICULATA)
Superfamily SPIRIFERACEA Waagen 1883
Family SPIRIFERIDAE King 1846
Subfamily SPIRIFERINAE Schuchert 1913
Genus SPINOCYRTIA Fredericks 1916

Type species. *Delthyris granulosa* Conrad 1839.

Diagnosis. See Cooper (*in* Shimer and Shrock 1944, p. 323).

Spinocyrtia ascendens (Spriestersbach)

Plate 1, figs. 1-7

- non* 1842 *Spirifer mediotextus* Archiac and Verneuil, p. 370, pl. 35, figs. 9, 9a-c.
- 1871 *Spirifer mediotextus* var. Kayser, p. 573, pl. 11, fig. 1.
- 1900 *Spirifer mediotextus* Scupin, p. 21, pl. 2, figs. 4-6.
- 1935 *Spirifer ascendens* Spriestersbach, p. 498, pl. 45, figs. 1, 2.
- 1942 *Spirifer (Spinocyrtia) ascendens* Paeckelmann, p. 16, text-fig. 14; pl. 1, fig. 4.
- ? 1950 *Hysterolites mediotextus* Termier and Termier, p. 77, pl. 107, figs. 21-23; pl. 108, fig. 4; pl. 109, figs. 1, 2.
- 1959 *Spinocyrtia ascendens* Vandercammen, p. 29.

Description. Shell medium to large, unequally biconvex, spiriferoid, apsacline; cardinal extremities rounded; hinge-line straight, greatest width a little anterior to the hinge-line. Surface of shell lateral to fold and sinus with 13 to 18 costae (observations from 10 specimens); each costa high and rounded in the umbonal region, gradually becoming low, gently convex, and wider towards the anterior margin; furrows between costae rounded, deep and narrow in the umbonal region, becoming gently concave and wider near the anterior margin. Growth-lines of two types; prominent widely spaced, and numerous fine, closely spaced types, which are crossed by fine radiating microfila; tear-granules appear to be situated at the intersections of microfila and growth-lines.

Pedicle valve convex. Sinus broad, shallow, subangular; median depression marked near beak. Lateral slopes curved. Beak prominent and incurved. Area high, slightly concave, with fine transverse and longitudinal striations. Delthyrium open, a little higher than wide. Internal features unknown, except for the long divergent dental plates.

Brachial valve less convex than pedicle. Fold prominent, broad, low, not greatly elevated above level of the costae; faint median groove towards the beak. Lateral slopes gently convex. Umbonal region elevated only slightly above hinge-line. Beak inconspicuous. Area narrow; notothyrium wide; cardinal process low; dental sockets widely divergent, groove-like, as seen in one specimen.

Dimensions. Measurements were made from 19 reasonably complete specimens, 11 of the brachial valve, 8 of the pedicle valve. The following are the average measurements in mm. (the number of measurements made is given in brackets with each average value):

Length around margin of pedicle valve	29.0 (5)
Height of brachial valve	21.8 (10)
Height of area in pedicle valve	12.5 (7)
Thickness of pedicle valve	11.0 (3)
Thickness of brachial valve	5.9 (10)
Maximum width	31.7 (13)
Hinge width	29.5 (16)
Angle of sinus	30° (3)
Angle of fold	26° (9)

Remarks. A comprehensive description of the type species *Spinocyrtia granulosa* (Conrad) and related species from North America by Ehlers and Wright (1955) allows a much closer comparison between American and European forms than was hitherto possible. One of the diagnostic features of the genus is the presence of tiny tear-shaped granules, which many of the European forms ascribed to this genus seem to lack, or they have not been observed. Perhaps the poor state of preservation in many of the European forms explains the frequent absence of the micro-ornament. Latex impressions of an external mould of *Spinocyrtia ascendens* from west Somerset produced indubitable tear-shaped granules.

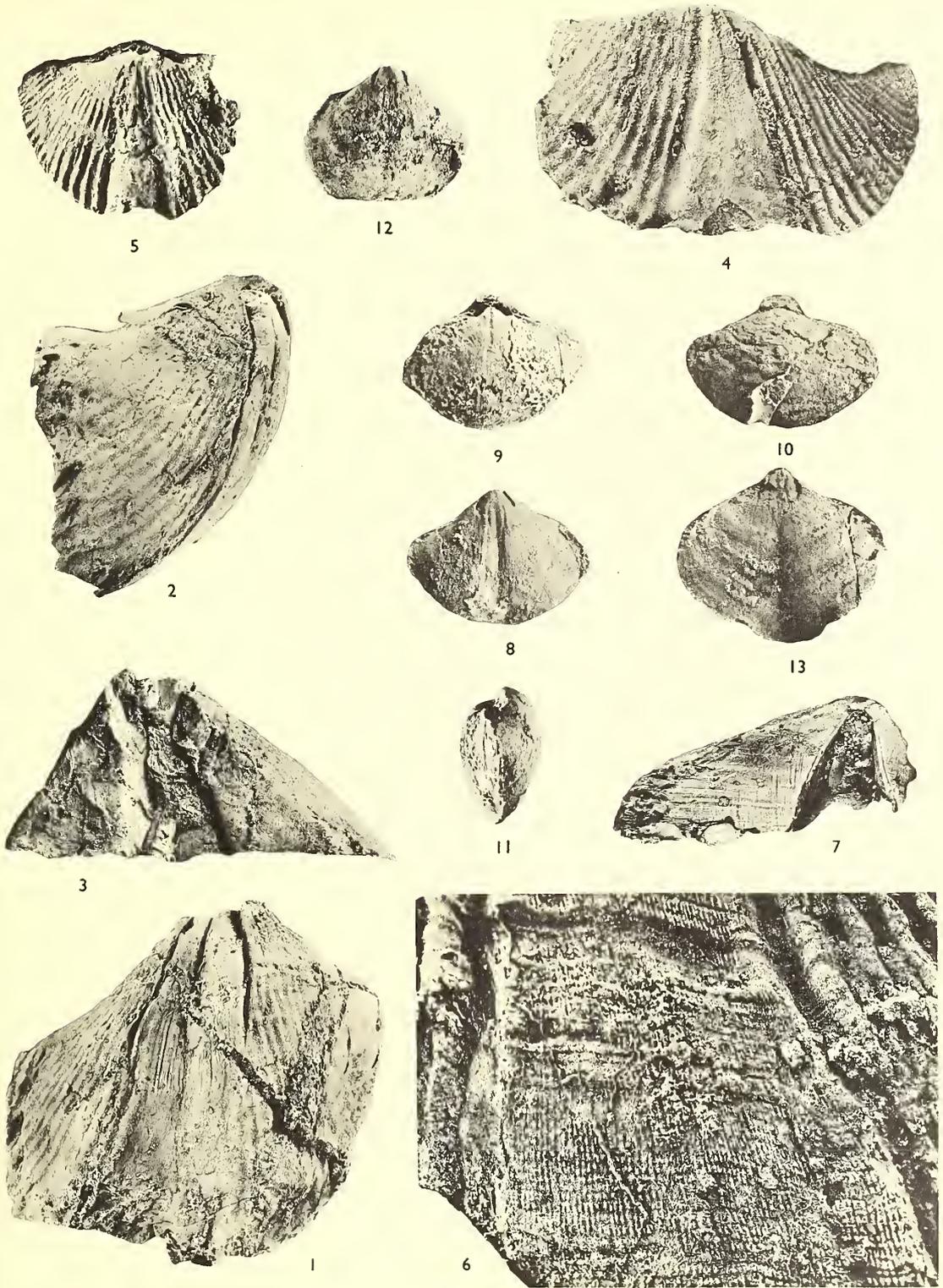
In a redescription of *Spinocyrtia mediotexta* (Archiac and Verneuil), Vandercammen (1959) considered the differences between the related forms, *S. subcuspidata* (Schnur) from the Upper Emsian, *S. geesensis* (R. and E. Richter) from the Couvinian, *S. ascendens* (Spriestersbach), *S. ascendens* var. *plicatula* Paeckelmann, and *S. mediotexta* from the Givetian. According to Vandercammen, the differences between these forms are slight: *S. mediotexta* can be distinguished in having a slightly concave fold, and 21 to 29 costae per flank, although the specimens of *mediotexta* from Gerolstein have only 15 to 18 per flank; *S. ascendens* can be separated from its variety *plicatula*, which has a marked

EXPLANATION OF PLATE I

All figured specimens are from the Oaktrow Sandstone at Oaktrow quarries (National Grid Ref. SS939402).

Figs. 1-7. *Spinocyrtia ascendens* (Spriestersbach). 1, BU 18126, $\times 1.5$, ventral view of internal mould of pedicle valve showing sinus, costae on the lateral slopes, and long divergent dental plates. 2, BU 18126, $\times 1.5$, lateral view of internal mould of pedicle valve showing strong convexity of valve, and the high, slightly concave area. 3, BU 18126, $\times 1.5$, posterior view showing internal mould of area in the pedicle valve. 4, BU 18128, $\times 1.5$, internal mould of brachial valve exhibiting fold and costae on the lateral slopes. 5, BU 18130, $\times 1.5$, internal mould of the brachial valve of a small specimen. 6, BU 18127, $\times 7$, detail of latex impression of external mould of the brachial valve showing a portion of the fold with micro-ornament of tear-granules which appear at the intersection between fine radiating microfila and growth-lines. 7, BU 18129, $\times 2$, latex impression of external mould of the area of pedicle valve showing fine transverse and longitudinal striations.

Figs. 8-13. *Thomasaria gibbosa* Vandercammen. 8, BU 18132, $\times 3$, ventral view of internal mould of pedicle valve showing weakly developed sinus and short divergent dental plates. 9, BU 18132, $\times 3$, dorsal view of internal mould of brachial valve. 10, BU 18132, $\times 3$, latex impression of external mould of brachial valve showing faint concentric growth-lines. 11, BU 18132, $\times 3$, lateral view of internal mould of both valves. 12, BU 18134, $\times 3$, ventral view of internal mould of pedicle valve. 13, BU 18133, $\times 3$, ventral view of internal mould of pedicle valve of a large specimen showing projecting tongue-like anterior margin.



WEBBY, Devonian brachiopods

median depression from the beak to the anterior margin on the fold; and only small differences separate *S. subcuspidata*, *S. geesensis*, and *S. ascendens*—12 to 14 costae per flank in *S. subcuspidata*, ± 13 in *S. geesensis*, and 13 to 18 in *S. ascendens*.

Occurrence. This species is present in the Givetian of both the Eifel and the Bergisches Land, Germany. In west Somerset it is fairly common in the Harwood Beds and the Oaktrow Sandstone of the Avill Group. Some of the Belgian specimens formerly identified as *Spirifer mediotextus* probably belong to this species. A similar form is reported from Morocco.

Subfamily AMBOCOELIINAE George 1931
Genus THOMASARIA Stainbrook 1945

Type species. *T. altmbona* Stainbrook 1945.

Diagnosis. See Vandercammen (1956, p. 19).

Thomasaria gibbosa Vandercammen

Plate 1, figs. 8–13

1956 *Thomasaria gibbosa* Vandercammen, p. 19, text-figs. 12–19; pl. 1, figs. 28–44.

Description. Shell small, unequally biconvex, subcircular to pentagonal in outline; cardinal extremities rounded; wider than long, with the greatest width anterior to the hinge-line; area small, elevated and curved; catacline. Some specimens exhibit a weak fold and sinus towards the anterior margin; anterior commissure uniplicate. Fine concentric growth-lines present at widely spaced intervals.

Pedicle valve strongly convex; sinus weak, commencing as a shallow depression away from the beak, and widening to the anterior margin where it projects slightly as a rounded, tongue-like projection. Area small, concave, twice as wide as high. As the specimens are moulds, details of internal structures are lacking, except for the divergent dental plates.

Brachial valve less convex than pedicle valve. No fold observed. Umbonal region slightly elevated; internal mould of beak short, pointed, and slightly incurved; a shallow, narrow median groove extends across the incurved beak region. Two small, slit-like teeth sockets seen in one specimen.

Dimensions. Measurements in mm.

	BU 18132	BU 18133	BU 18135	BU 18136	BU 18134
Length around margin of pedicle valve	7.5	11.1	5.2	5.0	8.1
Height of brachial valve	6.3	—	4.5	4.0	—
Height of area in pedicle valve	1.0	1.8	—	1.0	1.5
Thickness of pedicle valve	2.8	3.6	2.3	1.6	2.7
Thickness of brachial valve	1.4	—	1.2	0.5	—
Maximum width	9.6	11.0	6.1	5.4	8.0
Hinge width	5.9	8.0	3.1	2.9	4.1

Remarks. The Oaktrow specimens are moulds, and while they do not show all the features given in the type description (Vandercammen 1956), they do exhibit all the diagnostic characters. Vandercammen noted that *Thomasaria gibbosa* differs from *T. parallela* Vandercammen in having strongly divergent dental plates.

Occurrence. In Belgium, *T. gibbosa* occurs as a rare species in a number of localities, ranging in age from Upper Givetian throughout the Frasnian. In the Brendon Hills, it is moderately abundant in the Oaktrow Sandstone.

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TAXONOMIC CRITERIA IN THE CLASSIFICATION
OF THE PENNSYLVANIAN PRODUCTOID
JURESANIA NEBRASCENSIS

by J. A. FAGERSTROM and JOHN D. BOELLSTORFF

ABSTRACT. Biometrical and qualitative analysis of the form of the cardinal process in a sample of 123 brachial valves of *Juresania nebrascensis* (Owen) indicates that this feature is more variable than the size and shape of the valve proper. This relatively greater variability suggests that the form of the cardinal process has only limited value as a taxonomic criterion in the classification of this species.

MOST biometrical studies involving the Brachiopoda have concentrated on the relations between the various overall valve dimensions, especially length, width, and thickness, and have generally ignored for one reason or another the dimensions of the internal features of the valves. Recent discovery of a faunal assemblage containing numerous well-preserved brachial valves of *Juresania nebrascensis* (Owen) presented the opportunity to make both biometrical and qualitative evaluations of the relative significance of external and internal features in the classification of this species. Such a study is especially pertinent in view of the emphasis that has been placed on the form of the cardinal process in productoid taxonomy.

The sample was collected in June and July 1962 from a layer one foot thick of interbedded yellowish-brown shale and light gray, crystalline limestone in the upper portion of the Bonner Springs shale (the uppermost unit of the Kansas City group), outcropping in an abandoned quarry near the centre of the SE $\frac{1}{4}$, SE $\frac{1}{4}$, Sec. 7, Eight Mile Grove Twp., Cass Co., Neb., about 1 $\frac{1}{2}$ miles south-west of the village of Cedar Creek. At this locality the Bonner Springs shale is abundantly fossiliferous, containing trilobites, ostracods, and bryozoa as well as several species of brachiopods. Most of the larger specimens of *J. nebrascensis* had weathered free of the matrix, and so were randomly collected from the surface of the outcrop which extends for about 500 feet along the quarry face. The smaller specimens were picked from bulk samples, which had been boiled to free the valves from the matrix.

Juresania nebrascensis is one of the most common brachiopod species in the Pennsylvanian system of the northern mid-continent region and is well known to most palaeontologists and stratigraphers familiar with these rocks. The species has been adequately described and illustrated (Dunbar and Condra, 1932, pp. 195-8, pl. 22; Muir-Wood and Cooper, 1960, pls. 79, 80) so neither a formal systematic description nor illustrations of complete specimens are necessary for the purposes of the present paper.

It is a pleasure to acknowledge the help of Roger Pabian who discovered the faunal assemblage and called it to the attention of the senior author. A grant from the National Science Foundation defrayed the field expenses, and allowed the authors to devote their full attention to the study during the summer of 1962.

BIOMETRICAL DATA

The sample consists of 123 brachial valves, in various states of completeness, numbered 3300–3422 in the invertebrate palaeontological collection of the University of Nebraska State Museum (UNSM). On all unbroken specimens five dimensions were measured: length (Lbv) and width (Wbv) of the valve, length of the hinge-line (Lhl), length of the cardinal process (Lcp) measured from the hinge-line to the posterior extremity, and width of the cardinal process (Wcp) measured at the widest spread of the myophore lobes. As many of these dimensions as possible were measured on incomplete specimens; all specimens have at least three measurements. Attempts to measure the length and width of the adductor muscle scars proved to be futile since the outline was so indistinct that objective measurements were not possible; therefore, biometrical study of this internal feature was not undertaken.

Table 1 lists the number of specimens on which each dimension could be measured (N), the sample range (OR), sample mean (\bar{X}), sample standard deviation (s), and the coefficient of variation (V) for each dimension. Since the values for the sample range indicate that the sample is very heterogeneous with respect to biologic age, biometrical assessment of variability based on univariate analysis is not appropriate (Imbrie, 1956, p. 238). Therefore, bivariate analysis of variability was undertaken; the simplest measures of bivariate variability are the correlation coefficient (r) and the coefficient of relative dispersion about the reduced major axis (D_d ; Imbrie, 1956, pp. 239–41). Both these measures have been computed for every pair of dimensions and are listed in Table 2 in order of increasing values of D_d .

TABLE 1. Statistics based on dimensions of brachial valves

	N	OR (mm.)	\bar{X} (mm.)	s (mm.)	V
Wbv	87	7.6–30.0	22.1	5.3	23.98
Lbv	68	6.9–20.4	15.3	2.9	18.95
Lhl	109	6.2–22.8	15.8	3.8	24.05
Lcp	118	0.4–3.4	2.1	0.5	23.80
Wcp	120	0.7–3.4	1.8	0.5	27.77

VARIABILITY

For the purposes of the present paper the term ‘variability’ refers to the relative spread of the points on a scatter diagram about a line such as the reduced major axis, Bartlett’s ‘best fit’ line (Simpson, Roe, and Lewontin, 1960, pp. 232–7), &c. The sample correlation coefficient (r) and the coefficient of relative dispersion about the reduced major axis (D_d) give good measures of this relative spread if the conditional variances are homogeneous.

In addition to their inappropriateness in heterogeneous samples, as noted above, univariate measures of variability are limited by the fact that they merely express variation in linear dimensions rather than variation in shape. Thus the value of D_d (Table 2) for Lcp–Wcp expresses relative variation in the shape of the cardinal process and the values of D_d for Wbv–Lbv, Wbv–Lhl, and Lbv–Lhl express the relative variation in the

shape of the valve proper. The values of D_d for the paired dimensions involving one dimension of the cardinal process and one dimension of the valve proper, i.e. Lcp-Wbv, Wcp-Lhl, &c., express relative variation in the size of the cardinal process in relation to the size of the valve.

TABLE 2. Total correlation coefficients (r) and coefficients of relative dispersion about the reduced major axis (D_d) for (n) paired dimensions of brachial valves

	n	r	D_d
Wbv-Lbv	67	0.96	6.36
Wbv-Lhl	77	0.92	9.59
Lbv-Lhl	59	0.88	10.68
Lcp-Lbv	65	0.80	12.14
Lcp-Wbv	82	0.79	15.59
Wcp-Lbv	66	0.64	16.29
Lcp-Lhl	104	0.74	17.36
Wcp-Wbv	84	0.65	20.09
Wcp-Lhl	106	0.64	20.44
Lcp-Wcp	117	0.66	20.94

On the basis of the values of D_d (Table 2), the following generalizations concerning variability in the brachial valve of *J. nebrascensis* can be made:

1. The shape of the cardinal process is far more variable than the shape of the brachial valve proper.

2. During growth the size of the cardinal process is only moderately related to the size of the valve proper. In general Lcp is more closely related to the dimensions of the valve than Wcp.

3. Wbv is the one dimension most closely related to all aspects of shell development; Wcp is the least closely related. Wbv-Lbv is the least variable pair of dimensions and should therefore be used in the biometrical discrimination of samples of *J. nebrascensis* from other geographic localities and stratigraphic horizons.

It is important to realize that these generalizations have limitations; they are based on only one sample and apply only to *J. nebrascensis*. To apply them to other productoid species would be an unwarranted extension beyond their intended meaning.

In addition to size and shape, there are two more attributes of the form of the cardinal process that deserve analysis; these are the number of lobes in the myophore and the nature of the shaft. As will be shown below, neither of these attributes is amenable to biometrical analysis, since both undergo progressive change in form during ontogeny. Therefore, this aspect of variability must be approached on a purely qualitative basis.

The shaft may be thought of as consisting fundamentally of two primary lobes extending posteriorly from the hinge-line, approximately in the plane of the valve. The posterior half of each primary lobe bears a groove of variable depth on the dorsal and ventral surfaces, except in very small specimens where the groove is absent on the ventral surface. Typically these grooves join posteriorly to form a prominent narrow incision on the end of the myophore giving it a quadrilobed appearance. In quadrilobed specimens the inner lobe of each primary lobe of the shaft is here termed the inner secondary lobe; the outer lobe is the outer secondary lobe. Such quadrilobate cardinal

processes, with the primary lobes of the shaft separated throughout their entire length, are characteristic of the smaller specimens and comprise about 25 per cent. of the sample.

The most common form of the cardinal process is a variation of the quadrilobed type, which involves an inward twisting of the secondary lobes, especially the inner secondary lobes. This inward twisting generally results in partial or complete fusion of the inner secondary lobes to form a trilobate cardinal process. With only partial fusion the two primary lobes of the shaft remain separate anteriorly, whereas in complete fusion the shaft is one piece, generally with a prominent groove on the ventral surface. With both complete and incomplete fusion the central lobe is usually wider and longer than the lateral lobes and bears a median incision of variable depth on the posterior face. Such trilobate processes, with the inner secondary lobes of the shaft either partially or completely fused, are characteristic of the larger specimens and comprise about 75 per cent. of the sample.

This suggested ontogenetic development from an immature quadrilobate stage to an adult trilobate stage is quite imperfect. The sample contains numerous large quadrilobate specimens as well as several small trilobate specimens. However, the fact that there is a gradational transition from generally small quadrilobate forms to partially fused intermediate trilobate forms and finally to completely fused large trilobate forms supports this suggested ontogeny (Pl. 2, figs. 1-13). During the biometrical portion of this study, an attempt was made to segregate the sample into quadrilobate and trilobate sub-samples to see if this would strengthen the correlations between the dimensions of the cardinal process and the external valve dimensions. This segregation proved to be impossible, since there were so many gradational specimens that could not be objectively placed in either of these groups.

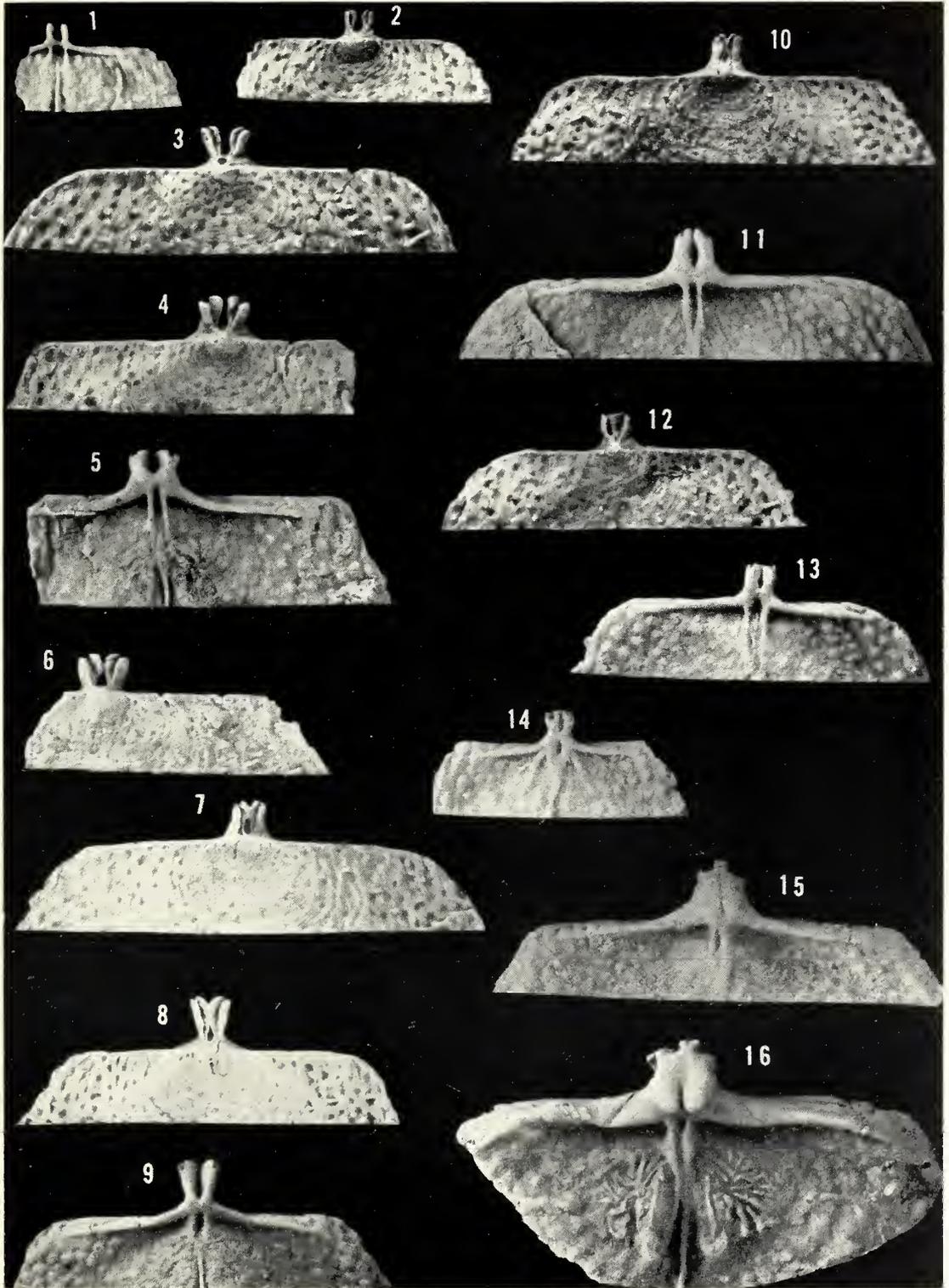
It is perhaps significant to note that there is no evidence that the cardinal process in *J. nebrascensis* conforms to the ontogenetic changes described by Kozłowski (1914, pp. 12-13) and Sarycheva (1949, p. 59). The trilobed form does not arise from a hollow cup or tube.

To explain the cause of variability in fossil animals is largely speculative. None the less it seems quite likely that there must be some relation between the rather spacious umbonal cavity of the pedicle valve in *J. nebrascensis* and the variability of the com-

EXPLANATION OF PLATE 2

All figures $\times 3$.

Figs. 1-16. *Juresania nebrascensis* (Owen). 1, UNSM 3304, ventral view showing double-shafted cardinal process. 2, UNSM 3303, dorsal view showing double-shafted quadrilobate cardinal process. 3, UNSM 3309, dorsal view of large quadrilobate cardinal process with divergent shafts. 4, 5, UNSM 3330, dorsal and ventral views showing incipient inward twisting of secondary lobes of cardinal process. 6, UNSM 3302, dorsal view showing initial fusion of inner secondary lobes of quadrilobate cardinal process. 7, UNSM 3336, dorsal view showing incomplete fusion of trilobate cardinal process. 8, 9, UNSM 3326, dorsal and ventral views of partially fused trilobate cardinal process. 10, UNSM 3331, dorsal view showing nearly complete fusion of trilobate cardinal process. 11, UNSM 3327, ventral view showing nearly complete fusion of trilobate cardinal process. 12, 13, UNSM 3360, dorsal and ventral views of completely fused trilobate cardinal process. 14, UNSM 3390, ventral view showing additional cardinal process buttress plates. 15, UNSM 3396, ventral view of thickened trilobate cardinal process and inconspicuous alveolus. 16, UNSM 3423, ventral view of thickened trilobate cardinal process and deeply incised adductor muscle scars.



FAGERSTROM and BOELLSTORFF, *Juresania nebrascensis*

paratively small cardinal process, which only partially fills the cavity when the valves are closed. The size and shape of the cardinal process was apparently not restricted in any way during growth by the size and shape of the umbonal cavity, thereby allowing such great diversity.

In addition to variability resulting from unrestricted growth, there must have been considerable inherent genetic variability in the form of the cardinal process. The sample contains specimens where the cardinal process is not in the centre of the hinge-line, quadrilobate specimens where one shaft is considerably larger than the other, and trilobate specimens where the lobes of the myophore are distinctly asymmetrical. One specimen has an extra pair of buttress plates at the base of the cardinal process (Pl. 2, fig. 14).

TAXONOMIC SIGNIFICANCE OF CARDINAL PROCESS

For many years, brachiopod taxonomists have recognized the importance of the so-called 'stable' internal features in the erection and discrimination of superspecific categories. This has been recently emphasized with regard to the cardinal process in the Productoidea (Muir-Wood and Cooper, 1960, pp. 26-27). The remainder of the present paper consists primarily of an evaluation of the cardinal process as a 'stable' feature in the classification of *J. nebrascensis* proposed by these authors (pp. 255, 266-7).

To properly evaluate the classification of Muir-Wood and Cooper, it is necessary to review briefly the taxonomic history of *J. nebrascensis* and another very similar species, *J. symmetrica* (McChesney). Both these species were originally described over a century ago, and were placed in the genus *Juresania* by Dunbar and Condra (1932). In the classification of the family Productidae used by these authors prime consideration was given to features of ornamentation.

Then in 1954, Stehli subdivided the Productidae and established, among others, the family Echinoconchidae which included the genus *Juresania* (1954, p. 326). Again, prime evidence was placed on ornamental features.

Finally, Muir-Wood and Cooper (1960, pp. 67-69) redefined Stehli's Echinoconchidae, and distributed the genera he included in two new families, the Overtoniidae and the Buxtoniidae, as well as the revised Echinoconchidae. In addition, Muir-Wood and Cooper redefined the genus *Juresania* (pp. 266-7), and created a new genus *Pulcratia* (pp. 249-50) to include some of the species formerly placed in *Juresania*. One result of this revision was to place *J. nebrascensis* in the family Buxtoniidae, and what was formerly *J. symmetrica* (now *Pulcratia symmetrica*) in the family Echinoconchidae.

At both the family and genus levels in the classification of these species, Muir-Wood and Cooper have repeatedly stressed the importance of the cardinal process (pp. 243, 249-50, 255, 267). However, the results of the present study indicate that the form of the cardinal process (form = size + shape + number of myophore lobes + degree of fusion of the shaft) in *J. nebrascensis* is the most variable aspect of the brachial valve. Therefore, the cardinal process cannot be considered a stable internal feature and is not a suitably diagnostic taxonomic criterion for the establishment and recognition of families and genera in the classification of this species. (See Sutton and Summerson, 1943, p. 324; Burma, 1948, p. 753; Mayr, Linsley, and Usinger, 1953, pp. 106, 123-4.)

Nor, at the species level, is the form of the cardinal process a useful taxonomic criterion in the classification of *J. nebrascensis*. The experience of the senior author in identifying

specimens of *J. nebrascensis* and *J. symmetrica* from the Pennsylvanian rocks of eastern Nebraska indicates that the form of the cardinal process is of no value in distinguishing between these two species. The presence of a small pit, or alveolus, near the base of the cardinal process shaft in *J. nebrascensis* and the relatively larger, more deeply impressed muscle scars in *J. symmetrica* have proven to be far more useful than the form of the cardinal process. Unfortunately, neither the alveolus nor the impressed muscle scars can be used with absolute certainty in all cases. (See Pl. 2, figs. 15, 16.)

At just which level in classification the presence of the pit or alveolus near the base of the cardinal process shaft in *J. nebrascensis* should be stressed, must await further study of this and other closely related species. Until such time, the status of the genus *Pulcratia* is uncertain. None the less, it does seem firmly established on the basis of this study and the work of Dunbar and Condra (1932) that *J. nebrascensis* and *J. symmetrica* are closely related and in any classification of productoid brachiopods they should be placed in the same family and perhaps in the same genus.

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A SEED MEGASPORE FROM THE DEVONIAN OF CANADA

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ABSTRACT. A megaspore tetrad, *Cystosporites devonicus* sp. nov., is described from the Upper Devonian of Scaumenac Bay, Quebec, Canada. *Cystosporites* megaspores have previously been reported only from the Carboniferous, where they have been found in the lycopod seed *Lepidocarpon*. The occurrence of this Canadian *Cystosporites* shows that a level of heterospory equivalent to that reached by *Lepidocarpon* had already been attained by the late Devonian.

THIS paper is an account of some Devonian fossil megaspore exines (briefly described in Chaloner and Pettitt 1963) which had, in at least one respect, reached the level of differentiation achieved in the seed plants. They consist of isolated tetrads, each consisting of one large (about 2 mm.), oval (presumably fertile) megaspore, and three very much smaller (presumably abortive) spores. They closely resemble the seed megaspores formed inside the Carboniferous lycopod seed *Lepidocarpon*. Hitherto the highest degree of heterospory reported in Devonian fossil plants is that in which many megaspore tetrads reached maturity in each megasporangium (e.g. in *Cyclostigma kiltorkense*, *Archaeopteris latifolia*) and were apparently shed, much as in the living *Selaginella* or *Isoetes*. The fossils described here show that a level closely approaching that of seed formation had already been attained in the Devonian.

Materials and methods of investigation. The material from which the megaspore tetrads were obtained was collected from the Upper Devonian Escuminac Formation of Scaumenac (Escuminac) Bay, Quebec, Canada, in 1934 and 1937 by W. Graham-Smith and deposited in the Department of Palaeontology, British Museum (Natural History). The Escuminac Formation is generally accepted as being of early Upper Devonian age (Cooper *et al.* 1942, McGregor 1959). One of the samples, a hard sandstone, bears compressions of *Archaeopteris* foliage and sporangia, whilst the second, a more indurated finer-grained sandstone from the Acanthodian Bed of the same locality, bears compressions of a thickly cutinized plant axis of unknown affinity.

The sandstone was mechanically crushed into small pieces and disaggregated further in commercial (40 per cent.) hydrofluoric acid for several hours. After washing and sieving, the megaspores were picked out and macerated individually in Schulze's solution (potassium chlorate in nitric acid) for 2 to 3 hours, until they were sufficiently transparent for examination by transmitted light. When this oxidative maceration was complete the spores were transferred to dilute ammonia solution for a few minutes and then washed and mounted in glycerine jelly, 'Clearcol' or Canada balsam. Spores of the same type were also seen on the bedding planes of the Acanthodian Bed and one of these spores was removed from the matrix with a needle and treated as outlined above.

To help in resolving the structure of the spore wall, serial sections of several of the macerated specimens were cut. These were dehydrated in 95 per cent. alcohol and cleared in methyl benzoate followed by a solution of 1 per cent. celloidin in methyl benzoate.

After a brief period in benzene, the spores were infiltrated with paraffin wax of melting point 45° C and then transferred to wax of melting point 54° C for about 45 minutes to complete embedding. Serial sections were cut on a microtome at 6 μ ; the sections were dewaxed and mounted in Canada balsam.

All the preparations are in the collections of the Department of Palaeontology, British Museum (Natural History), registered numbers V45428 to V45450.

Acknowledgement. We wish to express our thanks to Mr. J. V. Brown for his patient help in taking the photographs.

SYSTEMATIC DESCRIPTION

GENUS *CYSTOSPORITES* Schopf 1938

Cystosporites devonicus sp. nov.

Plate 3, figs. 1–6; Plate 4, figs. 1–3, 6

Diagnosis. Isolated megaspore tetrads composed of one large, elongated megaspore (presumed fertile), and three small ones (presumed abortive). Fertile spore up to 2,550 μ in length; abortive spores typically 130–70 μ in diameter. Open triradiate suture (laesure) visible at apex of fertile spore when abortive spores are missing; sutures typically 100–150 μ long. Weakly differentiated contact faces on fertile spore correspond to position of abortive spores. Exine of fertile spore minutely granular in texture, without discernible sculpture as seen in profile, 10–15 μ thick. Wall of abortive spores typically 10–12 μ thick, ornamented with conical processes 1–2 μ high and 1–2 μ apart. Distal extremity of fertile megaspore exine sometimes extended as a solid, tapering, truncated stalk-like process.

Holotype. V45428, Department of Palaeontology, British Museum (Natural History); Pl. 3, figs. 1, 2.

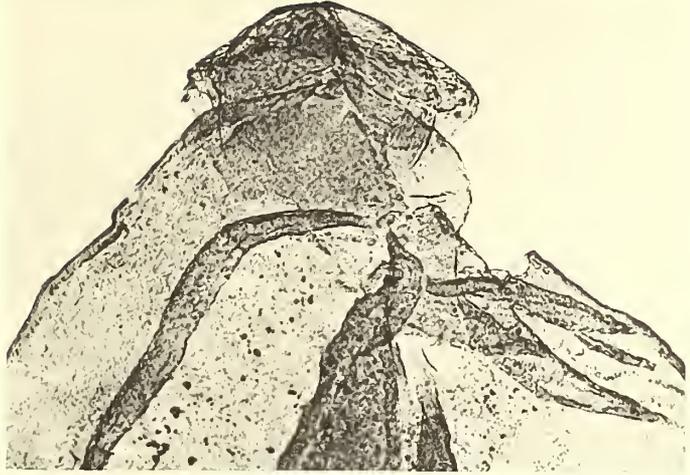
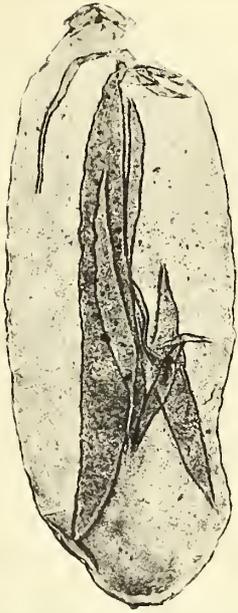
Type Locality. Escuminac Formation, Upper Devonian; Scaumenac Bay, Quebec, Canada.

Description

Variation in size and shape. The large fertile megaspore of each tetrad is typically ellipsoidal, being elongated along its polar axis (Pl. 3, figs. 1, 3). The largest is 2,550 μ long, and a typical specimen about 2,000 μ . This is very much larger than average Upper Devonian megaspores of presumably free-sporing type with normal tetrad development. A single, very much smaller, tetrad was isolated (Pl. 3, figs. 4, 7) in which the largest spore was 250 μ in length, and only slightly elongated (Pl. 3, fig. 7); the abortive spores (diameter 50–62 μ) became detached from it during mounting (Pl. 3, fig. 4). It is questionable

EXPLANATION OF PLATE 3

Figs. 1–7. *Cystosporites devonicus* sp. nov., from the Escuminac Formation, Scaumenac Bay, Quebec, Canada. All the photographs were taken by transmitted light; all the slides are in the British Museum (Natural History). 1, Holotype, V45428; \times 50. 2, Part of the same specimen showing the three abortive spores at the apex; \times 200. 3, Larger specimen, V45429; the irregular mosaic of pale areas on the exine is attributed to impressions of coarse particles of matrix; \times 50. 4, 7, The smallest tetrad found, V45430; the three abortive spores (4) became detached from the fertile spore (7) in mounting; \times 200. 5, Fertile spore which ruptured along three splits extending from the triradiate sutures, to form three partial valves, V45431; \times 25. 6, Transverse section of a seed megaspore showing the homogeneous character of the exine and a longitudinal secondary fold, V45447; \times 200.

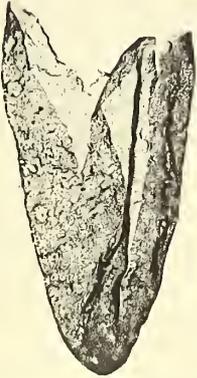


2



1

4



5



7



6



3

how far the observed size variation represents ontogenetic stages; evidently all the spores were sufficiently cutinized to survive fossilization and eventual maceration in Schulze's solution. Chaloner (1952) has observed considerable size variation in the seed megaspores (*Cystosporites*) contained within otherwise typical sporophylls of *Lepidocarpon waltoni*. It may be that some of the smaller tetrads represent those formed in sporophylls near a cone apex, rather than merely immature forms. But the thin (3–4 μ) wall and extremely small size of the tetrad of Plate 3, fig. 4 rather suggests immaturity.

Most of the fertile spores are darker at the ends (poles) and lighter (and probably thinner) in the central (equatorial) region. A number of secondary folds are usually developed, mainly parallel to the long axis presumably corresponding to collapse of an originally ellipsoidal body (Pl. 3, figs. 1, 3; also seen in section in Pl. 3, fig. 6). The polar axial elongation of the fertile spore, which is usually about three times the equatorial width, is a significant feature of agreement between these Devonian spores and the Carboniferous *Cystosporites*. In free-sporing heterosporous plants in which all four members of the megaspore tetrad develop equally, the spore body (aside from any special apical feature such as a gula) is typically more or less equidimensional, or even foreshortened axially. In Carboniferous *Cystosporites* (and possibly in the present case) the polar axial elongation corresponds to the spore expanding to fill the radially elongated sporangium characteristic of the Lepidodendrales.

Abortive spores and haptotypic features. Most of the fertile spores still have the abortive members of the tetrad adhering to the proximal pole (Pl. 3, figs. 1–3). The abortive spores show a sculpture of minute conia, 1–2 μ high and 1–2 μ apart. This ornament is variable, and in some specimens is barely discernible. The substance of the abortive spore exine is more or less granular, as in the fertile spores. The fertile spores show a clear triradiate suture when the three abortive spores have been removed (Pl. 4, fig. 1). In one case (Pl. 3, fig. 5) splitting had extended from the original sutures almost to the distal pole to divide the spore into three valves; this may have occurred before fossilization, or as a result of compaction in the matrix. In those spores where the proximal polar area of the fertile spore is visible, the areas of contact with the abortive spores are rather thinner than the adjacent exine and so are paler in colour (Pl. 4, fig. 1). The contact faces are bounded by weakly developed arcuate ridges, which appear darker than the surrounding exine.

The nature of the exine. The wall of the fertile megaspore is typically 10–15 μ thick, and under $\times 500$ magnification it shows a small-scale heterogeneity of a finely porous or granular nature (Pl. 4, fig. 6). Superimposed on this is an irregular, much larger scale pattern, of slightly thinner areas (Pl. 3, fig. 3; Pl. 4, fig. 1) which we attribute to coarse grained particles in the enclosing matrix which have left their impression on the exine. There is no clearly defined exine stratification; in section the fertile megaspore shows a more or less uniform exine (Pl. 4, fig. 6) with the fine granular texture extending throughout.

The basal stalk. Several of the fertile megaspores have at their base (the distal end with respect to the tetrad) an irregular prolongation of the exine in the form of a tapering, usually abruptly truncated, 'stalk' (Pl. 4, fig. 3). A closely similar feature has been described by Bochenski (1936) in *Cystosporites giganteus* found inside *Lepidocarpon*

major (Brongt.) Piérart (1961), and also on isolated *Cystosporites giganteus* (Dijkstra 1946).

Associated miospores. Several of the fertile megaspores have miospores adhering to them. While some of these are rather obscure, others have a prominent triradiate mark and an equatorial feature (Pl. 4, fig. 2), and may be assigned to the dispersed spore genus *Lycospora*. *Lycospora*, in addition to representing the microspores of many *Lepidostrobus* species, probably includes the microspores of *Lepidocarpon* (see, for example, Felix 1954). The occurrence of *Lycospora* in this context is of particular interest in view of the paucity of lycopod macrofossils at this horizon (see below). However, this occurrence of the *Lycospora* appressed to several of the specimens of *Cystosporites devonicus* cannot be regarded as being anything more than a suggestive association.

ASSIGNATION TO *CYSTOSPORITES*

In making the genus *Cystosporites* Schopf (1938) begins the diagnosis, 'Seed megaspores . . .'. It is amply demonstrated that many species of *Cystosporites* were borne on *Lepidocarp* megasporophylls (e.g. *C. giganteus*, *C. varius*) and were in this sense seed megaspores, but this is a piece of information which is not derived from an innate character of the dispersed megaspores themselves, and is only deduced from the circumstances of occurrence of certain specimens. The genus *Cystosporites*, which is based on dispersed megaspores, must be defined in terms of the megaspores alone, although it may be surmised that most (probably all) species included in the genus do indeed represent *Lepidocarp* seed megaspores. The main feature of *Cystosporites* is the development of the tetrad in such a way that the fertile spore becomes very large and sack-like in shape while the three abortive members of the tetrad remain relatively small and rounded. A further feature on which Schopf lays considerable emphasis is the fibrous character of the fertile spore exine. He reasonably correlates this with the supposition that this made it possible for food reserves to pass into the seed megaspore from the parent plant at a late stage in its development (while still enclosed in the sporangium). The thick continuous exine of the megaspores of *Lepidostrobus* and *Sigillariostrobus* (free-sporing plants) would presumably have prevented the inward passage of food reserves after the development of the spore wall was complete.

Since Scott's original (1901) description of petrified *Lepidocarpon* a number of species based on compression fossils have been put in the genus. The main problem involved in doing this is one commonly encountered in palaeobotany—that of extending a genus

EXPLANATION OF PLATE 4

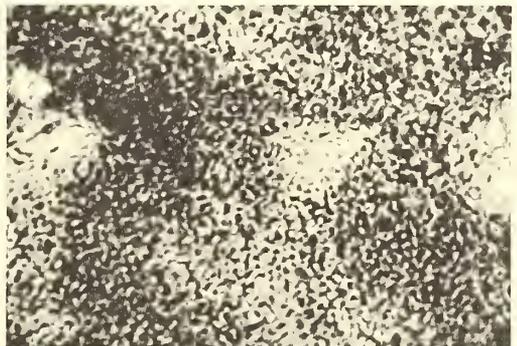
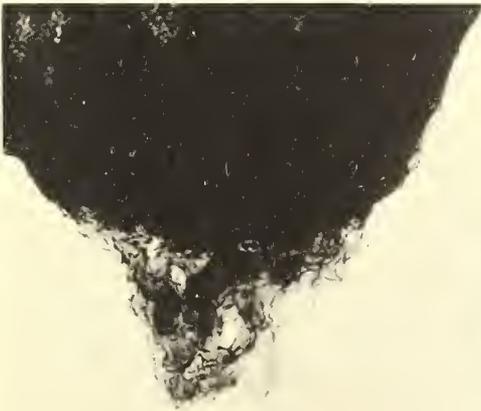
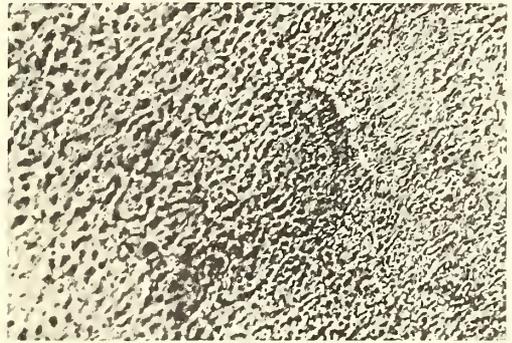
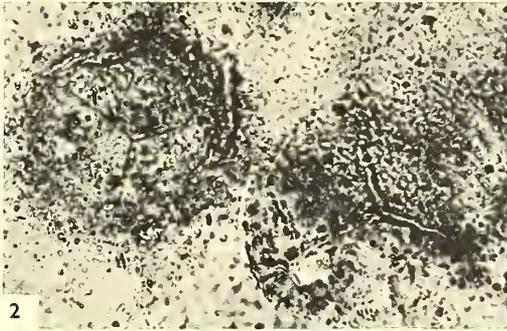
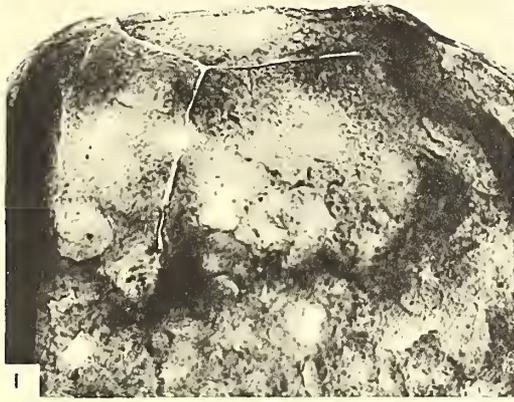
Figs. 1, 3, 6. *Cystosporites devonicus* sp. nov. 1, Fertile spore apex showing triradiate sutures (laesurae) and pale areas of the contact faces, V45428; $\times 200$. 3, Distal end of a fertile spore showing the 'stalk', V45433; $\times 200$. 6, Exine, showing its porous-granular character, V45434; $\times 500$.

Fig. 2. Two miospores, cf. *Lycospora* sp., adhering to the exine of a fertile spore of *Cystosporites devonicus*, near to the distal end, V45432; $\times 500$.

Fig. 4. Exine of *Cystosporites giganteus* (from the holotype of *Lepidocarpon waltoni*, from the Lower Carboniferous of Scotland) showing the fibrous character of the fertile spore wall, V45451; $\times 500$.

Fig. 5. Exine of *Cystosporites verrucosus* (from *Lepidocarpon braidwoodensis*, Upper Carboniferous of England), showing the more or less granular character of the fertile spore wall, and two spines, V45452; $\times 500$.

All the slides are in the British Museum (Natural History).



based on a petrification to include species based on compressions which do not show all the features seen in the petrified material. In this particular case, compressions of *Lepidocarpon* could hardly be expected to show clear evidence of the thin integumentary flaps, an important character of *Lepidocarpon* as seen in the petrified state. Schopf (1941), Chaloner (1952), Bharadwaj (1959), and Piérart (1961) have reviewed the basis for extending *Lepidocarpon* to include such compression fossils. In effect the possession of *Cystosporites* megaspores contained in otherwise *Lepidostrobus*-like sporophylls has been accepted by these authors as a legitimate basis for assigning the sporophylls to *Lepidocarpon*. We regard this as a more reasonable and preferable expedient to the alternative of assigning such sporophylls to *Lepidostrobus*.

Two Upper Carboniferous species of *Lepidocarpon* based on compressions are particularly relevant in their bearing on our Devonian *Cystosporites*: *Lepidocarpon major* (Brongt.) which contains *Cystosporites giganteus* megaspores and *Lepidocarpon braidwoodensis* (Arnold) Piérart, which contains *Cystosporites verrucosus* (of which Arnold's *Lagenicula saccata* is a synonym—see Dijkstra 1955). Both of these *Lepidocarpon* species were previously assigned to *Lepidostrobus*, but have been reassigned by Piérart (1961) on the basis of their containing *Cystosporites*.

The *Cystosporites giganteus* megaspores enclosed in *Lepidocarpon major* were shown by Bochenski (1936) to have a basal stalk (Stiel) extending from the megaspore to the adaxial end of the sporangium. A similar but much larger structure extends from the megaspore to fill the whole adaxial half of the megasporangium in *L. braidwoodensis*. (This can be seen in the specimens of this species figured by Chaloner 1954 as *L. monospora*, a species now shown to be a later synonym of *L. braidwoodensis*—see Dijkstra 1955.) We accordingly regard the similarity of the stalk in our *Cystosporites* to that in *C. giganteus*, which is known to be a *Lepidocarp* seed megaspore, as a significant feature of agreement.

The probable biological significance of the fibrous character of the exine in some *Cystosporites* has been mentioned above. That of *C. giganteus* is shown in Plate 4, fig. 4. However, *C. verrucosus* has a much more compact, homogeneous texture (Pl. 4, fig. 5), and is ornamented with small ridges and spines near the apex. These two species may be said to show the extremes of wall texture among those already assigned to *Cystosporites*. The exine of *C. devonicus* (Pl. 4, fig. 6) is not significantly less porous or granular than that of *C. verrucosus*, and we accordingly discount its non-fibrous exine as a basis for excluding it from *Cystosporites*.

In summary, our megaspore tetrads show the following features in common with Carboniferous species of *Cystosporites*:

1. Development of one member of the tetrad, the fertile spore, at the expense of the three abortive members, which adhere to the fertile spore apex.
2. The fertile spore is elongated axially to between two and three times its width.
3. Some of our spores have a basal stalk, similar to that of *C. giganteus*.
4. The exine is of a granular or porous character, similar to that of *C. verrucosus*.

These features form the basis of our assigning *C. devonicus* to that genus. We do not consider that this assignation begs the question of whether or not it represents a *Lepidocarp* seed megaspore, or even whether its enclosing sporangium was integumented, although both of these are likely.

COMPARISON WITH SIMILAR STRUCTURES

Cystosporites devonicus compares most closely with the several Carboniferous species of this genus. It may also be compared in more general terms with the seed megaspore enclosed in the Carboniferous lycopod seed *Miadesmia*. This is of comparable size to *C. devonicus*, but *Miadesmia* did not apparently form an exine on the three abortive members of the (presumed) megaspore tetrad, and only a single large seed megaspore is seen in the megasporangium. The *Miadesmia* megaspore also differs from *Cystosporites* in lacking any visible tetrad mark or other haptotypic features. We have examined Scott's material of *Miadesmia* seeds in the British Museum (Natural History) in which the megaspore membrane, although apparently yellow and translucent, was thin and uniform in texture.

The megasporangium of the Lower Carboniferous coenopterid fern *Stauropteris burntislandica* represents an instance in which a single megaspore tetrad was reduced to two fertile and two abortive spores (Surange 1952, Chaloner 1958)—a situation analogous to the more extreme reduction in *Lepidocarpon*. The similarity of the megaspore tetrad in *S. burntislandica* and *Cystosporites* does not extend beyond this; but the situation in *S. burntislandica* is of interest in that while it is a megaphyllous plant it parallels *Lepidocarpon* in having a modified single tetrad, but in this case in a non-integumented megasporangium.

Comparison with *Hirsutocarpon extensum*, described by Maslov (1957) from a section of Devonian limestone, is limited by our rather meagre knowledge of this Russian fossil. Maslov compared it with *Lepidocarpon* and with *Miadesmia*, but as it is known only in one plane of section, its real shape and the nature of the enclosed megaspore (if any) is quite conjectural and its similarity to these or any other seeds is problematical (see Banks 1960, Chaloner 1960).

Finally, *Cystosporites devonicus* may be compared with the megaspore membranes isolated from Lower Carboniferous Pteridosperm seeds—for example, those of *Eosperma oxroadense* (Barnard 1959) and *Geminitheca scotica* (Smith 1959). These and other Carboniferous seed megaspore membranes resemble our fossil in being more or less oval, elongated sack-like structures. They all differ from this and other species of *Cystosporites* in having no abortive spores or haptotypic features at the apex, and no basal stalk to the megaspore membrane.

THE PARENT PLANT OF *CYSTOSPORITES DEVONICUS*

All the fructifications in which Carboniferous *Cystosporites* megaspores have been found so far may be included in the genus *Lepidocarpon* s.l., or at least in the Lepidocarpaceae (Schopf 1941, Chaloner 1952, Bharadwaj 1959, Piérart 1961). Indeed, the various features which characterize the *Cystosporites* tetrad correspond to its retention to constitute the seed megaspore inside a Lepidocarp seed. Accordingly the most obvious interpretation of our fossil is simply that it represents a Devonian Lepidocarp seed megaspore. However, such an interpretation would presuppose the nature of the parent megasporangium, and, in particular, that it was integumented. A considerable number of large, and probably arborescent, lycopod genera are now known from the late Devonian, including *Cyclostigma*, *Archaeosigillaria*, *Lepidosigillaria*, and *Lepto-*

phloeum. Any of these are possible parent plants for a lycopod (*Lepidocarpon*-like) fructification. However, lycopod macrofossil remains in the Escuminac beds are rare. Dawson (1882) reported *Knorria* (a genus representing a variety of arborescent lycopods in a decorticated state) and an 'obscure' *Lepidostrobus* from Scaumenac Bay. These appear to be the only lycopod macrofossils recorded from that locality.

Archaeopteris, on the other hand, is relatively common at Scaumenac Bay (Arnold 1936). One species of this genus was shown by Arnold (1939) to be heterosporous, and Beck (1960), on the basis of its wood anatomy and other features, has grouped *Archaeopteris* with some similar genera in a new group, the Progymnospermopsida. Fertile pinnae of *A. cf. jacksoni* Dawson from Scaumenac Bay have been found by one of us (J. M. P.) to bear sporangia which contain either 9 to 48 megaspores 202–370 μ in diameter, or several hundred microspores 45–70 μ in diameter. It is evident that heterospory was not confined to one species of *Archaeopteris*, and it may have been general in the genus. It is at least conceivable that *Cystosporites devonicus* could represent a megaspore tetrad of a plant similar to *Archaeopteris* in which reduction of the megaspore number had reached the *Lepidocarpon* level. In this case, similarity of *C. devonicus* to *Lepidocarpon* megaspores would constitute a remarkable degree of parallel evolution in the lycopods and a macrophyllous plant. But whatever the nature of its parent plant, the character of the *C. devonicus* tetrad itself indicates the attainment of a level of heterospory previously unknown in the Devonian.

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MICROPLANKTON FROM THE CAMBRIDGE GREENSAND (MID-CRETACEOUS)

by I. C. COOKSON and N. F. HUGHES

ABSTRACT. Thirty-eight species of dinoflagellates (including hystrichospheres) and of acritarchs of uncertain systematic position are recorded from the Cambridge Greensand; eight of these are new, and several others are recorded for the first time in Europe. Rock samples studied include six from the Gault immediately below, and five from the lowest Chalk Marl which continues above the 'greensand'. Evidence for the early Cenomanian (Varians Zone) age of the Cambridge Greensand is discussed.

ALTHOUGH during the last century the Cambridge Greensand was exposed in phosphate diggings over an outcrop length of about 50 miles from West Bedfordshire through Cambridge to north of Soham, there are now few available exposures; the material here studied was collected in 1959 and 1960 in the south-west corner of the then Eastwood's Cement Pit (Nat. Grid Ref. TL 393507), near Barrington. A general map of the location is given in Sparks (1952, p. 164); the pit is now owned by the Rugby Portland Cement Co.

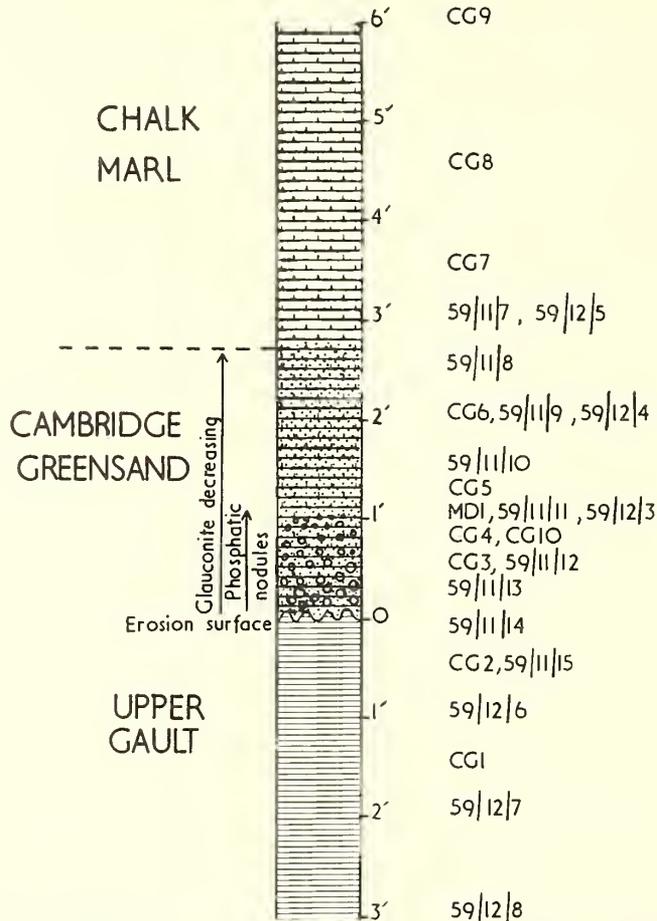
The samples used come from a suite of twenty-eight collected on separate visits by Dr. Mary Dettmann (MD 1), by Mr. G. Norris, and by N. F. H. (CG 1-10); their stratigraphical position is given on text-fig. 1. The samples were taken from a freshly excavated face, and measurements were taken up and down from the clear unconformity at the base of the Cambridge Greensand. At this locality, the Cambridge Greensand is a grey calcareous clay or marl with prominent glauconite grains and dark phosphatic nodules up to about 2 inches in diameter; the sand fraction is composed of the glauconite grains. The bed is from 1 to 2 feet thick, and grades off upward into the Chalk Marl above, which is much paler and in which the glauconite grains finally disappear at about 4 to 5 feet above the unconformity; below the unconformity there is undisturbed stiff blue Gault Clay, without diagnostic macrofossils at this locality.

Stratigraphy. The Cambridge Greensand was described by Cowper Reed (1897) as lying within the Varians Zone (now basal Cenomanian), although this appears to have been determined on the convenience of the unconformity rather than on the presence of any cephalopods. Spath (1943, p. 749) concluded that the formation of the bed occurred in Dispar Subzone times of the uppermost Albian; he described the large *derived* ammonite fauna as being principally from the two preceding subzones (of *substuderi* and *aequatorialis*) with only comparatively rare forms from the Dispar Sub-zone.

There are in the Sedgwick Museum three specimens of *Schloenbachia* which are probably from the Cambridge Greensand. Two of these were mentioned by Spath (1928, p. 245); B1679 is a fragment of a large specimen preserved in dark phosphate as are most of the derived fossils, but B10965 is a small and more complete specimen preserved in relatively light coloured phosphate. The third, B80557, is a mould of a small specimen, identified as *Schloenbachia* indet. cf. *subplana* (Mantell) by Mr. A. G. Brighton, it was found at Barrington Cement Works in 1954 by N. F. H., weathered out loose and lying about a foot above the phosphatic part of the Cambridge Greensand outcrop; the

matrix of the specimen contains prominent glauconite grains similar to those seen in the 'greensand' and in the first 3 feet above the unconformity.

It thus seems slightly more likely that the Cambridge Greensand should be considered as of basal Cenomanian age (Varians Zone), than of uppermost Albian (Dispar Zone) for which there is as yet no positive faunal evidence.



TEXT-FIG. 1. Collection levels of samples from the Cement Works Pit, north of Barrington, Cambridgeshire.

Distribution of microfossils. Most of the figured specimens are mounted and ringed on separate slides, the numbers of which in the Sedgwick Museum, Cambridge (prefaced by the letter K), are given in the Plate explanations; these numbers are accompanied by stage readings for Leitz Ortholux microscope No. 491249.

Selected strew preparations from the three samples CG1, CG3, and CG8, have been counted to 200 specimens (+rare forms ex-count) to give a preliminary idea of distribution in the section studied; it is important, however, to record that the flora is not complete in that a few small forms have been omitted. Table 1 gives the distribution of

TABLE 1. Records of counts from three selected samples, CG 1, CG3, and CG8, with occurrences of the species in microplankton floras from other Cretaceous stages. Legend: ×, recorded in literature; —, not recorded; +, record of < 1 per cent; (+), record from uncounted slides; numerals above the column total are percentages.

	Hauterivian/Barremian (Gocht, Alberti)	Aptian (Eisenack)	Aptian/Albian (Australian)	CG 1, Upper Gault	CG 3, Greensand	CG 8, Chalk Marl	Senonian (Australia/Europe)	Senonian
<i>Ascodinium scabrosum</i> sp. nov.	—	—	—	+	2	—	—	—
" <i>verrucosum</i> sp. nov.	—	—	—	—	2	5	—	—
<i>Scriniodinium campanula</i>	×	×	—	2	1	+	—	—
<i>Gonyaulax cassidata</i>	—	—	×	—	3	1	×	—
" <i>edwardsi</i>	—	—	×	1	1	2	×	—
<i>Hystrichodinium alatum</i>	—	—	×	2	1	+	×	—
<i>Palaeohystrichophora infusorioides</i>	cf.	—	—	—	(+)	(+)	×	×
<i>Canningia minor</i> sp. nov.	—	—	—	+	1	—	—	—
<i>Cyclonephelium membraniphorum</i>	—	—	×	—	(+)	(+)	×	—
<i>Hystrichosphaera furcata</i>	×	×	—	10	6	2	—	×
" <i>ramosa</i>	—	—	—	4	7	10	—	×
<i>Achomosphaera ramulifera</i>	×	—	—	2	1	1	×	×
<i>Hystrichosphaeridium ancoriferum</i>	—	—	×	+	1	(+)	×	—
" <i>arundum</i>	—	—	×	+	—	—	—	—
" <i>complex</i>	×	×	×	4	—	1	×	×
" <i>recurvatum polytypes</i>	—	—	×	+	+	—	×	—
" <i>siphoniphorum</i>	—	—	×	3	4	6	×	—
" <i>stellatum</i> (Tertiary species)	—	—	×	(+)	1	+	×	—
<i>Carpodinium obliquicostatum</i> sp. nov.	—	—	—	+	(+)	1	—	—
<i>Palaeoperidinium castanea</i>	—	—	×	—	+	+	×	×
" <i>spinatum</i> sp. nov.	—	—	—	—	×	—	—	—
<i>Stephodinium europaicum</i> sp. nov.	—	—	—	1	+	2	—	—
<i>Pseudoceratium dettmannae</i> sp. nov.	—	—	—	2	+	—	—	—
" <i>turneri</i>	—	—	×	—	(+)	—	—	—
<i>Apteodinium grande</i> sp. nov.	—	—	—	—	(+)	(+)	—	—
<i>Odontochitina</i> spp.	×	×	×	8	+	2	×	×
cf. <i>Rottnestia borussica</i> (Tertiary species)	—	—	—	1	+	2	—	—
<i>Hexagonifera chlamydata</i>	—	—	?	(+)	+	—	×	—
<i>Chlamydothorella nyei</i>	—	—	×	56	56	57	×	—
<i>Fromea amphora</i>	×	×	×	(+)	—	—	×	—
<i>Baltisphaeridium ferox</i>	×	×	×	—	+	(+)	×	×
" <i>hirsutum</i>	—	—	×	+	3	1	—	×
<i>Coronifera oceanica</i>	—	×	×	+	—	—	—	—
<i>Veryhachium reductum</i> (Long range species)	—	—	×	+	1	+	×	—
<i>Diplotesta anglica</i> sp. nov.	—	—	—	+	1	3	—	—
Object 'A'	—	—	—	(+)	+	1	—	—
<i>Michrystridium</i> spp.	—	—	—	+	4	1	×	×

Total %	100	100	100
Numbers identified and counted	240	267	200
Microplankton unidentified	60	37	27
Spores and pollen not identified	36	40	32

the more important elements of the flora together with records of their occurrence in floras so far described from two or three stratigraphical stages above and below. It must be emphasized that none of the floras concerned can be regarded as complete in the literature.

Some specimens in the Greensand will have been derived from the Upper Gault; this could have occurred without appreciable damage. It is unlikely that the time break represented by the unconformity was very long, but it does coincide with a general facies change to more calcareous deposits in Britain.

SYSTEMATIC DESCRIPTIONS

As a temporary measure while changes are being made to bring the nomenclature of these fossils under the Botanical Code (see Downie, Evitt, and Sarjeant 1963), certain family names will be left with zoological endings; we do not wish to undertake the emendation or redescription of these families here.

Class DINOPHYCEAE

Family DEFLANDREIDAE

Genus ASCODINIUM Cookson and Eisenack 1960

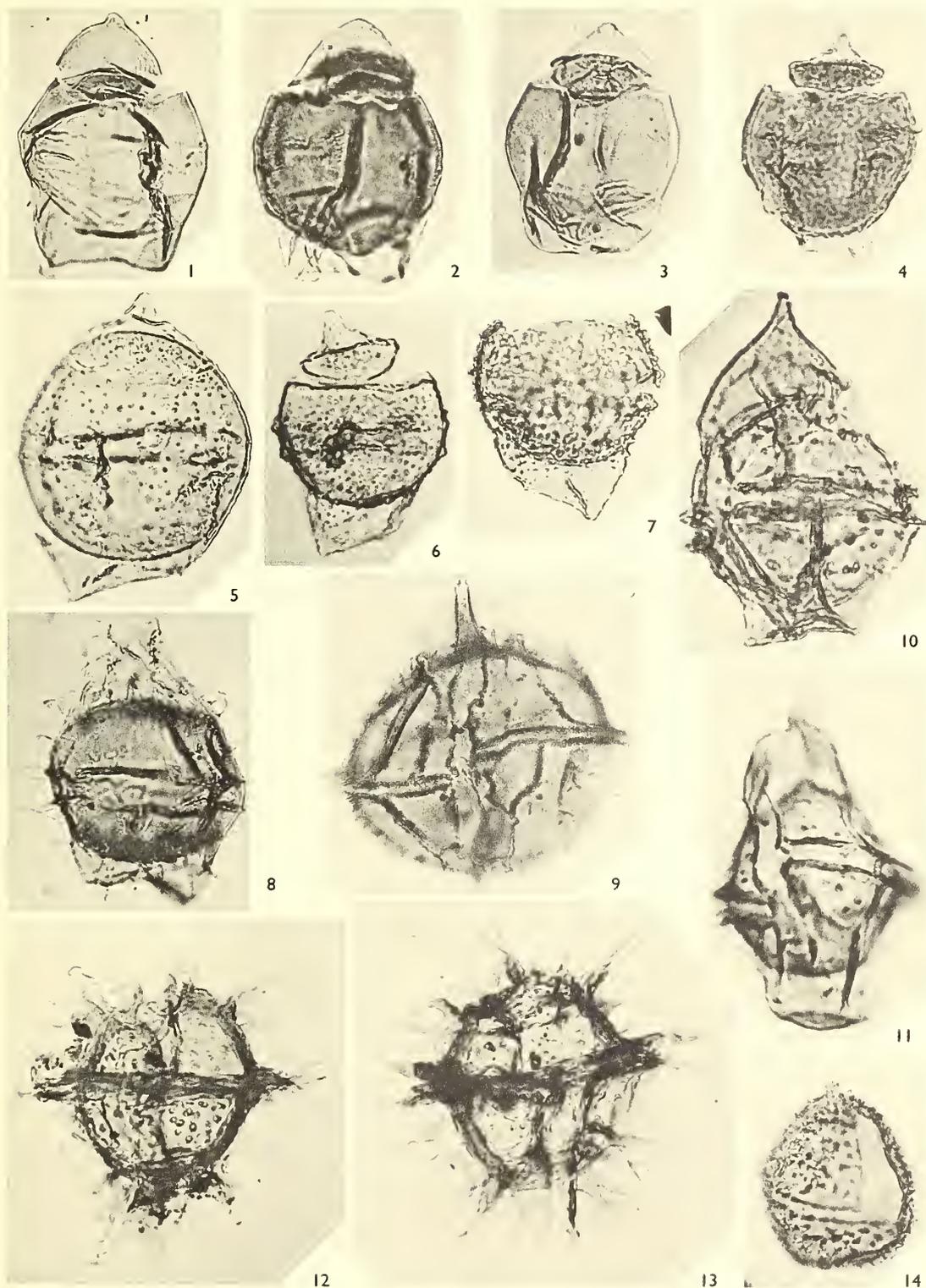
Comment. The genus *Ascodinium* was originally established for certain small, untabulated dinoflagellates which occur in Western Australian Albian–Cenomanian deposits. The main characters of this genus are, (1) the presence of an internal body or capsule which lies either freely in the cavity of the shell (*A. acrophorum* and *A. serratum* Cookson and Eisenack 1960a) or in partial contact with the shell-membrane laterally (*A. parvum* Cookson and Eisenack 1960a); (2) the opening of the shell by the removal of the apical region of both shell and capsule (apical archaeopyle). Two species occur in the Cambridge deposits which, although differing in detail from the above-mentioned species, seem best placed with them, at least for the present, as additional species of *Ascodinium*. Their mode of opening is similar but the wall of the capsule is in contact with the shell-membrane to a far greater extent, in fact to such a degree as to suggest that this layer may not mark the limit of an inner body or capsule but represent the inner layer of a two-layered shell-membrane.

Ascodinium scabrosum sp. nov.

Plate 5, figs. 1–3

EXPLANATION OF PLATE 5

- Figs. 1–3. *Ascodinium scabrosum* sp. nov. 1, Holotype, CG3; K5151, OR57 121.1, $\times 500$. 2, CG1; K5152, OR36 123.6, $\times c. 500$. 3, CG1; K5153, OR35.4 116.4, $\times c. 500$.
 Figs. 4–7. *A. verrucosum* sp. nov. 4, Holotype, 59/11/12; K5154, OR30.1 121.1, $\times c. 500$. 5, 59/11/11; K5155, OR46.7 122.8, $\times 500$. 6, MD1; K5156, OR41.4 119.7, $\times c. 500$. 7, CG8; K5157, OR49.3 127.8, $\times 500$.
 Fig. 8. *Palaeohystrichophora infusorioides* Defl., 59/12/5; K5162, OR44.6 118.5, $\times 560$.
 Fig. 9. *Gonyaulax edwardsi* Cooks. and Eisenack, CG3; K5163, OR39.3 120, $\times 500$.
 Figs. 10, 11. *G. cassidata* Cooks. and Eisenack. 10, CG8; K5164, OR42.2 124.1, $\times 800$. 11, CG3; K5161, OR36.9 121.9, $\times 875$.
 Figs. 12, 13. *Hystrichodinium alatum* Cooks. and Eisenack, CG8, $\times 500$. 12, K5159, OR31.3 123.7, 13, K5160, OR25.7 115.3.
 Fig. 14. *Palaeoperidinium castanea* Deflandre, 59/11/7; K5158, OR34.8 124, $\times 500$.



Diagnosis. Shell longer than broad with convex sides which curve inwards towards a bluntly pointed apex and slant slightly towards a somewhat truncate antapex. A circular girdle is faintly indicated in the equatorial region. The shell-membrane is very thin, not more than *c.* 0.5μ and densely covered with minute granules. The capsule wall, which is also 0.5μ thick, is unpatterned and closely opposed to the shell-membrane laterally. Opening is effected by the complete removal of the apical region of the shell and capsule.

Holotype. Plate 5, fig. 1; K5151, lowest 6 in. Cambridge Greensand (CG3).

Dimensions. Holotype 80μ long, 64μ broad. Range $52-80 \mu$ long, $42-64 \mu$ broad.

Occurrence. Upper Gault CG1, CG2, 59/11/14; Greensand, 59/11/12, CG3.

Ascodinium verrucosum sp. nov.

Plate 5, figs. 4-7

Diagnosis. Shell slightly longer than broad with strongly convex sides, a circular girdle and a short longitudinal furrow in the hypotheca. Shell-membrane completely adherent to the thicker wall of the capsule except at the extreme apex where it narrows towards a small, pointed, cap-like projection and antapically where it forms a prominent projection with a slanting asymmetrical base. The surface of the shell-membrane is ornamented with more or less densely arranged hollow verrucae; the wall of the capsule is unornamented, the two membranes together measure about $2-3 \mu$. Opening is effected by the complete detachment of the apical portion of the shell and capsule.

Holotype. Plate 5, fig. 4; K5154, 6 in. above base of Greensand (59/11/12).

Dimensions. Holotype 52μ long, 32μ broad. Range $55-80 \mu$ long, $40-59 \mu$ broad, the exceptionally large specimen ($98 \times 73 \mu$) shown on Plate 5, fig. 5 omitted.

Occurrence. Greensand, 59/11/12, CG3, CG4, CG10, 59/11/11, MD1; Chalk Marl, 59/12/5, 59/11/7, CG8.

Comment. Considerable variation both in size of shell and density of ornament has been observed amongst the individuals included in *A. verrucosum*, the larger shells having fewer and more widely spaced verrucae than the smaller ones. *A. verrucosum* is one of the commoner types in the Cambridge Greensand and Chalk Marl. It is particularly abundant in sample CG10.

Genus SCRINIODINIUM Klement 1957
Scriniodinium? *campanula* Gocht 1959

Plate 7, figs. 5-9

1959 *Scriniodinium campanula* Gocht, pl. 4, fig. 6, pl. 5, fig. 1.

1961 *Scriniodinium campanula* Gocht; Alberti, pl. 3, fig. 6.

Dimensions. Overall length $73-135 \mu$, width $60-100 \mu$, horn $9-15 \mu$ long, longest diameter of ventral opening $8-15 \mu$.

Occurrence. Upper Gault, CG1, CG2, 59/11/14; Greensand 59/11/12, CG3, CG4, CG10, MD1; Chalk Marl, 59/12/5, 59/11/7, CG8.

Comment. This species, whilst readily recognizable, is extremely difficult to interpret morphologically from surface views. It is therefore not at all surprising that both Gocht's description and consequent association of it with *Scriniodinium* are open to doubt.

In the Cambridge examples, which undoubtedly are specifically identical with the German forms, the dorsal surface of the shell is strongly convex and the ventral surface flat or slightly concave. The circular girdle which is usually deeply folded, crosses the dorsal surface somewhat above the equatorial line to end on the ventral surface a short distance within the margin of the shell. A fold in the middle of the dorsal convexity extends from the girdle to the antapex.

Our main disagreement with Gocht's description concerns the suggested presence of an inner body or capsule which is said to be separated from the shell-membrane by a wide space. One or more lines running parallel to and at some distance from the edge of the shell are clearly seen, but instead of regarding these lines as indicating the limit of an internal capsule of approximately the same shape as the shell we suggest that this appearance is due to the steepness of the gradient of the dorsal convexity. This idea is supported by transverse and longitudinal sections cut, at a thickness of $2\ \mu$, through two shells. In these sections there is no sign of a central body. Of course it may be argued that in reality an internal capsule is differentiated and that its wall is in direct contact with the shell-membrane. As far as our work has gone this seems unlikely since the shell-membrane is so thin that, as our photographs show, even in sections $2\ \mu$ thick no indication of a second layer can be seen. These sections were kindly prepared for us by Dr. Mary Dettmann.

As in most of the German specimens indications of surface markings suggestive of tabulation have been rarely seen in the Cambridge examples. On the other hand one feature, invariably present in them, which has not been mentioned in connexion with the German forms is a small round or oval opening on one side of the ventral wall towards the antapex. The significance of this feature is unknown.

The present record has extended the geological range of *S.?* *campanula* from Lower and Upper Hauterivian (Gocht and Alberti) to Cenomanian.

Family GONYAULACEAE Lindemann
Genus GONYAULAX Diesing 1866
Gonyaulax cassidata Cookson and Eisenack 1962

Plate 5, figs. 10, 11

1960 *Gonyaulax helicoidea* subsp. *cassidata* Eisenack and Cookson, p. 3, pl. 1, figs. 5, 6.

1962 *Gonyaulax cassidata* Cookson and Eisenack, p. 486, pl. 2, figs. 11, 12.

Comment. Specimens indistinguishable from the Australian Aptian–Cenomanian species *G. cassidata* occur regularly but infrequently. All have the small size, strongly helicoid girdle, oblique longitudinal furrow, and dome-shaped apex of this species. In addition the girdle and plates have the high ledges with serrate edges of *G. cassidata* and the plates are similarly ornamented with small tubercles.

Occurrence. Upper Gault, 59/11/14; Greensand, 59/11/12, CG3, CG4, 59/11/11, 59/11/9; Chalk Marl, 59/11/7, CG8.

Gonyaulax edwardsi Cookson and Eisenack 1958

Plate 5, fig. 9

Comment. Specimens which agree in general characters and in tabulation with those of *G. edwardsi* from Australian Albian to Cenomanian deposits occur in the Cambridge Greensand.

Occurrence. Greensand, 59/11/12, CG3, CG4, CG10, 59/11/11; Chalk Marl, CG8.

Family HYSTRICHODINIDAE

Genus HYSTRICHODINIUM Deflandre 1936

Hystrichodinium alatum Cookson and Eisenack 1962

Plate 5, figs. 12, 13

Comment. Specimens which agree in all respects with *H. alatum* from Western Australian ?Albian–Cenomanian deposits occur sparsely in most of the Cambridge deposits of comparable age. They have the tabulated shells of *H. alatum*, the whorls of hollow, pointed processes around the apex, antapex and girdle, the wing-like development of the outer membrane from which the processes arise, and the small tubercles with fine points which ornament the plates.

Occurrence. Upper Gault, 59/11/14; Greensand, 59/11/12, CG3, 59/11/9; Chalk Marl, 59/12/5, CG8.

Genus PALAEOHYSTRICHOPHORA Deflandre 1934 emend. Defl. and Cookson 1955

Palaeohystrichophora infusorioides Deflandre

Plate 5, fig. 8

1934 *Palaeohystrichophora infusorioides* Deflandre, *C.R. Acad. Sci.* **149**, 967, fig. 8.

1936 *Palaeohystrichophora infusorioides* Defl.; Deflandre, *Ann. Paléont.* **25**, 38, pl. 9, fig. 8.

1958 *Palaeohystrichophora infusorioides* Defl.; Cookson and Eisenack, p. 37, pl. 10, fig. 10.

Comment. In recording *P. infusorioides* from the Cambridge Greensand it must be noted that the short surface hairs characteristic of this species seem to be less numerous and prominent than those of the French Cenomanian and ?Senonian examples or the example from the German Senonian Alberti (1961; plate 3, fig. 24).

Occurrence. Greensand, CG3, CG4, CG10, 59/11/11; Chalk Marl, 59/12/7, CG8.

Family AREOLIGERACEAE Evitt 1963

Genus CANNINGIA Cookson and Eisenack (1960) 1961b

Canningia minor sp. nov.

Plate 8, figs. 1–3, 5

Diagnosis. Shell almost circular in outline, in well-preserved examples slightly longer than broad, opening by the removal of an apical segment along a zigzag line, the freed edge of the shell showing notches at intervals; apex with or without a short prominence, antapex usually unindented. Girdle absent; wall *c.* 1 μ thick, surface scabrate.

Holotype. Plate 8, fig. 1; K5184, Cambridge Greensand (CG10).

Dimensions. Holotype $70 \times 73 \mu$. Range $42\text{--}73 \mu$ long, $36\text{--}73 \mu$ broad.

Occurrence. Upper Gault, CG1, CG2; Greensand, CG4, CG10.

Comment. Of the three described species of *Cunningia*, *C. minor* most closely resembles the Australian Aptian species *C. colliveri* Cookson and Eisenack 1960*b*. However, it can be distinguished from this species by the less frequent occurrence of an apical prominence and indented antapex, its consistently smaller size (average dimensions of 19 specimens $56 \times 52 \mu$), and the finer ornamentation of the shell-membrane.

In the majority of specimens the apex is partially detached and crumpled so that a more accurate ratio of length to breadth has not been possible. Plate 8, fig. 4 shows a specimen with a girdle developed; in spite of several similarities to *C. minor*, we prefer to record this as *Cunningia?* sp.

Genus CYCLONEPHELIUM Deflandre and Cookson 1955
Cyclonephelium membraniphorum Cookson and Eisenack 1962

Plate 10, figs. 5, 6

Comment. A number of specimens which can safely be identified with *C. membraniphorum* from Western Australian ?Albian–Cenomanian deposits have been recovered. However, in them the membranes of the circumferential border-zone are proportionally more strongly developed and the radial supporting fibres less conspicuous than are those of the Australian examples.

Occurrence. Greensand, 59/11/12, CG3, CG4; Chalk Marl, 59/11/7, CG8.

Cyclonephelium cf. *densebarbatum* Cookson and Eisenack 1960

Plate 10, fig. 10

1960*b* *Cyclonephelium densebarbatum* Cookson and Eisenack, 253, pl. 38, figs. 9, 10.

Comment. A few specimens from one sample, although distinct from the type of *C. densebarbatum* in having longer and stouter appendages, are comparable with specimens from the Upper Jurassic deposits at Wallal in north-west Western Australia which were included by Cookson and Eisenack in *C. densebarbatum*. As in the latter the periphery of the shell is ornamented with short, rather densely arranged, free appendages with relatively broad apices.

Occurrence. Greensand, 59/11/9.

EXPLANATION OF PLATE 6

Figs. 1–6. *Carpodinium obliquicostatum* sp. nov. 1, Holotype, CG1; K5165, OR42 118, $\times c.$ 900. 2, CG8; K5166, OR38.5 114.3, $\times 750$. 3, 59/11/12; K5167, OR37 122.8, $\times 750$. 4, Dorsal surface, 59/11/12; K5168, OR37.4 117, $\times 625$. 5, As last—ventral surface (low focus). 6, Detail, CG3; K5169, OR36.1 117, $\times c.$ 1500.

Fig. 7. *Pseudoceratium turneri* Cooks. and Eisenack, 59/11/12; K5172, OR25.5 115, $\times 500$.

Figs. 8–9. *Apteodinium grande* sp. nov. 8, 59/11/12; K 5171, OR37 117.5, $\times 500$. 9, Holotype, 59/11/11; K5170, OR31 120, $\times 375$.



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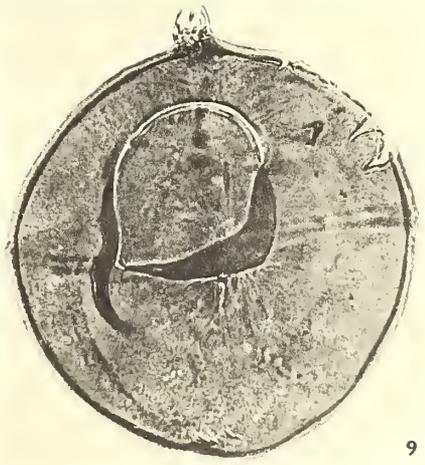
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Family HYSTRICHOSPHAERACEAE O. Wetzel 1933 emend. Evitt 1963

Genus HYSTRICHOSPHAERA O. Wetzel 1933

Hystrichosphaera furcata (Ehr.) O. Wetzel

Plate 9, fig. 1, 2

- 1838 *Xanthidium furcatum* Ehrenberg, *Abh. K. Akad. Wiss. Berlin*, 109–36, pl. 1, fig. 14.
 1933 *Hystrichosphaera furcata* (Ehrenberg) O. Wetzel, *Palaeontographica*, 77A, 34, pl. 5, figs. 1, 5, 9, 15, 16.
 1935 *Hystrichosphaera furcata* (Ehr.); Deflandre, *Bull. Biolog.*, 232, pl. 5, fig. 9; 1937, *Ann. Pal.* 26, 13, pl. 11, figs. 1, 3, 4.

Comment. Specimens agreeing with the description and illustrations of European forms attributed to *H. furcata* are regular components of the Cambridge Upper Gault, Greensand, and Chalk Marl deposits.

Hystrichosphaera ramosa (Ehr.) O. Wetzel 1933

Plate 9, figs. 4, 5

- 1838 *Xanthidium ramosum* Ehrenberg, *Abh. K. Akad. Wiss. Berlin* (1836–8), pl. 1, fig. 14.
 1933 *Hystrichosphaera ramosa* (Ehrenberg) O. Wetzel, *Palaeontographica*, 77, 35, 78: pl. 5, figs. 7, 8, 10, 10–12, 18, and 19.
 1937 *Hystrichosphaera ramosa* (Ehr.); Deflandre, p. 16, pl. 11, figs. 5, 7.
 1937 *Hystrichosphaera ramosa* (Ehr.); Lejeune, *Ann. Soc. Geol. Belg.* 60, B239–B260, pl. 1, figs. 1–4; pl. 2, figs. 5–10.
 1955 *Hystrichosphaera ramosa* (Ehr.); Deflandre and Cookson, pp. 263–4, pl. 2, fig. 1; pl. 5, fig. 6; pl. 6, fig. 1.
 1961 *Hystrichosphaera ramosa* (Ehr.); Gerlach, *N. Jb. Geol. Pal.* 112, 175, pl. 27, fig. 3.

Comment. Since writers such as Deflandre and Lejeune have stressed the difficulty of distinguishing *H. ramosa* from *H. furcata* it is with some diffidence that we record the occurrence of *H. ramosa* in the Cambridge deposits. The form so designated is consistently larger, has thicker-walled appendages, more strongly outlined fields, and wider membranes subtending the appendages than those referred to *H. furcata*. In these features the Cambridge specimens tend towards *H. wetzeli* Deflandre but differ from this species in that the appendages of the posterior part are radially arranged and not parallel to the long axis of the shell as Deflandre (1937) described them to be in *H. wetzeli*.

Occurrence. In Upper Gault, Greensand, and Chalk Marl.

Genus ACHOMOSPHAERA Evitt 1963

Achomosphaera ramulifera (Deflandre)

Plate 9, fig. 10

- 1935 *Hystrichosphaera* cf. *ramosa* Deflandre, *Bull. Biol.* 49, pl. 5, fig. 11.
 1937 *Hystrichosphaeridium ramuliferum* Deflandre, p. 26, pl. 14, figs. 5, 6; pl. 17, fig. 10.
 1952 *Hystrichosphaeridium ramuliferum* Deflandre; W. Wetzel, *Geol. Jb.* 66, 398, pl. A, fig. 9.
 1959 *Hystrichosphaeridium ramuliferum* Deflandre; Gocht, p. 71, pl. 3, fig. 9.
 1961 *Hystrichosphaeridium ramuliferum* Deflandre; Gerlach, *N. Jb. Geol. Paläont.* 112, 185, pl. 28, fig. 3.
 1963 *Achomosphaera ramulifera* (Defl.) Evitt.

Comment. Three specimens that appear to be referable to *A. ramulifera* have been recorded. Their appendages, although possibly somewhat shorter than those of the French types, are similarly branched and the shape of both shell and pylome is identical.

The sculpture of the shell-membrane, unfortunately not mentioned in the original description of *H. ramuliferum*, appears to be identical with that of the specimen illustrated by Deflandre on plate 14, fig. 6. Gocht (1959) in recording *H. ramuliferum* from German Neocomian deposits makes no mention of the development of surface sculpture whilst Gerlach (1961) indicates that in her Tertiary specimens the membrane is finely reticulate or unpatterned. Such an inclusion of smooth and sculptured shells in one species at once raises the question as to whether surface sculpture, evident in the one specimen of Deflandre's referred to above and indicated by dotting in his two other figures, should be regarded as a specific character. In the Cambridge specimens the pattern which has been constant and strongly developed and may even extend to the undivided portion of the appendages seems to be composed of small thickened areas of varying sizes and shapes separated by shallow grooves.

Occurrence. Greensand, CG3, CG4.

Genus CANNOSPHAEROPSIS O. Wetzel 1933
cf. *Cannosphaeropsis densa* Cookson and Eisenack 1962

Plate 10, fig. 4

Comment. The incomplete figured specimen was the only one of this type recovered from the Cambridge samples. The shell is somewhat smaller and the investing network less dense and prominent than in *C. densa* from ?Albian-Cenomanian of the Perth Basin, Western Australia. The straight or curved peripheral spine-like branches agree with those of *C. densa*.

Occurrence. Chalk Marl, CG8.

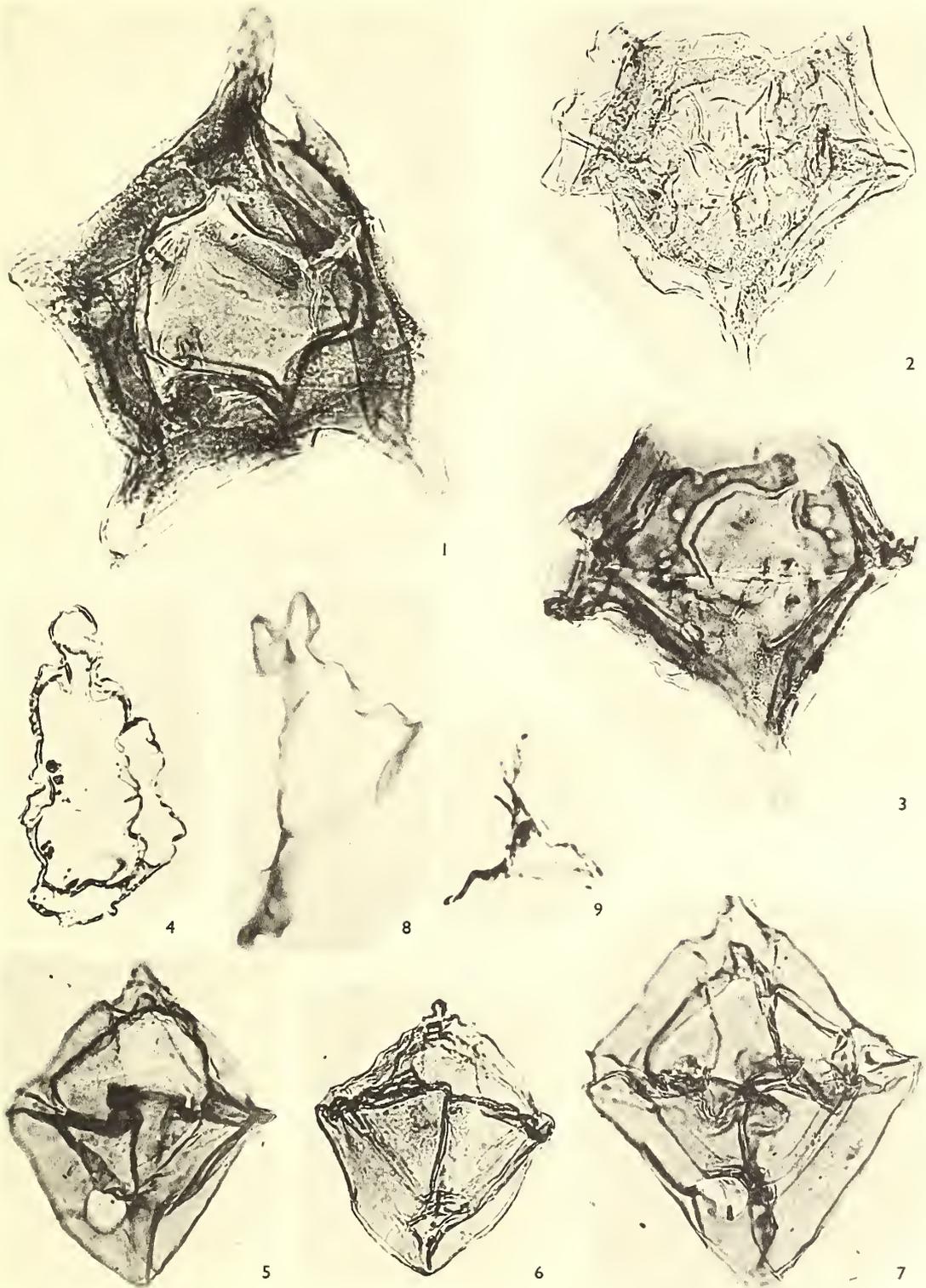
Family HYSTRICHOSPHAERIDIACEAE Evitt 1963
Genus HYSTRICHOSPHAERIDIUM Deflandre 1937
Hystrichosphaeridium complex (White)

Plate 9, fig. 6

- 1842 *Xanthidium tubiferum complex* White, *Micr. J.* **2**, pl. 14, fig. 11; 1844, *Trans. Micr. Soc.* **1**, 83, pl. 8, fig. 10.
1940 *Hystrichosphaeridium elegantulum* Lejeune-Carpentier, *Ann. Soc. Geol. Belg.* **63**, B222, figs. 11-12.
1946 *Hystrichosphaeridium complex* (White); Deflandre, *C.R. Soc. Géol. Fr.* 111.
1953 *Hystrichosphaeridium tubiferum*; Cookson, *Mem. Nat. Mus. Victoria*, **18**, 113, pl. 2, fig. 24.

EXPLANATION OF PLATE 7

- Figs. 1-4. *Pseudoceratium dettmannae* sp. nov. 1, Holotype, CG8; K5173, OR39.7 118.8, \times 500. 2, CG3; K5176, OR34.4 119, \times c. 500. 3, 59/11/12; K5175, OR52.6 120.2, \times c. 500. 4, Oblique section, CG3; K5177, OR40.5 125.5, \times 625.
Fig. 5-9. *Scriniodinium campanula* Gocht, CG3. 5, K5181, OR36.7 117.5, \times 500. 6, K5180, OR40.3 116, \times 500. 7, K5178, OR36.5 119.2, \times c. 500. 8, Longitudinal section; K5179, OR27.9 124.9, \times 850. 9, Transverse section; K5182, OR35 115.5, \times 500.



COOKSON and HUGHES, Mid-Cretaceous microplankton

- 1955 *Hystrichosphaeridium complex* (White); Deflandre and Cookson, p. 270, pl. 1, figs. 9, 10
 1956 *Hystrichosphaeridium* cf. *elegantulum* Lejeune-Carpentier; Weiler, *N. Jb. Geol. Paläont.* **104**, 140, pl. 12, figs. 7, 8; pl. 13, fig. 1.
 1958 *Hystrichosphaeridium complex* (White); Cookson and Eisenack, p. 42, pl. 12, fig. 10.
 1959 *Hystrichosphaeridium complex* (White); Gocht, p. 66, pl. 3, figs. 2, 3.

Comment. Since *H. complex* was first described from English Upper Cretaceous deposits it is not surprising that examples of it have been recovered from most of the Cambridge Albian and Cenomanian samples examined. In addition to the European occurrences referred to above, *H. complex* is widely distributed in Australian Aptian and Albian deposits.

Occurrence. Upper Gault, CG1, 59/11/14; Greensand, 59/11/11, MD1; Chalk Marl, 59/12/5, CG8.

Hystrichosphaeridium recurvatum (White) subsp. *polypes* Cooks. and Eisenack 1962

Plate 9, fig. 14

Comment. A few specimens have been observed in the Cambridge Greensand which agree with those occurring in Australian Cretaceous deposits upon which the subspecies *polypes* at present stands. All have many more appendages than typical examples of *H. recurvatum* and the 'hair-like' branches of the apical processes noted for the Australian examples have been seen. The wide geographical distribution of this subspecies demonstrated by the present record suggests that when better known this form will prove to be specifically distinct from *H. recurvatum*.

Occurrence. Upper Gault, CG2; Greensand, 59/11/12, 59/11/11, 59/11/9; Chalk Marl, 59/12/5.

Hystrichosphaeridium ancoriferum Cookson and Eisenack 1960a

Plate 9, fig. 7

Comment. Specimens which agree with *H. ancoriferum* from ?Upper Albian–Cenomanian deposits in Western Australia are common in the Cambridge deposits. Sometimes they are rather difficult to distinguish from the larger of the specimens of *Chlamydophorella nyei* Cookson and Eisenack 1958 with which they are frequently associated but usually their appendages are distinctly coarser than those of *C. nyei*, and they lack the outer membrane of this form.

Occurrence. Upper Gault, CG2, 59/11/14; Greensand, 59/11/12, CG3, CG4, CG10; Chalk Marl 59/12/5, 59/11/7, CG8.

Hystrichosphaeridium arundum Eisenack and Cookson 1960

Plate 9, fig. 16

Comment. Several specimens which approximate closely to the Australian Albian species *H. arundum* have been observed in preparations of one sample. The features in which they are in agreement with the Australian examples are the size and granular surface of the shell, the tubular form of the appendages, and the variability of their shape and size in one and the same example. The appendages of the Cambridge forms have either straight or slanting sides and some of the smaller ones are sharply conical. The presence

of the latter type was not noted in the description of *H. arundum* but in the present state of our knowledge this feature scarcely seems to be of diagnostic significance. The average diameter of six of the Cambridge shells is $33\ \mu$ and their overall diameter $51\ \mu$.

Occurrence. Upper Gault, CG2.

Hystrichosphaeridium siphoniphorum Cookson and Eisenack 1958

Plate 9, fig. 15

Comment. The Cambridge specimens agree closely with the type and other examples of *H. siphoniphorum* from ?Albian–Cenomanian deposits in the Perth Basin and deposits of approximately the same age in north-west Western Australia.

Occurrence. Upper Gault, CG2, 59/11/14; Greensand, 59/11/12, CG3, CG4, CG10, 59/11/11, MD1; Chalk Marl, 59/12/5, 59/11/7, CG8.

Hystrichosphaeridium stellatum Maier 1959

Plate 9, fig. 11

Comment. A few specimens conform to Maier's species and compare well with specimens from Western Australian Albian to Cenomanian deposits, recently referred to it by Cookson and Eisenack (1962).

Occurrence. Upper Gault, CG1, CG2; Greensand, CG3, 59/11/12; Chalk Marl, CG8.

Family INCERTA

Genus CARPODINIUM Cookson and Eisenack 1962

Carpodinium obliquicostatum sp. nov.

Plate 6, figs. 1–6

Diagnosis. Shell elongate-oval, divided almost equally by a circular girdle evident as lateral indentations $2\text{--}3\ \mu$ deep. Epitheca with a short tapering horn which arises from the outer membrane. Plates elongate, bordered by relatively high sutures with serrate edges; indications of an antapical plate have been seen and a large quadrangular pylome (pre-cingular archaeopyle) and longitudinal furrow are clearly evident in one specimen (Pl. 6, figs. 4, 5). The surface pattern of the plates provides the most distinctive specific feature; it consists of roughly triangular areas of variable size and shape which lie more

EXPLANATION OF PLATE 8

Figs. 1–3, *Cunningia minor* sp. nov., $\times 500$. 1, Holotype, CG10; K5184, OR37.9 119.2. 2, CG10; K5187, OR55.5 120. 3, CG10; K5183, OR 35.4 111.4. 5, CG10; K5185, OR43.8 109.8.

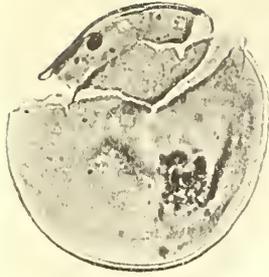
Fig. 4, *Cunningia?* sp., $\times 500$. CG2; K5186, OR29 116.

Figs. 6–8, *Palaeoperidinium spinosum* sp. nov. 6, CG3; K5189, OR42.9 125, $\times 500$. 7, CG3; K5193, OR42.4 118.6, $\times c.$ 500. 8, Holotype, 59/11/9; K5188, OR48 122.5, $\times 875$.

Figs. 9–17, *Stephodinium europaicum* sp. nov., 59/11/12. 9–12, Holotype rotated to various positions but mounted as in 12; K5190, OR41.5 115.4, $\times c.$ 500. 13, K5192, OR30 120, $\times 750$. 14, K5191, OR32 129, $\times c.$ 500. 15–17, Specimens rotated; K 5235, $\times c.$ 500. 15, Antapical view, high focus. 16, Low focus. 17, Oblique view.



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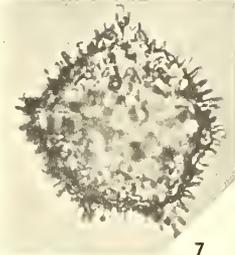
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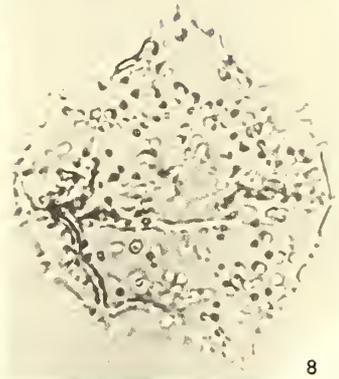
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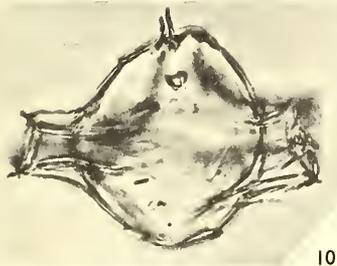
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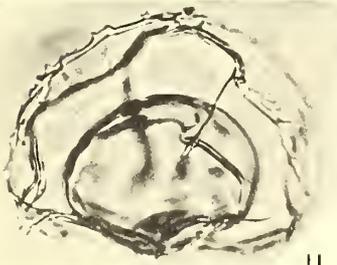
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or less obliquely to the long axis of the shell and are delimited by narrow anastomosing grooves.

Holotype. Plate 6, fig. 1; K5165, Upper Gault (CG1).

Dimensions. Holotype 73 μ long, 50 μ broad. Range 59–80 μ long, 36–50 μ broad.

Occurrence. Upper Gault, CG1, 59/11/14; Greensand, 59/11/12, CG3, CG4, 59/11/11, MD1, 59/11/9; Chalk Marl, 59/12/5, 59/11/7, CG8.

Comment. The general form and size of *C. obliquicostatum* is similar to that of the type species *C. granulatum* Cooks. and Eisenack 1962 from Australian Aptian and Albian deposits, but the two species are readily distinguishable by their surface patterns. *C. granulatum* has not, as yet, been recovered from Cenomanian deposits.

Genus PALAEOPERIDINIUM Deflandre 1935

Palaeoperidinium castanea Deflandre 1935

Plate 5, fig. 14

1935 *Palaeoperidinium castanea* Deflandre, *Bull. Biologique*, 49, 228, pl. 5, fig. 8; *Ann. Paléont.* 25, 29, pl. 6, figs. 1–4.

1962 *Palaeoperidinium castanea* Deflandre; Cookson and Eisenack, pl. 3, figs. 9–11.

Comment. Specimens agreeing closely with Deflandre's description of *P. castanea* from the French Senonian or Turonian have been recovered in small numbers. They have a helicoid girdle, the shell is ornamented with short spines and, as in the French specimens, the pylome extends from just beneath the apex to the girdle. Similar forms have recently been recorded by Cookson and Eisenack (1962) from Western Australian deposits of ?Aptian–Albian to Cenomanian age.

Occurrence. Upper Gault, 59/11/14; Greensand, 59/11/12, CG3; Chalk Marl, 59/11/7, CG8.

Palaeoperidinium spinosum sp. nov.

Plate 8, figs. 6–8

Diagnosis. Shell with convex sides, an arched apex with a slight central prominence, a slanting antapex, a shallow, circular, equatorial girdle, and a short, rather ill-defined longitudinal furrow. A capsule is not developed. Shell-membrane thin, covered with short, blunt, hollow outgrowths c. 2 μ long which usually give the wall a scalloped appearance. The shell opens by the detachment of the distal portion of the epitheca.

Holotype. Plate 8, fig. 8; K5188, Cambridge Greensand, 2 ft. above base (59/11/9).

Dimensions. Holotype; overall length 55 μ , overall breadth 46 μ . Range 55–67 μ long, 38–50 μ broad.

Occurrence. Greensand, CG4, MD1, 59/11/9; Chalk Marl, 59/11/7.

Comment. The genus *Palaeoperidinium* has been used for this species in the general sense in which it was created by Deflandre. *P. spinosum* resembles *P. caulleryi* Deflandre (1934) in its small size, the type of ornament, the scalloped shell outline, and the development of a slight projection on one side of the antapex. It differs, however, in having a denser ornamentation, a circular instead of helicoid girdle, and a less pronounced apical

prominence. The mode of opening of the shell in *P. caulleryi* was not specified by Deflandre.

Palaeoperidinium spinosum has not been generically associated with *Spinidinium* Cookson and Eisenack 1962, to the description of which it conforms in several respects, on account of its different mode of opening. In the type species *S. styloniferum* a pylome is present in the epitheca, in contrast to the detachment of the apex in *P. spinosum*.

Genus STEPHODINIUM Deflandre 1936

Stephodinium europaeicum sp. nov.

Plate 8, figs. 9–17

Diagnosis. Shell broadly oval with a definite surface tabulation composed of plates of varying sizes delimited by low, narrow ledges. An equatorial girdle incompletely encircles the shell leaving an untabulated area on the ventral surface which appears to represent a longitudinal furrow (Pl. 8, fig. 10). The girdle is bounded by two conspicuous flanges which extend from the shell in a plane at right angles to the longitudinal axis; the ledges of the pre- and post-equatorial plates adjacent to the girdle run radially across the flanges to their margins.

The exact tabulation has not been determined. Almost certainly there is a single four- or ?five-sided antapical plate (Pl. 8, fig. 13) and probably one four or ?five-sided apical plate from which a short horn projects (Pl. 8, fig. 14). A large and strongly outlined plate, comparable in position with plate 3" of many other dinoflagellates, extends on the dorsal surface from the apical plate to the margin of the pre-equatorial flange (Pl. 8, figs. 11, 12, 15). This plate, which marks the position of the pylome, widens considerably towards the girdle.

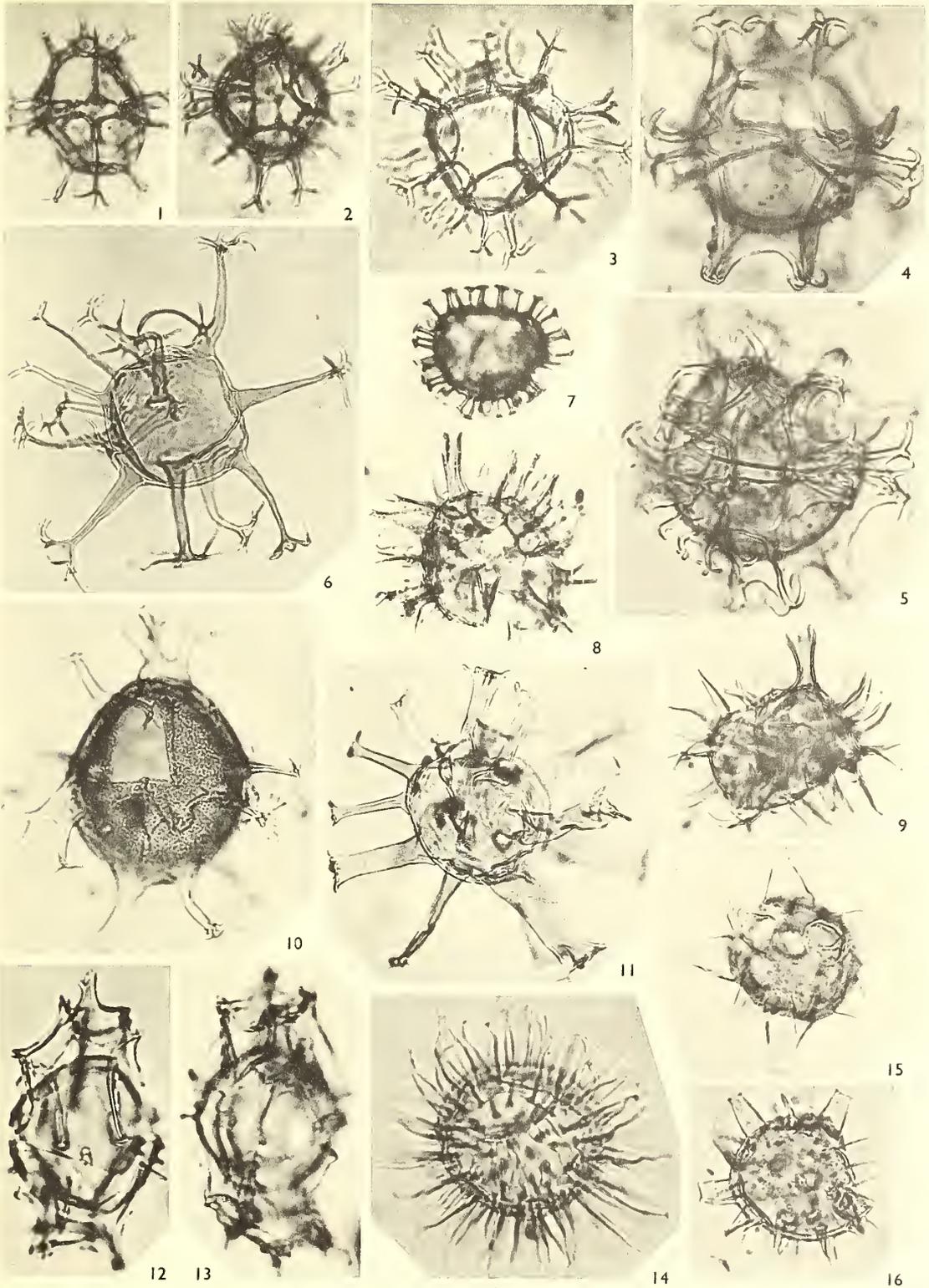
The shell-membrane is thin and smooth, except at the margins of the girdle-flanges which are minutely serrated.

Holotype. Plate 8, figs. 9–12; K5190, Cambridge Greensand (59/11/12).

Dimensions. Holotype body 59 μ long, horn 5 μ , body breadth 75 μ , overall breadth 46 μ . Range, body 52–60 μ long, 42–52 μ broad, overall breadth 67–78 μ .

EXPLANATION OF PLATE 9

- Figs. 1–5. *Hystrichosphaera* spp. 1, *H. furcata* (Ehr.) O. Wetzel, CG4; K5194, OR46 112.6, \times 500-2, *H. furcata*, CG3; K5195, OR50.6 123.8, \times 500. 3, *H. cf. furcata*, CG4; K5233, OR47.8 118, \times 500-4-5, *H. ramosa* (Ehr.) O. Wetzel, CG3, \times 500. 4, K5197, OR46 121. 5, K5196, OR37.2 118.4.
- Fig. 6. *Hystrichosphaeridium complex* (White), CG8; K5202, OR42.8 117, \times 400.
- Fig. 7. *H. ancoriferum* Cooks. and Eisenack, 59/11/14; K5212, OR29.8 114.4, \times c. 500.
- Figs. 8–9. *Coronifera oceanica* Cooks. and Eisenack, \times 500. 8, CG1; K5200, OR4 5117.8. 9, 59/11/12; K5201, OR47.7 121.
- Fig. 10. *Achomosphaera ramulifera* (Defl.), CG3; K5213, OR34.4. 115.8, \times 500.
- Fig. 11. *Hystrichosphaeridium stellatum* Maier, CG3; K5204, OR38.1 119.3, \times 500.
- Figs. 12, 13. cf. *Rottnechia borussica* (Eisenack), \times c. 700. 12, Dorsal aspect, CG4; K5208, OR54 111.5. 13, Ventral aspect, CG3; K5195, OR47.6 127.
- Fig. 14. *Hystrichosphaeridium recurvatum* subsp. *polypes* Cooks. and Eisenack, 59/11/9; K5211, OR30.1 122.4, \times c. 500.
- Fig. 15. *H. siphoniphorum* Eisenack and Cookson, 59/11/7; K5207, OR37.3 116.4, \times 500.
- Fig. 16. *H. arundum* Eisenack and Cookson, CG2; K5206, OR 33.7 113.6, \times c. 500.



COOKSON and HUGHES, Mid-Cretaceous microplankton

Occurrence. Upper Gault, CG1, 59/11/14; Greensand, 59/11/12, CG3, CG4, 59/11/11, MD1; Chalk Marl, 59/11/7, CG8.

Comment. In its general form and size *Stephodinium europaicum* conforms to Deflandre's species *S. coronatum*. However, as the description of this species was based on a single specimen preserved in a flint (?Senonian) it is not possible to compare the Cambridge forms with it.

Another species *S. australicum*, of comparable geological range, was recently described by Cookson and Eisenack (1962). All the available specimens of *S. australicum* were considerably flattened and in consequence difficult to interpret. However, in spite of some still existing uncertainties regarding the morphology of *S. australicum* there is no doubt that it is specifically distinct from *S. europaicum*.

S. europaicum is of special interest in that it completely confirms the dinoflagellate affinities of *Stephodinium* originally suggested by Deflandre, and gives a more accurate idea of the orientation of the shell than was previously possible. Furthermore, it provides the first clear evidence of the existence of a system of tabulation in a member of the genus as well as the presence of a transverse girdle previously postulated by Deflandre.

Unfortunately gaps in our knowledge still remain owing to the delicate nature of the shells and their consequent distortion and preferred orientation in permanent mounts. Most of the details and photographs had to be obtained from a few fully expanded examples that were removed for examination to hollow slides containing 50 per cent. glycerine solution, and later mounted in glycerine jelly.

Genus PSEUDOCERATIUM Gocht 1957

Pseudoceratium turneri Cookson and Eisenack 1958

Plate 6, fig. 7

Comment. Several examples referable to *P. turneri* have been recovered from the lowest part of the Cambridge Greensand. All agree in size, shape, and surface ornament with the Australian Aptian-Albian species. In this species the external processes usually unite forming lamella-like membranes which coalesce to form a net-like pattern, the meshes of which are of variable size and shape. In the German Neocomian species *P. pelliferum* Gocht 1957 the processes comprising the ornament are free from one another.

Occurrence. Greensand, 59/11/12.

Pseudoceratium dettmannae sp. nov.

Plate 7, figs. 1-4

Diagnosis. Shell approximately four-sided with a longish straight-sided apical horn and a short projection at each of the three angles. Indications of a \pm circular girdle occur in most specimens. The shell opens by the detachment of an apical segment along a straight or slightly oblique line. The surface of the shell is scabrate except for a relatively wide finely pitted band that encircles both dorsal and ventral surfaces. Transverse sections (cut by Dr. Mary Dettmann) have shown that the shell-membrane is two-layered, the two layers being in contact and traversed by elongated pits in the region of the pitted band mentioned above and widely separated from one another in the unpitted portions of the membrane.

Holotype. Plate 7, fig. 1; K5173, Cambridge Greensand (CG3).

Dimensions. Holotype $180 \times 150 \mu$. Range $104\text{--}132 \mu$ long, $78\text{--}99 \mu$ broad, horn *c.* 31μ .

Occurrence. Greensand, 59/11/12, CG3, CG4, MD1; Chalk Marl, 59/12/5.

Comment. Our reason for referring this species to *Pseudoceratium* is its superficial resemblance to *P. ludbrookii* (Cookson and Eisenack 1958) which was removed from *Ceratocystidiopsis* Deflandre by Eisenack (1961). However, at present we do not know whether the structure of the Cambridge species, as revealed by thin sections, is similar to that of either *P. ludbrookii* or the other species of *Pseudoceratium*.

Another important question that arises from the present investigation is whether or not a capsule is present in *P. dettmannae* or even in *P. ludbrookii* as was stated in the description of this species. As far as *P. dettmannae* is concerned the fact that the pits extend without a break through the entire wall of the pitted area rather suggests that the separation and development of 'air-spaces' in the intervening unpitted portions of the wall is not connected with the development of an internal capsule.

Genus APTEODINIUM Eisenack 1958

Apteodinium grande sp. nov.

Plate 6, figs. 8, 9

Diagnosis. Shell large, almost circular in outline with a lightly defined circular girdle; epitheca with a short median solid horn which in perfect specimens narrows towards a small bifurcate tip, although sometimes, as in the type, only the basal part of the horn remains. A large hoof-shaped pylome extends from the girdle to a short-distance beneath the horn. Shell-membrane about $2\text{--}4 \mu$ thick, minutely pitted, and of spongy texture.

Holotype. Plate 6, fig. 9; K5170, Cambridge Greensand (59/11/11).

Dimensions. Holotype, overall length 153μ , breadth 138μ , pylome $52 \times 57 \mu$. Range, overall length $111\text{--}153 \mu$, breadth $99\text{--}138 \mu$, horn $13\text{--}17 \mu$ long, wall $2\text{--}4 \mu$ thick.

Occurrence. Upper Gault, 59/11/14; Greensand, 59/11/12, MD1, 59/11/11; Chalk Marl, 59/12/5, 59/11/7.

Comment. *Apteodinium grande* is distinguishable from the German Aptian species *A. granulatum* Eisenack 1958 by its consistently larger size and the pitted character of its wall. It differs from the Australian Aptian-Albian species *A. maculatum* Eisenack and Cookson 1960 both in size and the absence of the small thickened areas with circular outlines that gives *A. maculatum* its characteristic appearance.

Genus ODONTOCHITINA Deflandre 1935

Plate 11, fig. 9

Comment. The genus *Odontochitina* is well represented in the Cambridge deposits, particularly so in the upper portion of the Gault. During this work no attempt has been made to identify specifically the individual types present. However, it is almost certain that these include the European Lower and Upper Cretaceous species *O. operculata*

(*O. Wetzel*) also recorded from Australia (Deflandre and Cookson 1955) and less certainly *O. striatoperforata* Cookson and Eisenack 1962 from ?Albian to Cenomanian deposits in Western Australia and possibly the closely related German species *O. costata* Alberti 1961.

Genus *ROTTNESTIA* Cookson and Eisenack 1961a
cf. *Rottnestia borussica* (Eisenack) 1954

Plate 9, figs. 12, 13

1954 *Hystrichosphaera borussica* Eisenack, pl. 9, figs. 5–7.

1955 *Hystrichosphaera borussica* Eisenack; Deflandre and Cookson, p. 268, pl. 5, figs. 9, 10.

1961a *Rottnestia borussica* (Eisenack); Cookson and Eisenack, pp. 41–42, pl. 2, figs. 1, 2; figs. a–d.

Comment. Some specimens resembling the Tertiary species *Rottnestia borussica* occur sparingly in the Cambridge samples. Taken as a whole the fields composing their surface tabulation are not so completely delimited as they are in *R. borussica* but considerably more so than in the apparently related species *Hystrichosphaera ovum* as illustrated by Deflandre (1937). The apical expansion is surmounted by a short median horn and the ledges outlining the fields have serrated edges; short forked appendages occur at the corners of the fields.

Occurrence. Greensand, 59/11/12, CG3, CG4; Chalk Marl, 59/12/5, 59/11/7.

Genus *BROOMEA* Cookson and Eisenack 1958
Broomea cf. *jaegeri* Alberti 1961

Plate 11, fig. 10

Comment. Three specimens referable to the genus *Broomea*, one complete (Pl. 11, fig. 10) and two represented only by their antapices, have been recovered. This genus was originally established on specimens from Jurassic deposits in north-west Western Australia and New Guinea, and subsequently recorded by Alberti (1961) from German Hauterivian and Lower Aptian sediments. The Cambridge specimens, although not identical with Alberti's figured examples of *B. jaegeri*, have been compared with this species firstly because their antapical horns are more sharply pointed than those of the Australian and New Guinea species *B. simplex* Cookson and Eisenack 1958 which they also resemble, and secondly because of their closer palaeogeographical and stratigraphical proximity.

Occurrence. Upper Gault, 59/11/14; Greensand, CG3.

Genus *HEXAGONIFERA* Cookson and Eisenack 1961
Hexagonifera chlamydata Cookson and Eisenack 1962

Plate 10, figs. 7–9

Comment. Specimens which are identical in all respects with those recorded from ?Upper Albian–Cenomanian deposits in Western Australia are widely distributed in the Cambridge deposits. As in the Australian examples the shells open by the removal of a six-sided portion of the wall at one end and are completely or partially enclosed in a smooth,

transparent outer membrane. The sculpture of the shell itself also varies from finely granular to verrucose.

Occurrence. Upper Gault, CG1, CG2, 59/11/14; Greensand, 59/11/12, CG3, CG4, CG10, 59/11/11, 59/11/9; Chalk Marl, 59/11/7.

Genus CHLAMYDOPHORELLA Cookson and Eisenack 1958

Chlamydoaphorella nyei Cookson and Eisenack 1958

Plate 6, fig. 12

Comment. *C. nyei* is one of the commonest types in these Cambridge deposits. Most of the examples, like their Australian counterparts, are seen in apical or antapical views. However, a few have been observed in lateral view (Pl. 6, fig. 12), including occasional shells in course of opening by the detachment of the apical region (Cookson and Eisenack 1962, pl. 7, fig. 16). As far as we know *C. nyei* has not previously been recorded from extra-Australian deposits. Its known geological range in Australia is from Aptian to Cenomanian.

Occurrence. Frequent in all samples examined.

Genus KALYPTEA Cookson and Eisenack 1960b

Kalyptea monoceras Cookson and Eisenack 1960

Plate 11, fig. 7

Comment. The figured specimen is one of two specimens that can be referred to *Kalyptea monoceras*. Others which appear to be comparable with them occur in samples CG1, CG4, CG10. However, although each of the latter consists of an approximately oval shell of comparable size which is enclosed in the characteristic kalyptean diaphanous 'veil', none has shown the slender horn of the figured specimen and of the type and paratype of *K. monoceras*. The present record of this Australasian species in Britain is of palaeogeographical interest.

Occurrence. Greensand, 59/11/12.

Genus FROMEA Cookson and Eisenack 1958

Fromea amphora Cookson and Eisenack 1958

Plate 10, fig. 3

EXPLANATION OF PLATE 10

Figs. 1, 2. *Baltisphaeridium hirsutum* (Ehr.), CG8. 1, K5221, OR39.5 126.4, \times 500. 2, Sculpture detail \times c. 1500.

Fig. 3. *Fromea amphora* Cooks. and Eisenack, 59/11/14; K5219, OR42.1 124.2, \times c. 500.

Fig. 4. cf. *Cannosphaeropsis densa* Cooks. and Eisenack, CG8; K5218, OR32.7 115.6, \times 500.

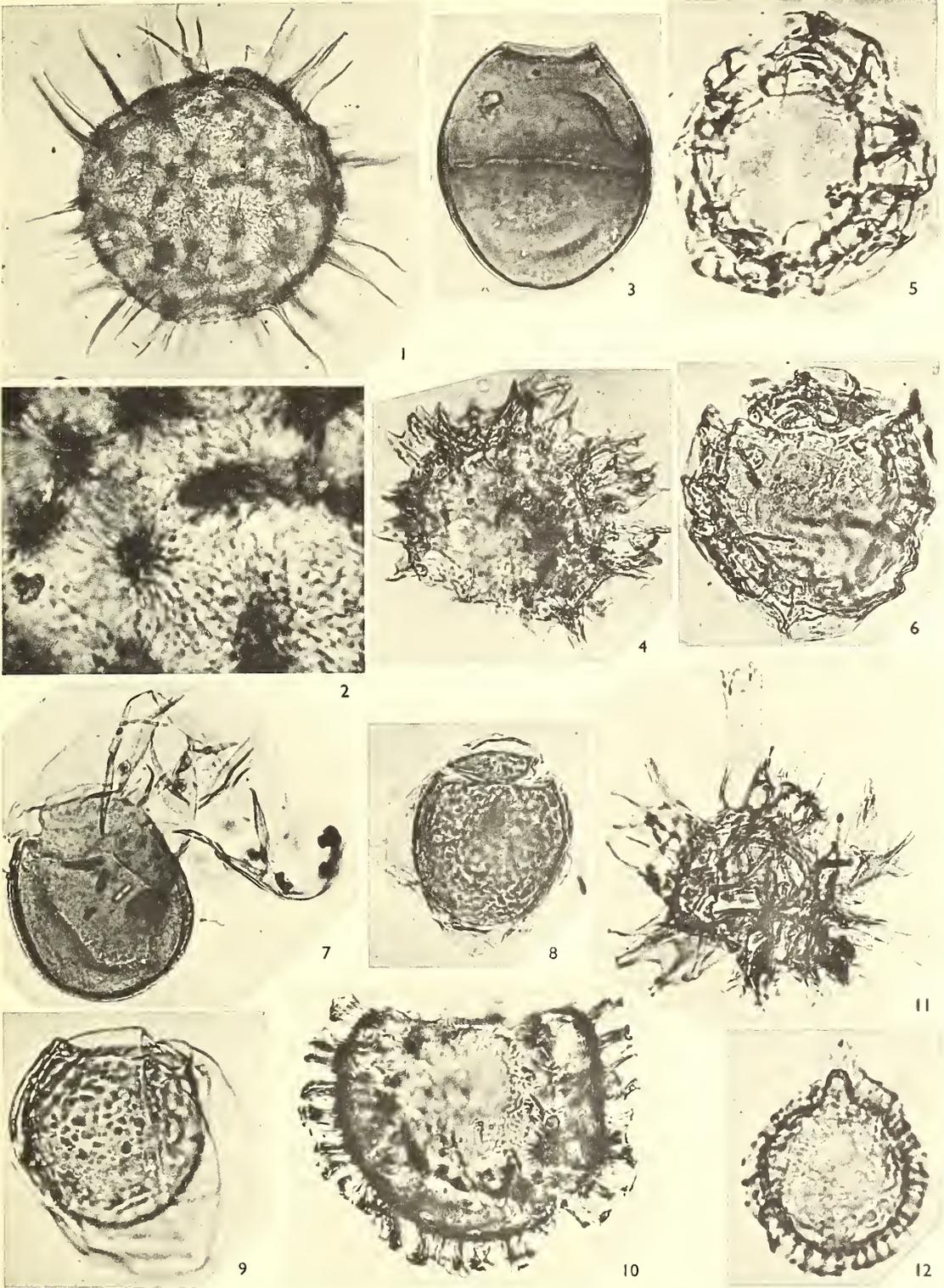
Figs. 5, 6. *Cyclonephelium membraniphorum* Cooks. and Eisenack, \times 500. 5, 59/11/7; K5215, OR35.5 119. 6, CG8; K5157, OR48 119.7.

Figs. 7-9. *Hexagonifera chlamydata* Cooks. and Eisenack. 7, CG3; K5216, OR49.7 118.8, \times c. 500. 8, CG8; K5221, OR36.7 109, \times 500. 9, 59/11/9; K5217, OR54.4 126.9, \times c. 800.

Fig. 10. *Cyclonephelium* cf. *densebarbatum* Cooks. and Eisenack, 59/11/9; K5209, OR59 127.8, \times 500.

Fig. 11. *Baltisphaeridium ferox* Deflandre, CG3; K5205, OR40.3 116.3, \times 500.

Fig. 12. *Chlamydoaphorella nyei* Cooks. and Eisenack, CG3; K5220, OR40.5 117, \times c. 800.



COOKSON and HUGHES, Mid-Cretaceous microplankton

Comment. Typical examples of *Fromea amphora* are sparsely represented in the samples mentioned. All have shown the equatorial 'girdle' so clearly indicated in the holotype and since seen by one of us (I. C. C.) in a relatively large number of Western Australian Albian and Cenomanian examples. The present stratigraphical range of *F. amphora* in Australia is from the Aptian to Cenomanian. Recently the same species was recorded by Alberti (1961) from Barremian deposits in Germany.

Occurrence. Upper Gault, CG1, 59/11/14; Greensand, MD1; Chalk Marl, 59/11/7.

Group INCERTAE SEDIS

Group ACRITARCHA Evitt 1963

Subgroup ACANTHOMORPHITAE Downie, Evitt, and Sarjeant 1963

Genus BALTISPHAERIDIUM Eis. emend. Downie and Sarjeant 1963

Baltisphaeridium hirsutum (Ehr.)

Plate 10, figs. 1, 2

- 1836 *Xanthidium hirsutum* Ehrenberg, *Abh. Kgl. Akad. Wiss. Berlin* (1838).
 1935 *Hystrichosphaera hirsuta* (Ehr.); Deflandre, *Bull. Biol.* **69**, pl. 9, fig. 4.
 1936 *Hystrichosphaeridium hirsutum* (Ehr.); Deflandre, *Ann. Paléont.* **26**, 30.
 1941 *Hystrichosphaeridium hirsutum* (Ehr.); Lejeune-Carpentier, *Ann. Soc. Geol. Belg.* **64**, B71-92, figs. 1-9.
 1963 *Baltisphaeridium hirsutum* (Ehr.); Downie and Sarjeant, p. 91.

Comment. In referring the relatively numerous and conspicuous Cambridge specimens of the *B. hirsutum* type to *B. hirsutum* itself the difficulty of distinguishing this form from the closely related species *B. cf. spinosum* (White), *B. spinosum* (White), *B. spinosum* var. *deflandrei* Lejeune-Carpentier, *B. pseudhystrichodinium* Deflandre, as reviewed by Lejeune-Carpentier (1941) has been borne in mind. However, the appendages of the Cambridge examples agree closely with those of *B. hirsutum* and divided ones occur in most specimens. The surface pattern of the shells (Pl. 10, fig. 2) is that of all members of the 'hirsutum' group.

Occurrence. Upper Gault, CG1, 59/11/14; Greensand, 59/11/12, CG3, CG4, CG10, 59/11/11, MD1, 59/11/9; Chalk Marl, 59/12/5, CG8.

Baltisphaeridium ferox (Deflandre) Downie and Sarjeant 1963

Plate 10, fig. 11

Comment. Specimens referable to *Hystrichosphaeridium ferox* as originally described by Deflandre (1937) from ?Senonian flints of the Paris Basin and subsequently recorded from the German Lower Cretaceous (Eisenack 1958, Gocht 1959) have been recovered from the Cambridge sediments. Comparable forms have also been recently reported from Western Australian ?Albian-Cenomanian deposits (Cookson and Eisenack 1962). In three of the Cambridge examples (e.g. Pl. 6, fig. 11) one of the larger appendages is longer, narrower, and less deeply divided than the others, a feature that is reminiscent of the 'tubular horn' of *Corouifera oceanica* Cookson and Eisenack 1958.

Occurrence. Upper Gault, CG2; Greensand, 59/11/12; Chalk Marl, 59/12/5, 59/11/7, CG8.

Genus CORONIFERA Cookson and Eisenack 1958
Coronifera oceanica Cookson and Eisenack 1958

Plate 9, figs. 8, 9

Comment. Several specimens identical in most respects with the holotype of *C. oceanica* Cookson and Eisenack (1958, pl. 12, fig. 6) have been observed. All agree with the type in having a prominent tubular horn with a toothed or fringed apex at one end of the shell, numerous fine, pointed, simple or bifurcate, flacid appendages, and a granular shell-membrane. The stiff spine mentioned in the specific description as occurring at the opposite end of the shell has not been apparent in the Cambridge specimens. One of the latter with fewer appendages than is usual shows clearly that their bases are united forming a net-like pattern (Pl. 9, fig. 8). *Coronifera oceanica* was originally described from two Western Australian Albian deposits. The specimen from the German Upper Aptian deposit (Eisenack 1958) has fewer and apparently larger appendages.

Occurrence. Upper Gault, CG1, 59/11/14; Greensand, 59/11/12, 59/11/9.

Subgroup POLYGONOMORPHITAE Downie, Evitt, and Sarjeant 1963
 Genus VERYHACHIUM Deunff 1954 emend. Downie and Sarjeant 1962
Veryhachium reductum (Deunff 1958)

Plate 11, fig. 8

- 1958 *Veryhachium trisulcum* (Deunff 1952) var. *reductum* Deunff, *Bull. Soc. Geol. et Min. Bretagne*, n.s. 2, 27, pl. 1, figs. 1, 3, 8, 10, 12, 14, 16, 17, 22, 23.
 1961 *Veryhachium reductum* (Deunff 1958) Jekhowsky, *Rev. Micropaléont.* 3, 210–12, pl. 2, figs. 22–37.
 1961 *Veryhachium reductum* (Deunff); Brosius and Bitterli, *Bull. Ver. Schweizer. Petrol-Geol.-Ing.* 28, 36, pl. 1, figs. 3–6.
 1962 *Veryhachium reductum* (Deunff); Cookson and Eisenack, 8, 492, pl. 4, fig. 16.

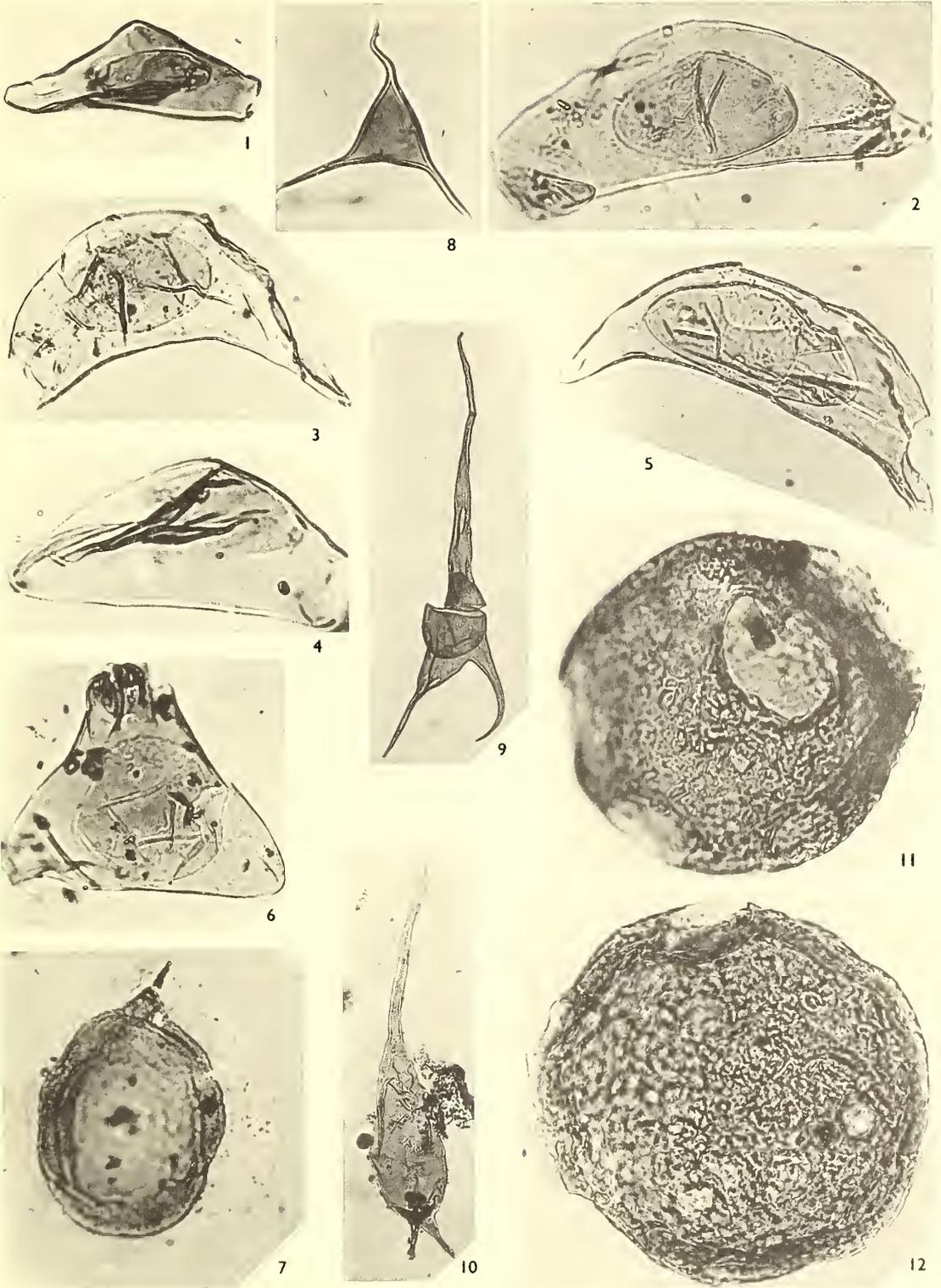
Comment. Occasional specimens, similar to the one figured, have been observed in preparations of most of the Cambridge samples.

Subgroup DINETROMORPHITAE Downie, Evitt, and Sarjeant 1963
 Genus DIPLOTESTA Cookson and Eisenack 1960
Diplotesta anglica sp. nov.

Plate 11, figs. 1–5

EXPLANATION OF PLATE 11

- Figs. 1–5. *Diplotesta anglica* sp. nov. 1, CG3; K5222, OR56.2 111.8, $\times c.$ 500. 2, Holotype, CG10; K5224, OR25.9 114.8, $\times 550$. 3, CG10; K5226, OR34 122.7, $\times c.$ 500. 4, 59/11/7; K5223, OR44.7 119.5, $\times 750$. 5, CG10, K5225, OR36 122.6, $\times 500$.
 Fig. 6. *Trigonopyxidina ginella* Cooks. and Eisenack, MD1; K5227, OR64.6 125.8, $\times 500$.
 Fig. 7. *Kalyptea monoceras* Cooks. and Eisenack, 59/11/12; K5228, OR45.4 116, $\times c.$ 500.
 Fig. 8. *Veryhachium reductum* (Deunff 1958), CG4; K5194, OR24.5 112.2, $\times 650$.
 Fig. 9. *Odontochitina* cf. *striatoperforata* Cooks. and Eisenack, CG3; K5231, OR37.6 119.3, $\times c.$ 150.
 Fig. 10. *Broomea* cf. *jaegeri* Alberti, 59/11/14; K5232, OR53 119.7, $\times c.$ 300.
 Figs. 11, 12. Object 'A', $\times 500$. 11, CG4; K5230, OR29.9 122.6. 12, MD1; K5229, OR37.6 121.5.



Diagnosis. Shell elongated with, in side view, one side straight or slightly concave, the other strongly convex, narrowing towards bluntly pointed apices one of which is usually open as the result of the partial or complete detachment of the wall along a straight line (Pl. 11, figs. 1, 3, 4). Capsule elongate-oval, strongly biconvex, narrowing somewhat towards both ends. The shell-membrane is scabrate.

Holotype. Plate 11, fig. 2; K5224, Cambridge Greensand (CG10).

Dimensions. Holotype 126 μ long, 44 μ broad; capsule 52 \times 24 μ . Range 34–80 μ long, 29–44 μ broad; capsule 25–54 μ long, 17–23 μ broad.

Occurrence. Upper Gault, 59/11/14, CG2; Greensand, CG3, CG10, 59/11/11, MD1; Chalk Marl, 15/12/5.

Comment. Shells of the *Diplotesta* type have been frequent in the samples studied but the majority have been badly crumpled. However, a few have clearly demonstrated the occurrence of this genus in the Cambridge deposits and permitted comparison with the three previously described species, namely *D. glaessneri* Cookson and Eisenack 1960*b* from Australian Upper Jurassic and Lower Cretaceous deposits, *D. luna* Cookson and Eisenack 1960*a* from ?Upper Albian–Cenomanian deposits in Western Australia, and *D. krutzschi* Alberti 1961 from the German Upper Barremian. *D. anglica* seems to be in closest agreement with *D. luna*, mainly differing in the plano-convex to slightly concavo-convex shell and to some extent in the shape of the capsule. Although Alberti (1961, p. 21) has described the shells of *D. krutzschi* as biconvex and so precluded reference of the Cambridge specimens to this species, his specimen shown on Plate 7, fig. 21 bears a strong resemblance to *D. anglica*.

Genus TRIGONOPYXIDIA (Cookson and Eisenack 1960*a*) C. and E. 1961*b*
Trigonopyxidia ginella Cookson and Eisenack (1960*a*) 1961*b*

Plate 11, fig. 6

Comment. The genus *Trigonopyxidia* was instituted for simple shells of triangular outline with a centrally placed capsule which were recovered from a certain Western Australian ?Upper Albian–Cenomanian deposit. The outline of the internal capsule was either circular or triangular but owing to the limited number of examples available both forms were included in the one species, *T. ginella*. Two specimens which can be accommodated in *T. ginella* in its present broad sense have been observed in the Cambridge Greensand. Although poorly preserved their triangular outline is clear and both contain a free internal capsule of sub-triangular outline similar to that of one of the Western Australian specimens (Cookson and Eisenack 1960*a*, pl. 3, fig. 18). *T. ginella* is a rare type; this is the first extra-Australian record.

Occurrence. Greensand, CG4, MD1.

INCERTAE SEDIS
 Object 'A'

Plate 11, figs. 11, 12

Description. Spherical body with wall approx. 6–7 μ thick. Sculpture pattern of short irregular ridges 1 μ across, 1 μ high, and up to 10 μ long. Some of these ridges form

regular circles or ovals up to $6\ \mu$ diameter enclosing a smooth area; the circles and ovals are irregularly distributed. Perforations of the main body are from $12\ \mu$ up to $44\ \mu$ diameter; each is surrounded by a low ridge ($1 \times 1\ \mu$). Irregularities in the outline of the body are due to these perforations.

Dimensions. Diameter $86\text{--}153\ \mu$; largest perforation (Plate 11, fig. 11), $44\ \mu$.

Occurrence. Upper Gault, CG1; Greensand, 59/11/12, CG3, CG4, CG10, 59/11/11; Chalk Marl, 59/11/7, CG8.

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A PROBABLE PTERIDOSPERM MICROSPORANGIATE FRUCTIFICATION FROM THE PENNSYLVANIAN OF ILLINOIS

by THEODORE DELEVORYAS

ABSTRACT. *Schopfitheca boulayoides* gen. et sp. nov., a new probable pteridosperm microsporangiate organ from an 'ironstone' concretion from the Mazon Creek area of Illinois is described as a pubescent, clavate-pyriform structure with large spores of the *Monoletes* (= *Schopfipollenites*) type.

UNDOUBTEDLY the most comprehensive paper devoted to an interpretation of supposed pteridosperm microsporangiate organs is that by Halle (1933). By using ingenious softening and embedding techniques, Halle was able to section compressed fertile structures and thereby reconstruct the three-dimensional configurations. Genera of probable pteridosperm microsporangia discussed by Halle are: *Goldenbergia*, *Whittleseyia*, *Boulaya*, *Aulacotheca*, *Codonothecca*, *Dolerotheca*, and *Potoniea*. *Zeilleria*, a problematic genus of synangia, was also described. Among the pteridosperm pollen-bearing organs elucidated by that author it has become obvious that there is a general structural plan which involves elongated sporangia in varying degrees of fusion.

Work in America includes the thorough treatise by Schopf (1948) on one of these genera, *Dolerotheca*, demonstrating actual anatomical structures and presenting ideas concerning the morphological interpretation and evolutionary significance of the genus. Schopf felt that *Dolerotheca* represented a septangium, derived from a septation of a simple sporangium.

Some years earlier Sellards (1903) found in 'ironstone' nodular concretions from the Mazon Creek area in northern Illinois specimens on which he based the genus *Codonothecca*, a microsporangiate fructification with fingerlike sporangia fused together at the base.

In such a small nodule from the mine spoil heaps just east of Coal City in Will County, northern Illinois, was found a flattened structure obviously related to some of the microsporangia discussed by Halle, Schopf, and others. The single specimen was compressed with almost no carbonaceous remains, but well-preserved spores were contained in it. Spores and impression features suggest that the specimen in question is another probable pteridosperm pollen-bearing organ.

SYSTEMATIC DESCRIPTION

Genus SCHOPFITHECA gen. nov.

Schopfitheca boulayoides sp. nov.

Plate 12, figs. 1-5; text-figs. 1, 2

Diagnosis. Stalked, clavate-pyriform microsporangiate fructification about 2 cm. long and 1 cm. wide; surface covered with closely spaced hairs. Contained microspores

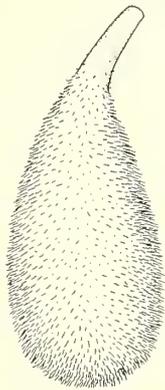
[Palaeontology, Vol. 7, Part 1, 1964, pp. 60-63, pl. 12.]

typically 420–480 μ in length and 325–590 μ wide, of the *Monoletes* (= *Schopfipollenites*) type; spore surface minutely granulose and waxy in appearance.

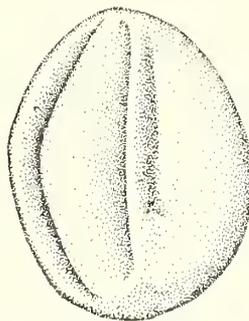
Stratigraphic occurrence. Francis Creek Shale, Carbondale Formation, Kewanee Group, Middle Pennsylvanian (Kosanke *et al.* 1960).

Holotype. Peabody Museum of Natural History, Yale University, Paleobotanical Collections No. 1003.

General description. The specimen is clavate-pyriform with the proximal end tapering imperceptibly into a stalk (Pl. 12, figs. 1, 2; text-fig. 1). It is just over 2 cm. in length and about 1 cm. wide in the flattened state; in life it was probably obovoid. The stalk is somewhat elongated, and there is no evidence of leaf material nearby, or of its mode of attachment to the parent plant.



TEXT-FIG. 1. Suggested reconstruction of *Schopfitheca boulayoides*; $\times 2$.



TEXT-FIG. 2. *Schopfitheca boulayoides*. Distal face of a microspore showing two prominent grooves; the apparent third groove on the right side is due to collapse of the spore coat. Drawing based on photograph in Plate 12, fig. 5; $\times 100$.

In places where the mineral material contained within the fructification has separated from the surrounding matrix it is possible to see closely-spaced fine pitting (Pl. 12, fig. 3). This feature suggests that the outer surface of the fructification was hairy, a characteristic reminiscent of the situation in *Goldenbergia* (Halle 1933).

Contained within the compressed specimen were a number of spores. Actual sporangia are not evident but on the basis of the similarity of all of the spores and the extremely large size of the spores, which were probably not easily transported, it may confidently be assumed they belong to the fructification.

Description of spores. Four of the spores were freed with dilute hydrochloric acid and mounted on slides. These spores are considerably flattened, rather opaque, and too delicate to be cleared, so only surface features are evident. The range in length of the spores observed is from about 420–480 μ ; the widest portion ranges from 325–390 μ . These spores, in the isolated state, would correspond to the genus *Monoletes* as defined by Schopf, Wilson, and Bentall (1944), or, as commonly referred to in Europe, *Schopfipollenites* Potonié and Kremp (1954). The proximal suture extends for nearly the entire

length of the spore (Pl. 12, fig. 4); two conspicuous grooves are on the distal side (Pl. 12, fig. 5; text-fig. 2). Minute granulations are evenly distributed over the waxy surface.

Comparison. In general structure *Schopfitheca* resembles most closely the genus *Boulaya* (Halle 1933). Like *Boulaya*, it is widest near the distal end and has large, monoete spores. There are some conspicuous differences, however, and because of inadequacies of preservation in both *Boulaya* and the new microsporangiate structure, it is impossible to compare certain additional features. No dimensions are given by Halle, but a photograph of the fructifications in his paper reproduced at natural size indicates they are 1.8 cm. long and about 0.6 cm. at their widest point. Kidston (1914) described similar fructifications as *Whittleseyia* (?) *fertilis*, but these were transferred to the genus *Boulaya* by Halle. Kidston's material included forms larger than those shown by Halle, reaching a maximum length of 2.4 cm., exceeding even that of *Schopfitheca*. Carpentier (1914) describing similar forms called *Whittleseyia* (?) *fertilis*, indicated a usual length of 1.0–1.1 cm. Also described by Carpentier (1925) is fragmentary material referred to *Boulaya*, but preservation is poor and the size is much smaller than *Schopfitheca*.

Microspores found in specimens referable to *Boulaya fertilis* do not exceed 240 μ in length (about half the size of the Illinois spores), so that there is a pronounced difference between them and those of *Schopfitheca*.

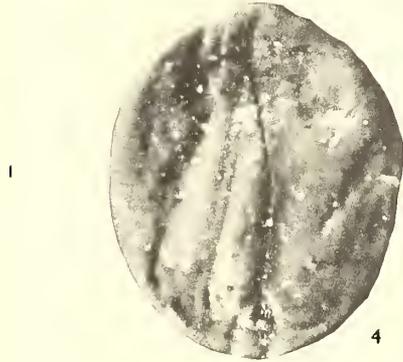
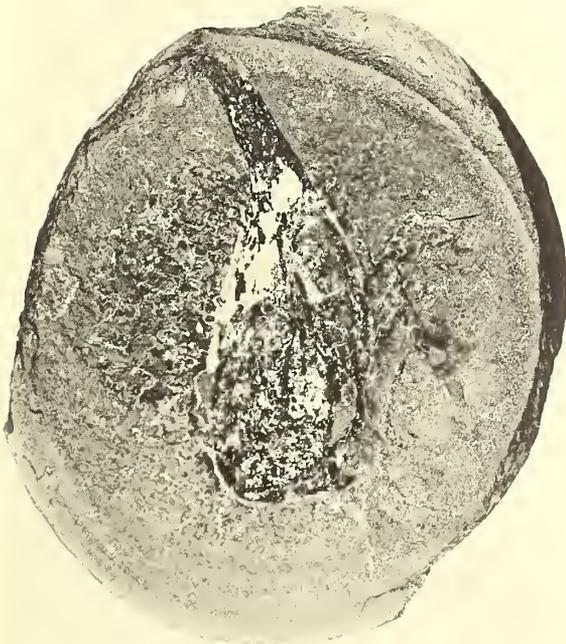
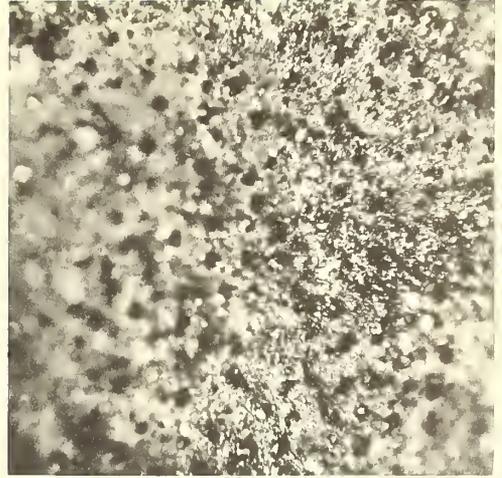
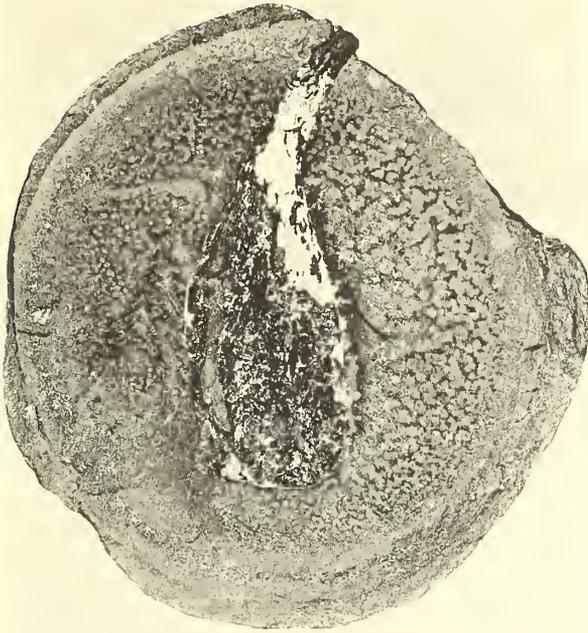
Goldenbergia (Halle 1933) is another form quite similar to both *Boulaya* and *Schopfitheca*. *Goldenbergia*, however, is generally smaller (6–8 mm. in length), although the spores are larger than those of *Boulaya* (300–400 μ), more closely approximating the size of those in *Schopfitheca*. Halle admitted a similarity between *Goldenbergia* and *Boulaya* but retained the generic distinction because it was not possible to demonstrate actual relationship. For the same reason the new material is assigned to a new genus. Poor preservation makes it impossible to determine sporangial structure, but spore size is impressive and greater than that found in the fructifications in the two other genera.

Spores of other pteridosperm fructifications such as *Doleritheca* and *Codonothea* compare favourably with those in *Schopfitheca* but are typically smaller. Schopf (1948), however, figured a spore from a compression of *Doleritheca* in an 'ironstone' nodule from southern Illinois that is as large as typical *Schopfitheca* spores.

Botanical affinities. It is impossible to indicate the natural affinities of *Schopfitheca* except to suggest relationships with the pteridosperms, more specifically with the medullosan seed-ferns. Carpentier's *Boulaya* was associated with alethopterid foliage, often thought to have been borne by medullosans. Because of mechanical and size considerations it would be logical to assume that *Schopfitheca* represents the microsporangiate structure of a plant that also bore large seeds. The unusually large size of the microspores means that the ovule that received the spores must have been sizeable, and the pollen chamber sufficiently commodious to contain these large microspores. It is among the seeds of the Trigonocarpales, usually considered to be medullosan, that such large micropyles and

EXPLANATION OF PLATE 12

Figs. 1–5. *Schopfitheca boulayoides*. 1, 2, Two halves of split nodule showing the compressed, stalked fructification, $\times 2$. 3, Surface of rock matrix surrounding the fructification with closely-spaced holes representing impressions of hairs, $\times 70$. 4, Proximal face of spore showing prominent suture, $\times 100$. 5, Distal face of another, somewhat smaller spore. Note the two grooves (compare with text-fig. 2), $\times 100$.



2

3

4

5

DELEVORYAS, Pennsylvanian pteridosperm fructification

pollen chambers are known. Until additional vegetative and seed material of the plants that bore *Schopfitheca* are known, however, its medullosan affinities remain only conjectural.

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TETRAPTERITES VISENSIS—A NEW SPORE-BEARING STRUCTURE FROM THE LOWER CARBONIFEROUS

by H. J. SULLIVAN and A. F. HIBBERT

ABSTRACT. *Tetrapterites visensis* gen. et sp. nov. is the name given to examples of a spore-bearing structure from two Lower Carboniferous shales. A spore tetrad is enclosed by a non-cellular membrane of basic tetrahedral shape with wing-like appendages at the apices. These apical modifications (herein designated skiadions) are also found as separate entities in the assemblages and resemble saccate spores. Detailed descriptions of the *Tetrapterites* capsule and component parts are given and an attempt is made to explain its unusual organization.

BOTH authors have been engaged in independent studies of miospores from Lower Carboniferous shales. H. J. S. has been concerned with an assemblage from a shaly intercalation in the Drybrook Sandstone of the Forest of Dean, Gloucestershire, and A. F. H. with plant microfossils from a shale in the Basement Series outcropping on the Caernarvonshire side of the Menai Straits, North Wales. The microfloras from these two shales contained many elements in common; in particular, they were characterized by the presence of pseudosaccate grains which, although usually occurring as separate entities, were also observed as part of a larger structure which is of considerable palaeobotanical interest since it appears to represent a spore tetrad unit of unusual organization. The purpose of this communication is to give a detailed morphological description of the tetrad unit on the basis of material obtained from both shale preparations. The pseudosaccate grains which are a constituent part of this structure may be expected to occur in other spore separations, and because of their distinctive morphology and known presence at similar horizons at two widely separated localities, they may prove to be useful stratigraphical indices.

Location and geological horizon of the samples. The specimen of shale from the Drybrook Sandstone was taken from a level 33 feet above the exposed base of this formation in the more easterly of two quarries on Plump Hill, near Mitcheldean, 160 yards south of the A 4136 Monmouth to Mitcheldean road (Grid ref. SO 661168). The shale was near the base of a 25 feet layer (preserved as a bluff in the quarry) interposed between massive, fine-grained, white, pink, or mottled sandstones with occasional bands of quartz pebbles.

The Drybrook Sandstone was placed in the Seminula Zone [S₂] of the Lower Carboniferous by Sibly (1918, p. 25) on the basis of brachiopods obtained from a calcareous intercalation (the Drybrook Limestone) which is present in the more southerly outcrops. Recently, Allen (1961) and Lele and Walton (1962) have described plant impressions from a siltstone layer in the Drybrook Sandstone of Puddlebrook on the western limb of the Wigpool syncline; the latter have also investigated the miospores from the bed. Lele and Walton (1962) believed that the plant mega- and microfossils indicated that the horizon of the Drybrook Sandstone was below that cited on the brachiopod evidence. However, it is doubtful whether such a conclusion was justified. Lele and Walton (1962,

pp. 149–50) compare their plant remains with similar forms found at the base of the Lower Brown Limestone of Dyserth, North Wales; and in the Calciferous Sandstone Series of Eskdale, in the Border region of Scotland. The fauna of the Lower Brown Limestone suggest a Lower Dibunophyllum [D_1] Zone age and, therefore, more likely to be younger rather than older than the Drybrook Sandstone. Lacey (1962) in his recent description of the plant remains from the Lower Brown Limestone admits (p. 154) they afford inconclusive evidence of age, but are likely to belong to the Upper Viséan. The correlation with the flora recorded by Kidston (1883) from Eskdale is, at present, of little value in determining the position in the coral/brachiopod zonal scheme because of the uncertainty regarding the equivalence of these rocks with the Dinantian sequences in the Central and Southern Provinces.

The miospores described by Lele and Walton (1962) from the siltstone lacked any distinctive forms on which any assessment of age could be based. The shale sample from the Drybrook Sandstone contained a varied and well preserved microflora (Sullivan, in press) which confirms the Upper Viséan age of these rocks.

The sample from the Basement Series of the Carboniferous Limestone of the Menaian region was collected from a lenticle of shale, maximum thickness 3 feet, referred to by Greenly (1928, pp. 420–1). The shale has an outcrop of 40 yards close to the Britannia Tubular Railway Bridge (Grid. ref. SH 541708) and when traced laterally wedges out into conglomerates.

The Basement Series of the Carboniferous Limestone in the Menaian region carries a fragmentary fauna, mainly of brachiopods. The lowest horizon containing abundant animal remains lies near the base of the overlying Lower Brown Limestone. There is a slight divergence of opinion regarding the age of these beds and they have been variously assigned to the base of D_1 or to the top of S_2 (Greenly 1928, Neaverson 1946, George 1958).

Plant remains known from these beds were first described by Walton in Greenly (1928, pp. 408–10) and the list of species later extended by Lacey (1952*a*, *b*). The plants recorded by Lacey (1952*b*, p. 376) were collected from the same shale band and at the same locality as the plant microfossils described in the present paper. Lacey (1952*b*, p. 376) also mentions the varied and well-preserved microflora in which Mrs. E. M. Knox recognized thirty spore types distributed through thirteen genera. A detailed account of this assemblage is being prepared by one of the authors (A. F. H.) as part of a doctoral dissertation on the Viséan and Namurian spores of North Wales.

It will be apparent from the foregoing account that there is a little doubt concerning the exact age of the shales from the Drybrook Sandstone and the Basement Series. A similarity in the composition of the miospore assemblages indicates that one is dealing with closely comparable horizons. An analysis of the stratigraphical information favours the view that the samples belong to the upper part of the Seminula Zone.

Preparation of the samples. The sample of shale from the Drybrook Sandstone was in a very weathered condition and much care was needed in its preparation. The addition of the normal 40 per cent. hydrofluoric acid produced a violent effervescence and so it was necessary to dilute the acid with three times its own volume of distilled water; the polythene container was also immersed in ice to arrest the rise in temperature. Even under these conditions the reaction was complete after only 2 hours. The acid was

decanted off and the residue washed with distilled water. No maceration was required, presumably because of the atmospheric oxidation, and the structureless organic debris was removed by the addition of 2 per cent. caustic potash.

The Menaian sample was treated with cold 40 per cent. hydrofluoric acid for several days until all the mineral matter had dissolved. The residue was macerated with fuming nitric acid for 2 hours, washed with progressively more dilute nitric acid and, finally, with distilled water. Both samples were non-calcareous and prior treatment with dilute hydrochloric acid was unnecessary.

SYSTEMATIC DESCRIPTION

Single and compound mounts were made either in glycerine jelly or in cellosize with a balsam cement (Jeffords and Jones 1959). The holotype of *Tetrapterites visensis* and other illustrated specimens have been deposited in the permanent collection of the Micropalaeontological Laboratory of the Department of Geology, Sheffield University.

To facilitate the description of *Tetrapterites*, several morphological terms have been introduced. We propose to apply the term *capsule* to the 'whole' *Tetrapterites* unit, i.e. a structure containing a tetrad of spores. Owing to the uncertainty regarding the precise function of *Tetrapterites*, it is possible that our use of this term may not conform to strict botanical practice, but it is intended to express quite simply the idea of a 'spore receptacle'. The capsule consists of a tetrad of spores surrounded by a non-cellular membrane which is basically tetrahedral in form (text-fig. 1). The outer covering is called the *wall membrane*. The wall membrane is extended into wing-like appendages at the apices. The apical portions of the capsule have been named *skiadions* (Gr. σκιάδειον, umbrella or cover). The skiadions become detached from the rest of the wall membrane and are composed of two distinct parts. The darker-appearing, originally bowl-shaped, central area is called the *cupule* and this encloses the distal hemisphere of the spore (text-fig. 2). The outer, and structurally lower, part of the skiadion is the *wing* (text-fig. 2).

Genus TETRAPTERITES gen. nov.

Type species. *Tetrapterites visensis* gen. et sp. nov.

Diagnosis. Spore tetrad enclosed by a non-cellular membrane which has a basic tetrahedral shape and possesses wing-like modifications at the apices.

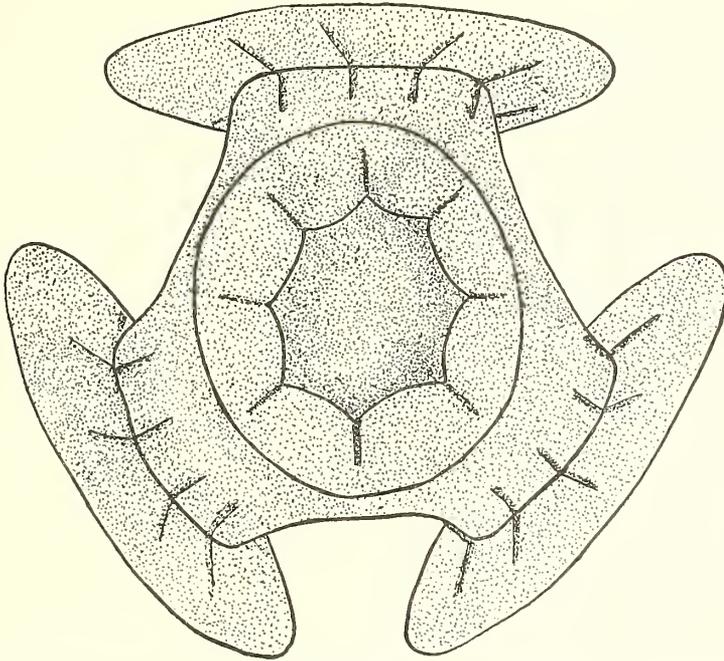
Tetrapterites visensis gen. et sp. nov.

Plate 13, figs. 2-5; Plate 14, figs. 1-6

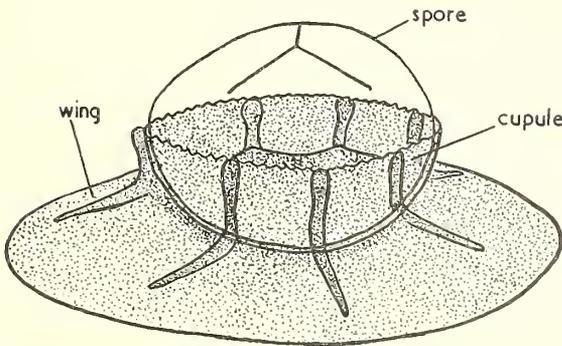
Holotype. The specimen illustrated (Plate 13, fig. 2) from a shale in the Basement Series of the Carboniferous Limestone of the Menai Straits, Caernarvonshire, North Wales.

Diagnosis. Dimension of capsule approximately 200 μ , diameter of holotype 190 μ ; spores radial trilete, amb circular to oval, exine laevigate, size 50-70 μ ; as sporae dispersae they would be classified as *Punctatisporites*; wall membrane opaque to translucent (depending on the degree of maceration); skiadions 105-155 μ in diameter, cupule about half of total radius, parallel-sided folds are located on the outer rim of the cupule and

continue across the upper surface of the wing; the base of the cupule has a characteristic cuspidate outline with seven to nine angles separated by concave margins; upper border of cupule is irregular.



TEXT-FIG. 1. Diagram to illustrate the basic tetrahedral symmetry of *Tetrapterites visensis* gen. et sp. nov.



TEXT-FIG. 2. Diagrammatic representation of a skiadion of *Tetrapterites visensis* and its associated spore.

Description. Examples of skiadions in their original apical positions are illustrated in Plate 13, figs. 1-2, 4-5. The specimen Plate 13, fig. 1 was photographed while in an open mount. Three skiadions and four spores are present; the fourth skiadion had been attached at the left hand side of the figure. During the preparation of this specimen as

a single-grain mount, one of the skiadions and its associated spore broke away from the remainder of the group. The two separated elements are shown as Plate 13, figs. 2, 3. The larger of these two portions (Pl. 13, fig. 2) has been selected as the holotype of *Tetrapterites visensis*. This has three laevigate spores enclosed by a wall membrane with two attached skiadions.

The wall membrane of the capsule (Pl. 13, fig. 4) is reddish-brown in colour and has a resinous texture. The wall is too thick to reveal the details of the spores inside the capsule, although their outlines can be discerned in the region of the apices. The skiadion below the capsule in Plate 1, fig. 4, was probably originally attached in the plane of the photograph. The opacity of the wall membrane is a function of the period of maceration; the Menaian specimens were treated with fuming nitric acid for 2 hours and as a result appear more translucent than those from the Drybrook Sandstone which were unmacerated. The skiadions seem less affected by maceration and the preservation in both separations was very similar.

The skiadion and its associated spore which became detached from the capsule (Pl. 13, fig. 2) is illustrated in Plate 13, fig. 3. It is preserved in semi-lateral view and clearly shows the bowl shape of the cupule (Pl. 14, fig. 2). Another example (Pl. 14, fig. 1) has become distorted during compression and the spore and the skiadion no longer bear their original relationship to one another. One of the rays of the tetrad scar can be seen in the portion of the exine not covered by the cupule (Pl. 14, fig. 3).

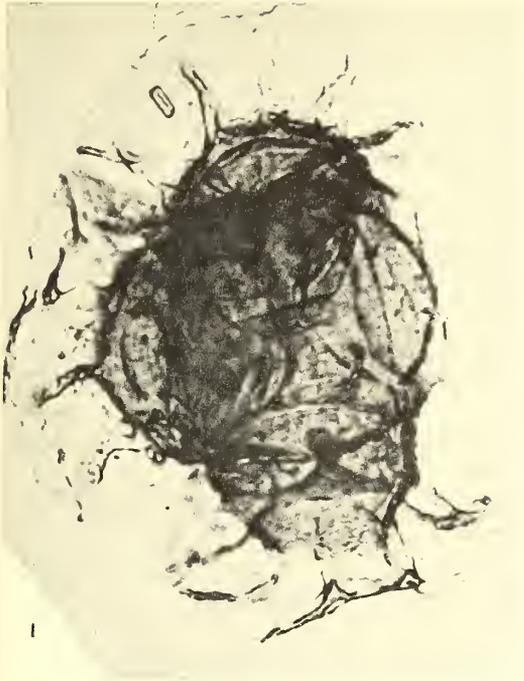
The spores which occur as tetrads within the capsule range from 50–70 μ in diameter. They have laevigate exines, often with crescentic secondary folds, and are circular to oval in outline: as spores dispersae they would be classified as *Punctatisporites*. It is presumed that the spores were not tightly clasped by the cupule because of the infrequency in which they occur together. Furthermore, in the rare cases when the spore is observed within the cupule, the position of the trilete is variable.

The most common remains recognizable as belonging to *T. visensis* are the skiadions (Pl. 14, figs. 4–6). They vary in size from 105 to 155 μ and are usually oval in outline (Pl. 14, figs. 4, 5), rarely circular. The cupule is sharply defined from the wing and occupies approximately half of the total radius of the skiadion. The cupule is composed of a depressed, saucer-shaped base surrounded by a rim about 10 μ high, but now compressed in the horizontal plane. The upper border of the cupule is ragged and it is along this line that the skiadion separates from the remainder of the wall membrane. This feature is clearly evident in Plate 14, fig. 6. The base of the cupule displays a characteristic cuspidate outline; there are between seven and nine cusps separated by concave margins (Pl. 14, fig. 6). There is a darker, and presumably thicker, zone around the base of the

EXPLANATION OF PLATE 13

Specimen references; DS, Drybrook Sandstone of the Forest of Dean; MS, Basement Series of the Carboniferous Limestone Series of the Menai Straits.

Figs. 1–5. *Tetrapterites visensis* gen. et sp. nov. 1, Capsule with three skiadions and four spores: this specimen separated into two parts on mounting; $\times 400$. 2, Holotype, MS1a; the larger portion of the group illustrated in fig. 1; $\times 400$. 3, Skiadion containing spore which separated from the base of the specimen illustrated in fig. 1, MS1b; $\times 500$. 4, Capsule with three skiadions attached at the apices and a fourth below the group which may possibly have been attached in the plane of the photograph, DS1/1; $\times 250$. 5, Enlarged view of one of the skiadions in fig. 4 (this plate); the folds can be seen to originate at a concentric zone of thickening above the cupule, DS1/1; $\times 1000$.



SULLIVAN and HIBBERT, Lower Carboniferous spore-bearing structure

cupule which has an ill-defined inner limit (e.g. Pl. 14, fig. 5). Parallel-sided folds are located at the angles of the cuspidate base and are disposed in a radial manner. The folds run down the exterior of the cupule rim and continue across the upper (proximal) surface of the wing. In the skiadion (Pl. 13, fig. 5) the folds appear to arise from a concentric zone of thickening below which the wall membrane ruptures. In some cases the folds at the cupule margin have terminal thickenings (Pl. 13, fig. 3; Pl. 14, fig. 2). There are usually the same number of folds as there are cusps at the base of the cupule, but it sometimes happens that folds are absent at one or two (never more) of the angles (e.g. Pl. 14, figs. 5, 6). In no instance were folds observed between the cusps.

The significance of the cuspidate outline of the base of the cupule is still a matter of conjecture. It may result from, or merely be accentuated by, compression. It is possible that the cusps may be the points at which the cupule is attached to the wing. Whatever the explanation, the constancy in the number and arrangement of the cusps is indicative of a control by some inherent structural character of the skiadion. The wing and the cupule are without ornamentation. The only visible structure is an irregular pitting which is probably due to corrosion.

Remarks. The capsules and skiadions of *T. visensis* were only minor elements in the preparations from the two samples. An estimated frequency is in the region of 0.02 per cent. This figure excludes the spores of *Punctatisporites* which may have arisen from tetrads enclosed within the wall membranes of *Tetrapterites*. The proportions of spores morphologically similar to those observed in *T. visensis* were 26 per cent. and 9 per cent. for the Drybrook and Menaian samples, respectively. These spores have been referred to *Punctatisporites platirugosus* (Waltz) by Sullivan (in press). It is unlikely that more than a small fraction of the total were derived from *Tetrapterites*. Indeed, *P. platirugosus* was observed in the Drybrook Sandstone preparations as large masses containing upwards of forty or fifty specimens and obviously represented the contents of sporangia. The number of complete or incomplete capsules (spores enclosed by a wall membrane which has two or more skiadions attached at their original apical positions) present in both assemblages was six. The skiadions totalled seventy-five and, of these, only two had retained the spore in the cupule. It was surprising that examples of wall membrane without skiadions or spores were not identified in the preparations. It is not implied that they do not exist, merely that they present problems in recognition.

Comparative morphology. The mode of occurrence of spores in sediments (spores dispersed) or in fructifications ('*spores in situ*' of Potonié (1962), but perhaps *spores inclusae* would be a better name) is either as individuals, or as isolated tetrads, or as tetrads making up the whole or part of a sporangial cluster. The contents of a mature sporangium can take the form of a single tetrad as is the case with many megasporangia, but in those cases the tetrad is surrounded by a sporangial wall which has a cellular structure. The wall membrane of *Tetrapterites* is non-cellular and cannot therefore be equivalent to a sporangial wall or even the remains of one.

The organization of *Tetrapterites* is unusual; a search through the literature of both living and fossil plants has not revealed any comparable structure. However, attention may be drawn to *Didymosporites scotti*, a megaspore tetrad described by Chaloner (1958) from the coenopterid fern *Stauropteris burntislandica*, consisting of two large fertile spores and two small abortive ones surrounded by a cuticular network. It is possible

that the wall membrane of *T. visensis* could have the same origin as that of the cuticular network of *D. scotti* which Chaloner (1958, p. 201) believes to be the remains of a tapetum. The remains of *D. scotti* have been observed in the Drybrook preparations, but the possible significance of its association with *T. visensis* is not known.

Certain features observed in living plants may have a bearing on the interpretation of the structural organization of *T. visensis*. In the Order Hepaticae certain species of the genus *Sphaerocarpus* liberate spores in the form of tetrads. A special wall develops between the spore mother cell wall and the individual spores. This wall is thick and is arranged in the pattern of the future ornamentation of the spore exine; it thickens distally before the spores themselves have completed wall formation on their proximal faces. A special wall would thus surround the tetrad and one would observe the following sequence of mutually enclosing membranes: sporangium wall, spore mother cell wall (which disappears at maturity), special wall and, finally, spore wall (exine). It is conceivable that the wall membrane of *T. visensis* could be equivalent to a special wall which is non-cellular.

Another possible explanation is that the laevigate spores represent the inner layer (intexine) of the exine and that the wall membrane is the outer layer (exoexine). In an immature condition the intexine may become separated at both poles whilst the exoexine is detached at the distal pole only. This stage in development has been observed in some species of *Pellia* (Hepaticae).

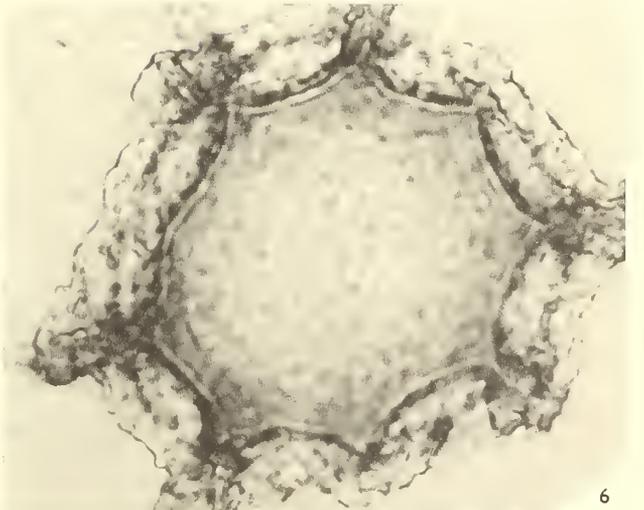
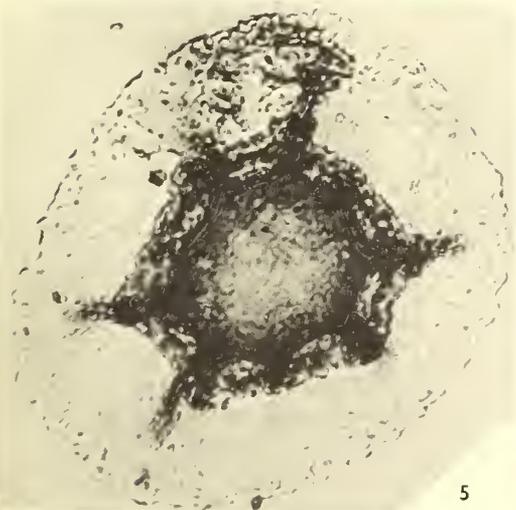
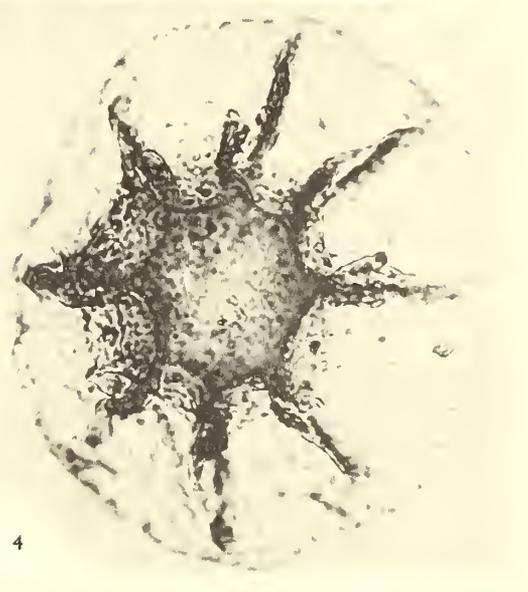
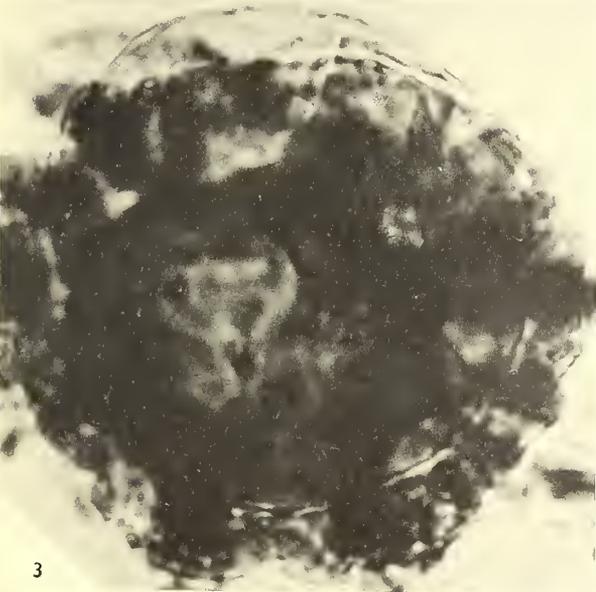
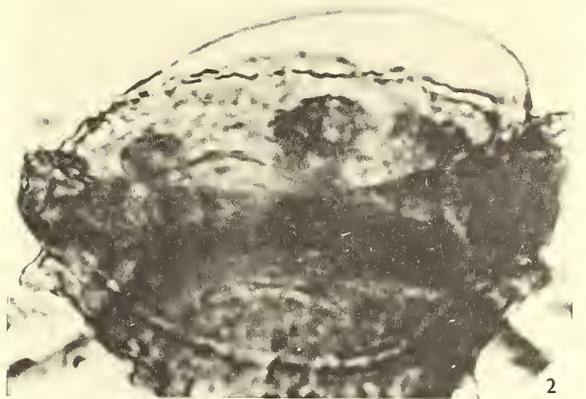
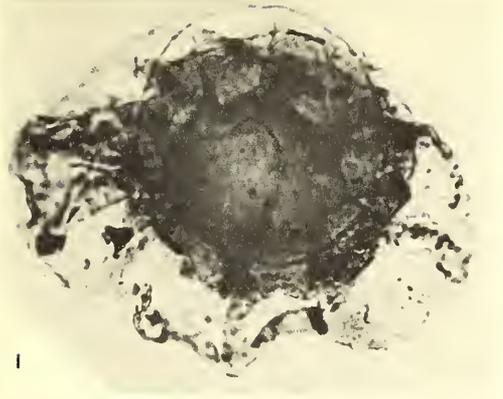
Whatever the explanation of the organization of *T. visensis* it is possible to suggest its function in the reproductive cycle. The wing-like modifications of the wall membrane are clearly a morphological adaptation to facilitate transport of the capsule through the air or water. The rupture of the wall membrane takes place near the apices and the skiadions separate to release the spores.

The separated skiadions of *Tetrapterites* do sometimes display a superficial resemblance to certain genera of Acritarchs. In the genus *Pterospermopsis* Wetzel 1952, the spherical capsule is surrounded by an equatorial wing which may bear radial folds, e.g. *P. helios* Sarjeant 1959 from the Cornbrash of Yorkshire. Several species of *Cynatiostphaera* (Wetzel 1933) Deflandre 1954, e.g. *C. mirabilis* Deunff 1958 from the Ordovician of Brittany and *C. miloni* Deunff 1957 from the Devonian of Canada, have membranes which are supported by rodlets: these on compression can simulate the wing of *Tetrapterites*.

Acknowledgements. The authors are deeply grateful to Prof. L. R. Moore, Dr. W. S. Lacey, and Dr. R. Neves for their critical reading of the manuscript. One of us (A. F. H.) is in receipt of a Department of Scientific and Industrial Research Award.

EXPLANATION OF PLATE 14

Figs. 1-6. *Tetrapterites visensis* gen. et sp. nov. 1, A skiadion with its associated spore, MS2; $\times 500$. 2, Enlarged view of the cupule and spore of the skiadion illustrated in Plate 13, fig. 3; note the bowl-shaped nature of the cupule, the thickened termini of the radial folds, and the irregular upper margin of the cupule, MS1b; $\times 1000$. 3, Enlarged view of portion of fig. 1 (this plate) to show the spore in the cupule; one of the rays of the trilete is clearly visible, MS2; $\times 1000$. 4-6, separated skiadions of *T. visensis*. 4, DS3/1; $\times 500$. 5, DS2/1; $\times 500$. 6, Enlarged view of cupule of skiadion illustrated in fig. 5 (this plate); to show the cuspidate outline of the base and the irregular upper margin, DS2/1; $\times 1000$.



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THE ONTOGENY OF *THERIOSYNOECUM* *FITTONI* (MANTELL)

by I. G. SOHN and F. W. ANDERSON

ABSTRACT. The carapaces of *Theriosynoecum fittoni* (Mantell) from the uppermost Weald Clay (Lower Cretaceous) of four English localities have been measured. Nine growth stages were recognized and the shape and ornament of each stage recorded. Though change in shape is considerable, the tubercles are generally constant in number and relative position throughout development. A lectotype for the species is designated, figured, and described.

SAMPLES of Weald Clay from the Cuckmere Brick Pit, near Berwick, Sussex, at a horizon 15 feet below the base of the Atherfield Clay have been examined independently by both writers, whose results have been combined in this account. In addition the second writer measured specimens of *T. fittoni* occurring in the upper part of the Weald Clay from three boreholes, i.e. at Warringham, Surrey; St. Margaret's Bay and Oxney, Kent.

These studies have made it possible to trace the ontogenetic development of *T. fittoni* from an instar, probably the first hatched, through eight other stages, of which the last was the adult and the first to show any marked sexual dimorphism.

Acknowledgements. The material examined by Sohn was collected in 1953 for the U.S. National Museum by Drs. H. T. and A. R. Loeblich (USNM loc. 4066). The writers are indebted to Dr. G. A. Cooper, U.S. National Museum, for permission to study these ostracods, and to Dr. E. Triebel, Senckenburg Museum, Frankfurt, for the loan of unfigured paratypes of Martin's species, and for permission to publish photographs of three of these specimens. The remaining samples were collected by officers of the Geological Survey of Great Britain. Sohn's visit to London in 1962 was arranged through the National Science Foundation.

Publication of these results has been authorized by the Directors of the Geological Surveys of Great Britain and the United States of America.

Genus *THERIOSYNOECUM* Branson 1936

Morrisonia Branson 1935 (*non* Grote 1874), p. 521.

Theriosynoecum Branson 1936, p. 323 (new name for *Morrisonia* Branson 1935).

Type species (monotypic). *Morrisonia wyomingensis* Branson 1935, p. 521, pl. 57, figs. 17-21. Morrison formation, Wyoming.

The reason why *Theriosynoecum* has had only one species for so many years is that the generic characters as originally defined were identical with the characters of the type species *T. wyomingense* (Branson). The orientation of Branson's original illustration (1935, p. 57, fig. 17) should be transposed left to right. It is of a right valve and not a left valve as indicated by Branson (1935, p. 520). Correct orientation shows the species to be bisulcate in the anterior half. Topotypes (USNM 75502) are dimorphic in width of posterior. Both dimorphs have nodes and ridges. Branson described the hinge of the genus (1935, p. 521), and of the type species (1935, p. 522) as 'Hinge straight, short, a ridge on the right valve fitting into a groove in the left valve in the central part of the hinge'. The blade-like teeth were not mentioned.

Single valves of *T. wyomingense* from the Morrison formation of the Black Hills of South Dakota and Wyoming (USGS localities 26897, 26910, 26916, 26921, 26922) have hinges with terminal dentition that are illustrated in text-fig. 1g and j. The muscle scars of this genus were not discussed by Branson, but the single valves mentioned above have a vertical row of four scars located below the median sulcus similar to those illustrated here on Plate 15, figs. 18, 20, 25.

Our present studies suggest that Mandelstam (1956, p. 138) was probably correct in considering the bisulcate Mesozoic species hitherto assigned to *Metacypris* and *Gomphocythere* as belonging to *Theriosynoecum* Branson. This matter has also been discussed by Grekoff (1958).

Theriosynoecum fittoni (Mantell)

Plate 15, figs. 1–35; text-figs. 1a–f, h, i; 3, 4

- 1836 *Cypris tuberculata* J. de C. Sowerby (part), in Fitton, p. 345, pl. 21, fig. 2a (non 2b, c; 2c is *Cypridea tuberculata*).
- 1844 *Cypris fittoni* Mantell, p. 545, pl. 119, fig. 2.
- 1878 *Cypridea? fittoni* (Mantell); Jones, p. 277.
- 1885 *Cythere fittoni* (Mantell); Jones, p. 333.
- 1888 *Metacypris fittoni* (Mantell); Jones, in Prestwich, p. 263, fig. 137a.
- 1940 *Gomphocythere berwickensis* Martin, p. 344, pl. 12, figs. 176–81, text-figs. 1, 2; p. 340, pl. 6, figs. 95–97; pl. 7, figs. 98–100.
- 1957 *Gomphocythere fittoni* (Mantell); Wicher, p. 270, pl. 2, figs. 4a–c, 5a–c.
- 1958 '*Metacypris*' *fittoni* (Mantell); Grekoff, p. 26, pl. 2, fig. 19.
- 1961 *Theriosynoecum berwickense* (Martin); Branson, p. 247.

Lectotype. GSM Mik(M) 1905001 (ex Geological Society of London Collection, No. 2479). A complete carapace, adult female.

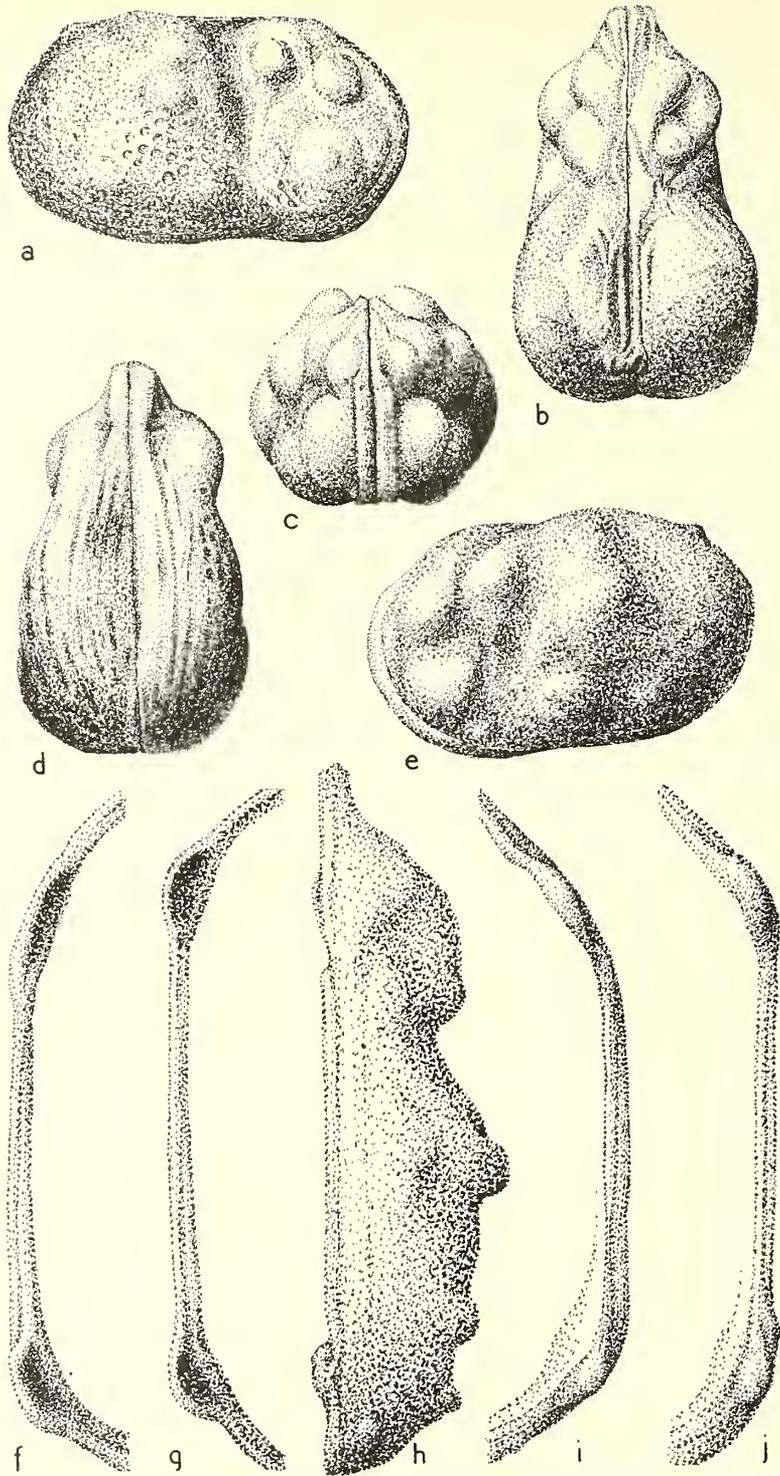
Dimensions. Length 0.950 mm., height 0.580 mm., width 0.575 mm.

Locality. Punfield Cove, Swanage Bay, Dorset.

Horizon. Uppermost Wealden, i.e. Wealden Shales, 34 ft. 6 in. thick.

Diagnosis. In lateral view an oblong carapace with anterior and posterior margins evenly rounded, but with marked antero- and postero-dorsal angles. Adductor muscle scar anterior to centre of valve and a little below the middle line, consisting of a vertical row of four longitudinally elongate scars. Two vertical, slightly sinuous sulci in anterior dorsal quadrant, one running from the muscle-scar to the dorsal margin and the other, shorter and shallower, anterior to this.

Description. The hinge in the lectotype is not visible, but in other specimens the articulation in the right valve consists of an anterior flange-like tooth and a posterior, more conspicuous, peg-like tooth. These are connected by the thickened shell margin, which is slightly excavated on the inner side. In the left valve are sockets to correspond, joined by a narrow, rounded bar. End margins with simple, widely spaced radial pore canals. The outer surface is rather coarsely punctate. The ornament consists of large blunt tubercles or rounded bosses. Sexual dimorphism well marked. In both sexes the carapace is wider behind the centre, but in the female the posterior is much more swollen than in the male. In the adult male there are usually four swellings or tubercles anterior to the



TEXT-FIG. 1. *Theriosynoecum fittoni* (Mantell) and *T. wyomingense* (Branson). *a-e*, *T. fittoni*, lectotype $\times 50$, adult female; *a*, right side; *b*, dorsum; *c*, anterior; *d*, venter; *e*, left side. *f*, *T. fittoni*, GSM Mik(M)644037, hinge of left valve. *g*, *T. wyomingense*, USNM 131912, hinge of left valve. *h*, *T. fittoni*, GSM Mik(M)113093, dorsal view of right valve. *i*, *T. fittoni*, GSM Mik(M)644059, hinge of right valve. *j*, *T. wyomingense*, USNM 131913, hinge of right valve.

adductor muscle scar and six posterior to it, with sometimes additional minute auxiliary tubercles near the anterior and posterior margins. In the adult female the ornament is reduced, especially in the posterior half, where the tubercles are sometimes barely detectable. In juveniles, except for the earliest instars, all ten tubercles are present.

Discussion. This species was first described by J. de C. Sowerby, together with another quite different form, as *Cypris tuberculata*. In his fig. 2, three forms were illustrated. That in fig. 2a is recognizable as the one later named *Cypris fittoni* by Mantell; fig. 2b is not recognizable, whilst fig. 2c remains as *Cypridea tuberculata*.

Sowerby stated that the specimen illustrated as fig. 2a came from Swanage. The type material consists of a small fragment of rock covered with numerous examples of the species *Theriosynoecium fittoni*. It is impossible to identify the specimen actually figured by Sowerby, and a lectotype has therefore been selected from this material.

The allocation of the species *fittoni* to the Recent genus *Metacypris* by T. R. Jones (1888) has caused much discussion in recent years. Martin (1940), working with immature moults from the Weald Clay of Berwick, Sussex, renamed the species *berwickensis*, referring it to the Recent genus *Gomphocythere* Sars, 1924. Wicher (1957) relegated *berwickensis* to a subspecies of *fittoni* in *Gomphocythere*. In 1958 Grekoff made a critical study of the systematic problems involved and came to the conclusion that *fittoni* could not be satisfactorily assigned to either *Metacypris* or to *Gomphocythere* and proposed using these names only in parentheses or alternatively, following Russian workers (Lubimova 1956), in allocating *fittoni* and related species to the genus *Theriosynoecium*. The hingement in *Theriosynoecium* is not very different from that of *Metacypris* but clearly differs from that of *Gomphocythere*. In the type of *Metacypris cordata* Brady and Robertson (BMNH 1900.3.6.171) the two valves are firmly closed, and the hinge cannot be seen.

The species to be considered are the Wealden *fittoni* and the Purbeck *forbesi* allocated by Jones to *Metacypris*, and the two Purbeck species *striata* and *silvana* allocated by Martin to *Gomphocythere*. These four are similar in hinge structure and adductor muscle scars, and if Grekoff is correct in his interpretation of the hinge in *Gomphocythere*, none of them can be allocated to that genus. On the other hand Grekoff's illustrations of the hinge in *Metacypris cordata* (1958, pl. 2, fig. 18a-d) differ from those of the original authors, Brady and Robertson (reproduced by Grekoff 1958, pl. 1, figs. 3-6), who showed a hinge closer to that of *fittoni*. Thus, at present, the distinction between *Theriosynoecium* and *Metacypris* is not clear and the writers are uncertain as to the correct generic assignment of these apparently related species from the Purbeck beds, i.e. *M. forbesi* Jones 1885, *Gomphocythere striata* Martin 1940, and *G. silvana* Martin 1940.

GROWTH STAGES IN *THERIOSYNOECUM FITTONI*

The fact that living ostracods pass through a series of moult stages during their life history has been known for many years, and the dimensions of the successive instars of a number of species have been published.

Since Jones recognized juvenile forms in 1849 most authors writing on ostracods have from time to time referred to immature individuals. The fact that earlier instars may be very different in appearance from the adult, and the difficulty of recognizing as the same

species carapaces which differ in size, shape, ornament, and hinge-structure, has always proved an embarrassment to the systematist.

Though it is obvious that an ostracod species is incompletely known until all its growth stages have been described, little attention has been paid to this until comparatively recently. In 1945 Le Roy studied the development of *Cythereis simensis* (Le Roy) and *C. holmani* Le Roy, and in the same year Cooper described the developmental stages of *Ectodemites plummeri* Cooper. Since then a number of such studies have been published, and are critically examined in the immediately following paper by Anderson (1964). Nevertheless there remain a number of questions which have not yet been unequivocally answered, namely, whether it is possible to recognize individual instars by size alone; the number of moults required to reach maturity; the number of instars present in any one species, and whether this number is constant for the species; whether or not there are post-maturation moults; and what is the law of growth in the Ostracoda.

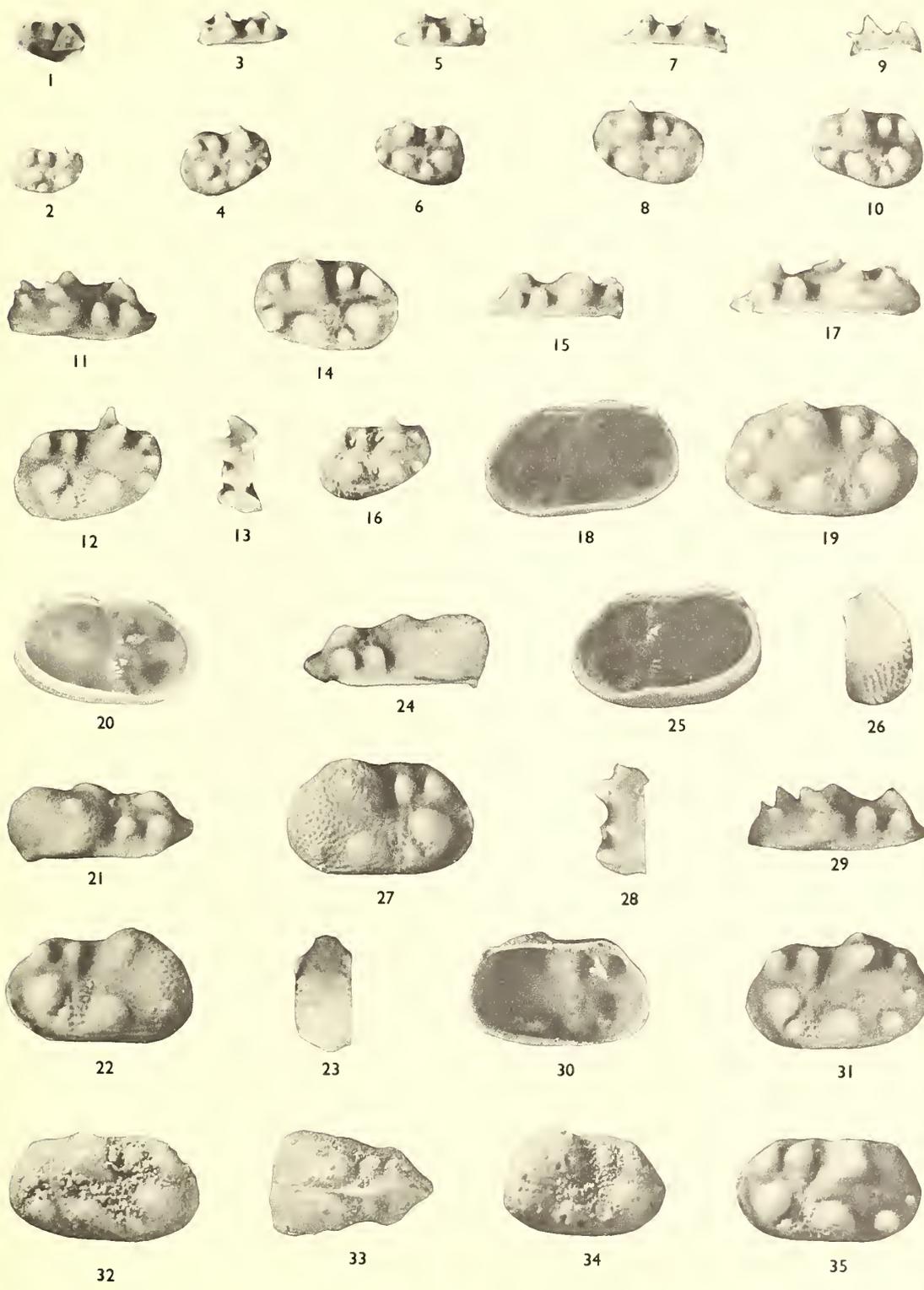
Material. For this study of the growth stages in *Theriosynoecum fittoni* samples of ostracod-bearing shale were taken from strata of approximately the same age, i.e. a horizon high in the Weald Clay (Lower Cretaceous) from four widely separated localities, Berwick (Sussex), St. Margaret's Bay and the Oxney boreholes (Kent), and the Warlingham Borehole (Surrey). In each case the ostracod fauna consisted almost entirely of the one species and in no case was any other species of the genus present. It was therefore a reasonable presumption that all the juveniles found were those of *T. fittoni*. Four different localities were selected in order to discover if the growth-rate was constant for the species. In every case early instars were deliberately sought, so that the numbers recorded for each instar do not bear any relation to the natural distribution of individuals in the instars.

1. *The Warlingham assemblage.* Horizon: 1,076 feet, i.e. 29 feet below the base of the Atherfield Clay at 1,047 feet. The length and height of 382 carapaces and separated valves were measured. Since the two valves differ very little in size they were not recorded separately. In text-fig. 2 length is plotted against height. The approximate position of the mean in each instar is apparent whenever a reasonable number of individuals has been measured. It is equally clear that the amount of growth between moults increases with age. Nine growth stages appear to be represented. They range in size from a mean

EXPLANATION OF PLATE 15

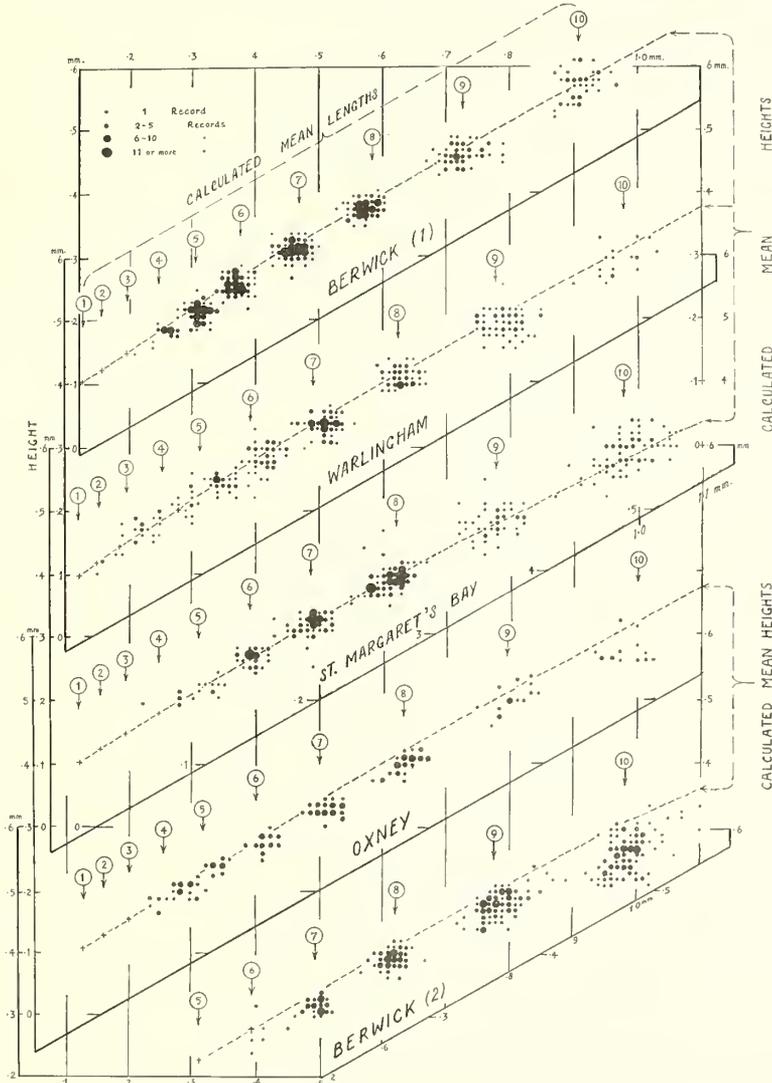
Theriosynoecum fittoni (Mantell). Magnification approximately $\times 30$.

Figs. 1, 2. Inside and outside of left valve, USNM 131231. 3, 4, Dorsal and outside of left valve, USNM 131232. 5, 6, Dorsal and outside of right valve, USNM 131233. 7, 8, Dorsal and outside of right valve, USNM 131234. 9, 10, Dorsal and outside of right valve, USNM 131235. 11-13, Dorsal, outside and posterior of left valve, USNM 131236. 14, 15, Outside and dorsal of right valve, USNM 131237. 16, Left valve, paratype, Senck.-Mus. No. X/E 2053. 17-19, Dorsal, inside and outside of right valve, male, USNM 131238. 20, Inside of left valve, female, USNM 131239; the spot anterior to vertical row of muscle scars is matrix. 22-23, Dorsal, outside and posterior of left valve, female, USNM 131240. 24-27, Dorsal, interior, posterior and outside of right valve, female, USNM 131241. 28-31, Posterior, dorsal, inside and outside of left valve, male, USNM 131242. 32, Right view of carapace, male; paratype, Senck.-Mus. No. X/E 2504. 33-34, Dorsal and right views of carapace, female; paratype, Senck.-Mus. No. X/E 2055. 35, Left valve, male, node 5 missing, USNM 131243.



length of 0.158 mm. and height of 0.115 mm. to mature individuals of average length 0.961 mm. and height 0.585 mm.

2. *The Berwick assemblage.* Horizon: 15 feet below the base of the Atherfield Clay. From this fauna 918 complete carapaces and single valves were measured. In this case only eight growth stages were identified, the last being the mature adult, which averages 0.904 mm. in length and 0.568 mm. in height in Anderson's material and 0.986 mm.



TEXT-FIG. 2. Growth stages in the ostracod *Theriosynoecum fittoni* (Mantell). Measured lengths and heights of carapaces are plotted for samples from four localities. Calculated mean lengths (see immediately following paper by Anderson 1964) are indicated by an arrow for each growth stage and heights by means of a broken line. Growth-stage numbers are shown within a circle. Too few well-preserved specimens of early instars were found to compensate for the pressure effect on these very delicate shells. This diagram illustrates clearly the difficulty of determining mean dimensions in early instars.

long and 0.561 mm. high in Sohn's. Sohn's material, probably collected from a different level, gives results that differ slightly from those Anderson obtained from Berwick, but coincide almost exactly with those from Warlingham. Anderson's measurements are plotted on text-fig. 2 as 'Berwick (1)' and those by Sohn are shown as 'Berwick (2)'.

3. *The St. Margaret's Bay assemblage.* Horizon: 6 inches below the base of the Atherfield Clay. The 400 specimens measured from St. Margaret's Bay also show that here the growth rate is greater than in Berwick (1), leading to an average size for the mature carapace of 0.980 mm. in length and 0.590 mm. in height. Here only seven instars were recognized, the earliest of which is growth stage 4.

4. *The Oxney assemblage.* Horizon: 8 inches below the base of the Atherfield Clay. The 199 individuals from this locality again represent seven growth stages.

Morphological changes during development

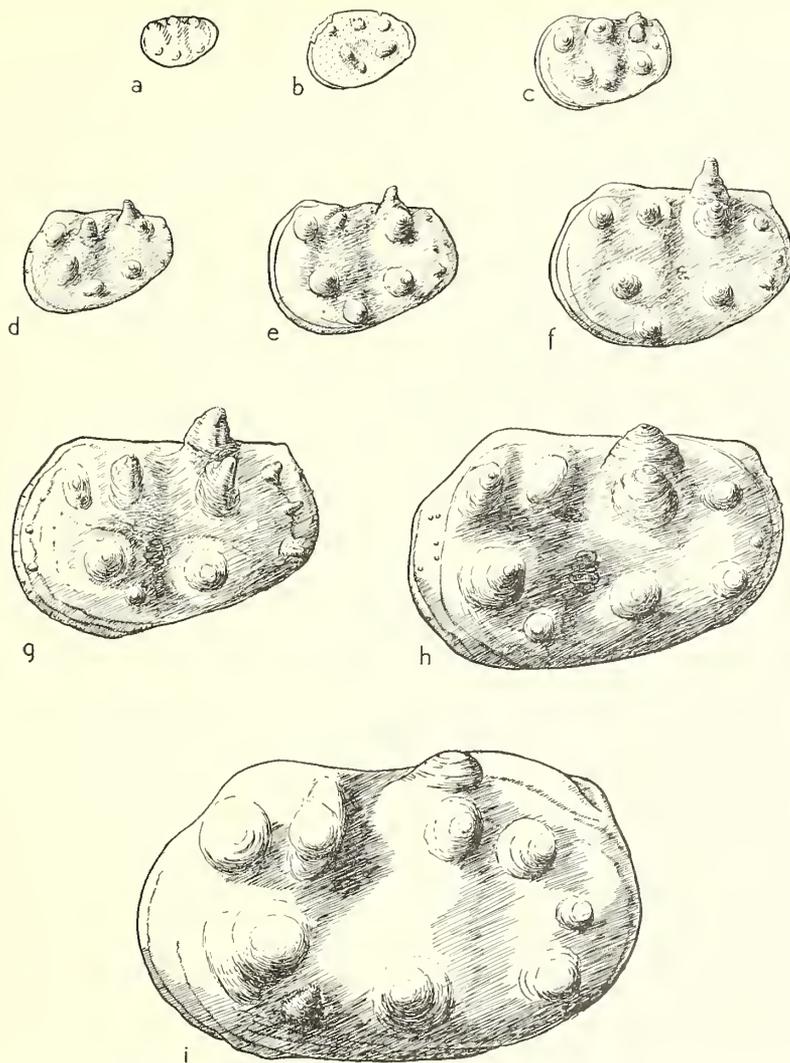
(i) The earliest instar seen; according to the system of notation used by Anderson (1964), this is recorded as *growth stage 2*. Only four examples of this stage have been seen, all from Warlingham. Three of them are thin-shelled and partly damaged, 0.160 mm. long and 0.120 mm. high, and one, apparently uncrushed, is 0.150 mm. long and 0.100 mm. high (text-fig. 3a). The mean of these measurements is 0.158 mm. and 0.115 mm. The dimensions, calculated by the method described in the immediately following paper by Anderson, could be expected to be 0.158 mm. and 0.126 mm. No examples of a comparable instar were recovered from any of the other localities.

The shell is extremely thin. It is oval in outline with its greatest height well anterior to the centre (text-fig. 3a). The dorsal margin is almost straight, anterior and posterior margins smoothly rounded and joining it without the characteristic angles seen in most of the later instars. Anteriorly and posteriorly the shell bears a narrow marginal flange. The radial pore canals are plainly visible and evenly distributed, but are relatively widely spaced. Tubercles are only faintly indicated as low rounded bosses. Six primary tubercles appear to be present, the lumbar pair (text-fig. 4, *Fa, Fb*) being represented by a single tubercle, whilst the posterior tubercles (text-fig. 4g, *h, i*) are missing. The length of shell anterior to the rudimentary sulcus is 1.80 times that behind. If an earlier instar ever existed it would probably have been 0.126 mm. long and 0.103 mm. high, and may have been without tubercles.

(ii) *Growth stage 3*. Sixteen examples of this stage were recovered, fifteen from Warlingham, averaging 0.207 mm. in length and 0.164 mm. in height; and one from Berwick, 0.215 mm. in length and 0.150 mm. in height. In outline the shell is similar to that of the previous instar but a little less ovate. Six tubercles are still present (text-fig. 3b). The ratio between anterior and posterior portions of the shell is now 1.75. The sulcae are not yet evident.

(iii) *Growth stage 4* (text-fig. 3c). Thirty-six examples were measured: 11 from Warlingham, with average length 0.248 mm. and height 0.182 mm.; 14 from St. Margaret's Bay, average length 0.276 mm., height 0.201 mm.; 5 from Berwick, average length 0.246 mm., height 0.182 mm.; and 6 from Oxney, average length 0.244 mm., height 0.188 mm. The anterior-posterior length ratio is 1.66.

With this instar there is marked change of shape. The carapace has now developed an evident postero-dorsal angle and is more oblong than ovate. The tubercles are now clearly seen and all six primaries are present, with the addition of several minute



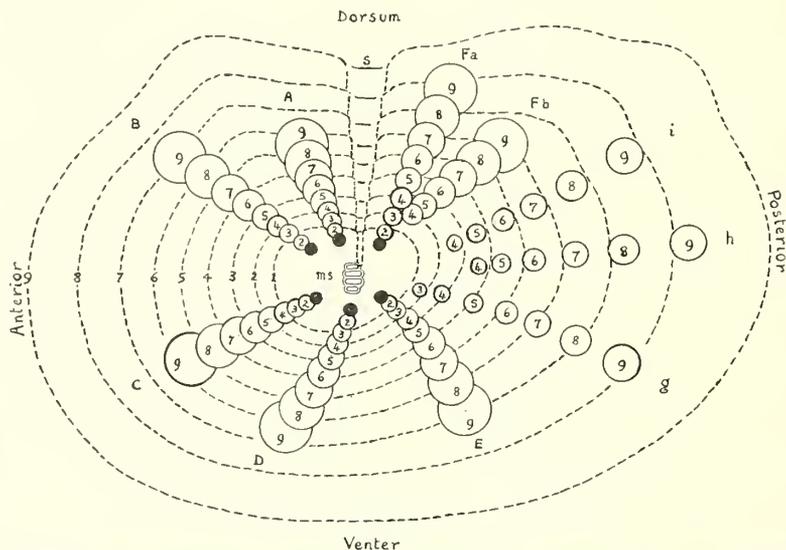
TEXT-FIG. 3. *Theriosynoecum fittoni* (Mantell). Growth stages, all left valves. *Camera lucida* drawings. *a*, Growth stage 2. Length 0.150 mm. Warlingham borehole. GSM Mik(M)637060. *b*, Growth stage 3. Length 0.215 mm. Berwick. GSM Mik(M)386067. *c*, Growth stage 4. Length 0.260 mm. Berwick. GSM Mik(M)388064. *d*, Growth stage 5. Length 0.315 mm. Berwick. GSM Mik(M)388042. *e*, Growth stage 6. Length 0.370 mm. Berwick. GSM Mik(M)338062. *f*, Growth stage 7. Length 0.450 mm. Berwick. GSM Mik(M)388040. *g*, Growth stage 8. Length 0.585 mm. Berwick. GSM Mik(M)387082. *h*, Growth stage 9. Length 0.720 mm. Berwick. GSM Mik(M)385100. *i*, Growth stage 10. Length 0.920 mm., male. Berwick. GSM Mik(M)385012.

posterior tubercles. The lumbar (*F*) is now divided into two divergent tubercles with a common base (*Fa*, *Fb*). The radial pore canals are distinct, relatively large, and more closely set than before, and the shell surface is now very finely punctate.

(iv) *Growth stage 5* (text-fig. 3*d*). Two hundred and thirty-four examples were measured: 40 from Warlingham, with average length 0.314 mm., height 0.235 mm.;

12 from St. Margaret's Bay, average length 0.310 mm., height 0.215 mm.; 131 from Berwick, average length 0.303 mm., height 0.213 mm.; and 51 from Oxney, average length 0.318 mm., height 0.225 mm. The anterior-posterior length ratio is 1.56. All six primary tubercles are present and are conical rather than dome-shaped. The lumbar tubercles are clearly seen to be a closely set pair confluent at the base and with vertical axes diverging at about 45° . Three or more secondary tubercles are again present posterior to the lumbar-furcal line, and there may be three or four minute tubercles on the anterior flange.

(v) *Growth stage 6* (Pl. 15, figs. 1, 2; text-fig. 3e). Two hundred and thirty-three examples were measured, 68 from Warlingham, average length 0.405 mm., height 0.273 mm.; 46 from St. Margaret's Bay, average length 0.397 mm., height 0.269 mm.; 98 from Berwick, average length 0.373 mm., height 0.259 mm. (Anderson), 0.400 mm. and 0.270 mm. (Sohn); and 21 from Oxney, average length 0.412 mm., height 0.275 mm. The anterior-posterior length ratio is 1.44. The tubercles are relatively larger and more spinose, the lumbar pair (text-fig. 4, *Fa, Fb*) being especially large and sharp.



TEXT-FIG. 4. *Theriosynoecum fittoni* (Mantell). Diagram representing the exterior of a left valve and showing the positions of the nodes at each growth stage. The six primary nodes are shown in solid black and their position in each subsequent growth stage by circles enclosing the growth stage number. Carapace outlines are shown by the broken lines.

(vi) *Growth stage 7* (Pl. 15, fig. 16; text-fig. 3f). Three hundred and eighty-four examples were measured, 92 from Warlingham, average length 0.509 mm., height 0.337 mm.; 83 from St. Margaret's Bay, average length 0.490 mm., height 0.323 mm.; 166 from Berwick, average length 0.465 mm., height 0.314 mm. (Anderson), 0.494 mm. and 0.318 mm. (Sohn); and 43 from Oxney, average length 0.513 mm., height 0.325 mm. The anterior-posterior length ratio is 1.32. The outline of the carapace is a little more oblong than in the previous instar as a result of the more rapid growth of the posterior half of the shell. The anterior sulcus is now less clearly defined than the median. All the

tubercles are spinose with large, spreading, swollen bases. The lumbar pair (text-fig. 4, *Fa*, *Fb*) are relatively larger and more conspicuous than the others. Three of the posterior tubercles become clearly defined, and presumably represent the tubercles *g*, *h*, and *i* (text-fig. 4). These three are constant in position and number in later growth stages.

(vii) *Growth stage 8* (Pl. 15, figs. 7–10, 16; text-fig. 3g). Four hundred and thirteen examples were measured, 68 from Warlingham, average length 0.630 mm., height 0.409 mm.; 114 from St. Margaret's Bay, average length 0.610 mm., height 0.385 mm.; 185 from Berwick, average length 0.580 mm., height 0.381 mm. (Anderson), 0.618 mm. and 0.444 mm. (Sohn); and 46 from Oxney, average length 0.638 mm., height 0.400 mm. The anterior–posterior length ratio is 1.16. The shape of the carapace is similar to that in the previous instar, but the posterior half is relatively larger so that the adductor muscle scar is now almost on the vertical axis. All primary tubercles are well-developed and spinose, the lumbar pair being especially prominent.

(viii) *Growth stage 9*. Three hundred specimens of this, the pre-maturation instar, were measured, 64 from Warlingham, average length 0.793 mm., height 0.500 mm.; 49 from St. Margaret's Bay, average length 0.777 mm., height 0.472 mm.; 170 from Berwick, average length 0.730 mm., height 0.470 mm. (Anderson), 0.783 mm. and 0.480 mm. (Sohn); and 17 from Oxney, average length 0.800 mm., height 0.500 mm. The anterior–posterior length ratio is 0.98, i.e. the posterior half of the shell is now longer than the anterior half but is still not quite so high. The outline of the carapace is a little more oblong and the tubercles are less spinose, now bluntly conical.

(ix) *Mature adult (growth stage 10)* (Pl. 15, figs. 17–35; text-fig. 3i). Two hundred and seventy-nine examples were measured, 20 from Warlingham, average length 0.961 mm., height 0.585 mm.; 82 from St. Margaret's Bay, average length 0.980 mm., height 0.590 mm.; 162 from Berwick, average length 0.904 mm., height 0.568 mm. (Anderson), 0.986 mm. and 0.561 mm. (Sohn); 15 from Oxney, average length 0.982 mm., height 0.575 mm. The anterior–posterior length ratio is 0.80. The maturation moult produces marked changes in the shell. The dorsal and ventral margins are now almost parallel so that the outline is rectangular, with evenly rounded, more or less semicircular anterior and posterior margins. The tubercles are now all rounded bosses or blunt cones and the lumbar pair (text-fig. 4, *Fa*, *Fb*) are clearly separated and no longer dominant. The anterior sulcus is barely perceptible and the adductor muscle-scar is well anterior to the middle line. Sexual dimorphism is pronounced; in the female the posterior half of the carapace is swollen (Pl. 15, figs. 21–23) and the tubercles are low and inconspicuous, sometimes absent; in the male the posterior half is much narrower and all the tubercles are well developed (Pl. 15, figs. 17–19, 28–31). In both sexes the posterior-dorsal margin is swollen and raised so as to hide the dorsal margin in side view.

RECOGNITION OF INSTARS

When length of carapace is plotted against height as in text-fig. 2, it is obvious that the later growth stages can be identified by size alone provided a sufficient number of individuals are measured and provided they are from the same horizon and locality. But since the growth-rate in *T. fittoni* is not absolutely constant it is evident that if the measurements of length and height were not plotted on a separate graph for each locality

it would not always be possible to distinguish the instars. Though the growth rate is evidently not constant for *T. fittoni*, this may be a feature peculiar to brackish-water species, since the data published by Neale (1959) for the Recent marine species *Normanocythere leioderma* (Norman), the specimens of which came from various localities though mainly from Spitzbergen, show very little evidence of a variable growth rate. Similarly, Anderson's (1964) study of *Pterygocythere jonesi*, for which specimens were collected from various localities in the Irish Sea, show very little deviation from the mean of each instar so that the growth rate cannot have differed greatly from place to place.

Apart from size the changes in shape and ornament enable a rough assessment of the growth stage to be made. It was noted during measurement that some specimens were atypical in that one or more of the posterior three nodes (text-fig. 4g, h, i) were missing (Pl. 15, fig. 35), and all the material on hand then was examined for atypical specimens. Out of 2,000 specimens examined, only 16 atypical specimens were found. These are similar to the rest in all respects except that one of the posterior nodes is missing. Only one of these specimens has two of the posterior nodes missing. The shell is smooth in the area where the node should be, indicating that its absence is not due to preservation. These specimens range in greatest length from 0.51 mm. to 1.06 mm., suggesting that the abnormality persisted through the entire ontogeny of the individual. These exceptions are considered to represent genetic sports, and as such do not alter the conclusion that in this species the number of nodes, and their relation to each other on the surface of the valve, are constant. This interpretation of genetic control argues against the hypothesis proposed by Wicher (1957, p. 269) that nodosity in this plexus is caused by outside influences, namely environment. According to him, a change in the salinity caused the development of nodes.

CONCLUSIONS

This study demonstrates that in *Theriosynoecium fittoni* (Mantell) the number of nodes is normally ten in adult males as well as in most of the younger growth stages. It is usually possible to see the remains of these nodes in adult females even though they are resorbed. The position of the nodes relative to each other is constant on the surface of the valve.

This principle of constancy of nodes may be used to discriminate between bisulcate brackish-water Mesozoic species, and may prove to apply as well to marine species in other ostracod genera. For example, Wicher (1957) illustrated and discussed specimens from north-west Germany that he assigned to *Gomphocythere fittoni berwickensis*. The German specimens figured have only nine nodes, and are stated to have from eight to nine nodes (1957, p. 270). The arrangement on the surface of the valve (Wicher 1957, pl. 2, figs. 4a-c, 5a-c) differs from that of *T. fittoni*, so that these specimens may not be conspecific with the English species. Grekoff (1958, p. 26) considers the *G. palhasapensis* (Roth) of Martin 1940, as synonymous with *G. berwickensis* Martin 1940, and refers both to '*Metacypris*' *fittoni* (Mantell) 1844. Martin's illustrations (1940, pl. 6, figs. 95-97; pl. 7, figs. 98-100) are of specimens that are probably not conspecific with *T. fittoni* since the number and arrangement of the nodes differ from the species illustrated by Martin (1940, pl. 12, figs. 176-81; text-figs. 1, 2), and also in this paper.

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ADDENDUM. The monograph entitled 'A Complete Revision of the Genera *Bisulcocypris* and *Theriosynoecum* (Ostracoda)', by I. D. Pinto and Y. T. Sanguinetti (1963, *Esc. Geol. P. Alegre Publ. Esp.* **4**) appeared after this paper had been completed and contains several controversial issues which require discussion. At the moment the present authors find no reason to change their allocation of '*Metacypris*' *fittoni* from the genus *Theriosynoecum* to the genus *Bisulcocypris*.

THE LAW OF OSTRACOD GROWTH

by F. W. ANDERSON

ABSTRACT. A method of calculating the dimensions of ostracod growth stages is described and applied to the analysis of already published data referring to 26 species ranging in age from Ordovician to Recent.

THE first attempt to formulate a law of growth for the Arthropoda was made by Brooks (1886). Working on *Coronis* larvae he found that the successive instar sizes could be approximately calculated by multiplying the length of the previous instar by 1.25. Fowler (1909) applied this rule to living ostracods from the Bay of Biscay and claimed that each stage increased by a fixed percentage of its length approximately constant for its species and sex. He named this rule 'Brooks's Law' and found that for species of Halocypridae the growth factors ranged from 1.26 to 1.78. In 1931 Przibram assumed a growth factor of 1.26 for all arthropods. This was based on the assumption that the mass is doubled at each moult, 1.26 being the cube root of 2.0. It is extremely unlikely that this is true and in fact the principle has been largely abandoned for arthropods in general. Animals which add to the number of appendages at each moult are not likely to obey this law even approximately, and certainly the method does not give satisfactory results for the ostracods.

Brooks's Law stated as a formula reads: $L_{n+1} = kL_n$, where L_n is the length of carapace at n th instar, and k is the growth factor. As has been demonstrated for *T. fittoni* (see preceding paper by Sohn and Anderson) the growth factor is not necessarily constant even for one species and, as will be shown subsequently, for ostracods generally there is a wide range of growth rates. Many ostracods, however, in the adult stage have lengths near to 1.0 mm. and should therefore, according to the method of calculation suggested below, have an incremental factor of 0.100, which is the logarithm of 1.259, i.e. approximately 1.26, so that the fact that Przibram's growth rate is not applicable generally is not always readily apparent.

In the search for a more satisfactory method of calculating instar sizes the dimensions of the individuals of *T. fittoni* were recorded as logarithms to the base 10. It was then apparent that the logarithms of the mean dimension of each instar were approximately equidistant. Thus the law which is immediately suggested is that which might have been deduced on purely theoretical grounds, i.e. some form of the compound interest formula $y = y_0 e^{kx}$, since growth is incremental and logarithmic. In this formula x is the time at which the size y is obtained, y_0 is a constant depending on the size at time 0, and k is a constant (the efficiency index). On taking logarithms, $\log y = \log y_0 + kx$, which simplifies subsequent operations. This is, of course, an expression of the general form $y = a + bx$, the equation for a straight line. The distribution of the measurements for length and height of *T. fittoni* suggests that the growth formula for this species at least is an equation of this kind. In the case of fossil ostracods, however, x cannot be expressed in units of time which are not determinable, but since the logarithms of the means of each instar size are equidistant, x can be legitimately replaced not by the instar number,

which again is not necessarily determinable, but by a growth-stage number. If it can be assumed that the first growth stage in all ostracods in which the adult is of the same order of size, has the same dimensions, and for all practical purposes this may well be true, then the incremental factors of growth in length (K_L) and in height (K_H) can be determined as follows:

$$K_L = \log L_n - \log L_{n-1}$$

$$\text{and } K_H = \log H_n - \log H_{n-1},$$

where n is the number of any growth stage. If K_L is taken as the length of the first growth stage then growth stage 10 will have the length $10K_L$. In *T. fittoni* and a number of other species growth stage 10 is the mature adult, i.e. the instar numbered 8 or 9 according to the author concerned.

In the calculation of height another factor, the length/height ratio, must be taken into account. Let r equal the fundamental L/H ratio, that of growth-stage 0, which will be constant for the species if the shape is to remain the same. During growth, however, there is a change of shape with each instar, usually in the form of an increase in the L/H ratio so that the shell becomes proportionately more elongate as growth proceeds. Thus another factor, p , again a constant for the species, must be introduced, which alters the value of r with each moult and must operate uniformly if the change in shape is to be gradual and incremental. This factor is simply the difference between the two growth rates K_L and K_H . The relationship between length and height in any growth stage is therefore expressed by:

$$\log L_n - r - pn = \log H_n.$$

Thus for the Berwick (1) individuals of *T. fittoni* the difference between $\log L_n$ and $\log L_{n-1}$ is 0.096 (K_L), and between H_n and H_{n-1} is 0.083, so that $p = K_L - K_H = 0.072$ and $r = \log L_0 - \log H_0 = 0.013$.

The L/H ratio in the female appears to be constant only in the pre-maturation moults, presumably because much of the increase in size at the maturation moult is in the *width* of the posterior half of the carapace. Thus in any assemblage which includes a large number of females the average length and height will be smaller than calculated. This is very evident in some of the data reproduced below.

In *T. fittoni* growth stage 10 is the mature adult and eight pre-maturation instars have been recognized. It does not follow that there are ten instars in the development of this species, and in the following discussion the growth stages which are arbitrarily taken to equal nK_L are not necessarily numerically equated with the instars.

The determination of ostracod instars has been thoroughly discussed by Kesling (1951, 1952, 1953), who has devised a circular slide rule (1953, fig. 2) to assist in the recognition of growth stages. The method, however, is based on Przibram's concept and is somewhat complex. In fact, the various methods of calculation so far suggested do not give results which differ greatly in the median range of ostracod sizes. The method adopted here, however, is simpler to operate than that advocated by Kesling and will give more satisfactory results for ostracods much smaller or larger than the average.

1. *Pteryocythereis jonesi* (Baird). Recent, marine, from bottom samples in the Irish Sea south of the Isle of Man. Measurements carried out by the writer. $K_L = 0.0882$, $K_H = 0.0680$, $r = 0.040$, $p = 0.0202$.

The method of calculating instar sizes suggested here can best be illustrated by taking

as an example measurements taken on the carapaces of a living species of ostracod, *Pterygocythereis jonesi*. In this species the adult is easily recognized by its development of a large clear hemispherical eye tubercle which is not present in earlier moults. The valves of 175 individuals were measured, right and left valves being recorded separately, but as the difference in length between the two was only 0.025 mm. in the adult it became apparent that this would have no significant effect on the scatter of the measurements.

Most valves (73) ranged from 0.713 to 0.813 mm. in length (mean 0.763) and from 0.400 to 0.488 mm. in height (mean 0.438). The next smallest instar (39 individuals) had lengths ranging from 0.588 to 0.675 mm. (mean 0.621) and heights ranging from 0.325 to 0.400 mm. (mean 0.363). The constant for growth in length (K_L) is therefore assumed to be close to 0.883 (log of 0.763) minus 0.793 (log of 0.621), that is about 0.090. Thus the instar with a length of 0.763 mm. would, according to the method described, be growth stage 10 and a closer approximation to K_L would be 0.088. In fact a value of 0.0882 for K_L gives the best fit between calculated and measured means.

The average difference between the logarithms of the heights in adjacent instars is 0.068. Thus the value for the constant p is 0.0202. The hypothetical growth stage 0 would therefore have the dimensions: length 0.100, height 0.091 mm., and the L/H ratio at growth stage 0 (r) = 0.040.

In Table 1 calculated means have been determined for each growth stage and compared with the means of those measured. It will be seen that the maximum difference between calculated and measured lengths is 0.006 mm., which is well within the standard deviation ($\sigma = 0.016$) of the measured lengths. Similarly the maximum difference between calculated and measured heights is 0.011 ($\sigma = 0.016$).

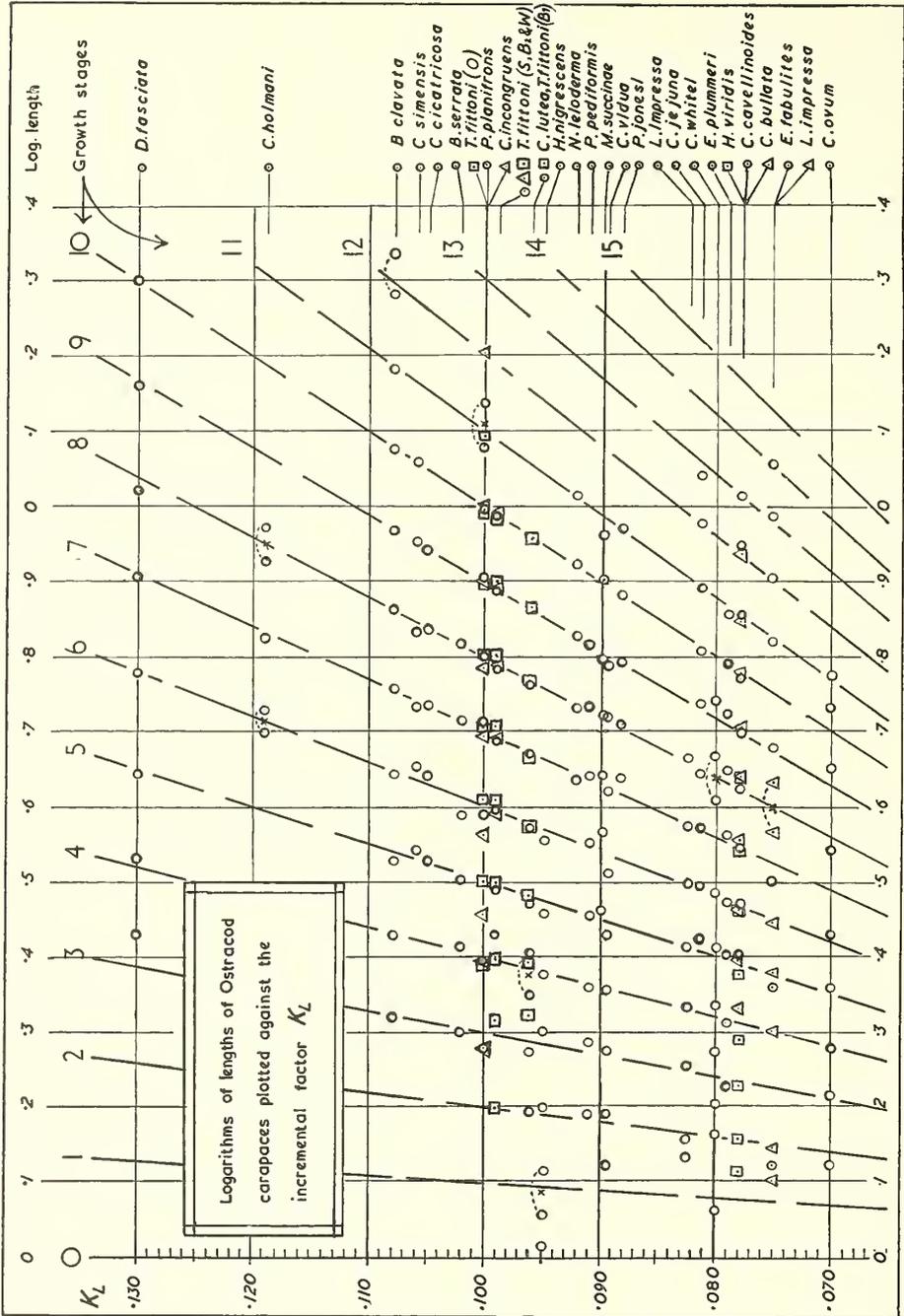
TABLE 1

Growth stage	Measured means (mm.)		Calculated means (mm.)		Number measured
	Length	Height	Length	Height	
7	0.438	0.275	0.414	0.273	1
8	0.513	0.313	0.508	0.319	8
9	0.621	0.363	0.622	0.373	39
10	0.763	0.438	0.762	0.437	73
*11	0.938	0.500	0.933	0.511	54

* Adult with eye tubercle

Much labour can be avoided by using the chart set out in text-fig. 1. All that is necessary is to mark off the logarithms of the means of the measured lengths of a species on the scale at the top of the chart and move down the vertical scale until the best fit for all growth stages is obtained, at which point the reading on the left hand scale will give the incremental factor K_L . It can be seen at a glance if any growth stages have been missed, or if two values have been obtained for the same instar. The method can be used to find both K_L and K_H , from which the other factors r and p can be calculated. Logarithms of means should fall on or near the broken lines.

Measurements of ostracod instars so far published indicate values for K_L ranging from a minimum of 0.070 (1.175) to a maximum of 0.128 (1.343). There appears to be no



obvious relationship between the number of possible growth stages and the dimensions of the ultimate instar (Table 28).

This method is here utilized to calculate dimensions for instars of those species for which measurements are available. Where differences between calculated and measured dimensions are greater than the standard deviation in any one growth stage further investigation is needed. It is suggested that errors are most frequently due to:

- (a) the number of individuals measured in any one growth stage being too small;
- (b) failure to collect representatives of some of the growth stages;
- (c) failure to recognize the growth stage to which individuals belong;
- (d) failure to recognize as the same species juveniles and adults which change markedly at the maturation moult, or to recognize sexual heteromorphs as the same species.

Most recent workers have recognized the importance of measuring a large number of individuals and it is usually only in older publications that the effect of measuring too few individuals becomes serious. More common is the omission of a growth stage, usually an early instar. Individuals belonging to the earlier growth stages are not easily found or abundant and are easily damaged, so that reliable means are difficult to obtain. Consequently individuals at extreme and opposite limits of the range for the instar may be thought to belong to different instars. Examples of this are illustrated below. It is suspected, but difficult to prove, that in some cases the juveniles have not been recognized as the same species as the adult. For example, if the eye tubercle in *Pterygocythereis jonesi* were taken to be a diagnostic feature of the species, then the pre-maturation moults would be excluded. Similarly in *Macrodentina retirugata* (Jones) the hingement changes sufficiently during development to place adult and early moults in distinct genera if a too rigid system of classification is adopted.

2. *Normanocythere leioderma* (Norman). Recent. From various localities, but mainly Spitzbergen. Data by Neale 1959. $K_L = 0.092$, $K_H = 0.072$, $r = 0.048$, $p = 0.020$.

TABLE 2

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Length	Height	Length	Height
7	0.435	0.280	0.441	0.286
8	0.540	0.330	0.545	0.337
9	0.675	0.400	0.673	0.398
10	0.840	0.470	0.832	0.470
11	1.030	0.550	1.028	0.555

Neale estimated the incremental factor to be 1.2445 (i.e. $K_L = 0.095$) and compared it with the generalized value of 1.256 given by Kesling (1953) (i.e. $K_L = 0.099$). He apparently assumed that the growth increment is the same for both length and height, but it is obvious that in this species this is not the case. Mean values are not given by Neale and the figures quoted above have been taken from the published graph (text-fig. 4). The maximum difference between measured and calculated means is 0.008 mm. Growth stage 11 is the mature adult. Neale assumes nine instars, thus his first instar

would be growth stage 3, for which the calculated dimensions are: length 0.189, height 0.147, compared with Neale's estimate of length 0.18 mm. It is not stated why earlier growth stages are not possible. Growth stage 2 is estimated to be length 0.153, height 0.125, a much closer approximation to the figures for *Cythere lutea* (length 0.156 mm.) and *Cyprideis littoralis* (length 0.150 mm.) given by Elofson (1941).

3. *Cypridopsis vidua* (O. F. Müller). Recent, marine, parthenogenetic. Material: culture from a single ostracod from Crystal Lake, Champaign County, Illinois. Data from Kesling 1952, p. 235, Table 2. $K_L = 0.0895$, $K_H = 0.080$, $r = 0.160$, $p = 0.0095$.

TABLE 3

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Length	Height	Length	Height
1	0.1322	0.0920	0.1229	0.0830
2	0.1555	0.1060	0.1510	0.1000
3	0.1882	0.1238	0.1856	0.1200
4	0.2268	0.1456	0.2281	0.1450
5	0.2698	0.1697	0.2802	0.1740
6	0.3334	0.2038	0.3444	0.2090
7	0.4180	0.2505	0.4232	0.2510
8	0.5280	0.3162	0.5200	0.3020
9	0.6170	0.3726	0.6390	0.3630

The correspondence between measured and calculated means is reasonably good, with a maximum difference of 0.022 mm., and this in the adult, which since the individuals were all females could have been anticipated. The effect of captivity on growth rate has not yet been demonstrated so that the figures given above may not be applicable to the species in its natural environment. Nine growth stages were recognized, of which the last is the adult moult.

4. *Hirshmannia nigrescens* (Baird). Recent, marine. Data from Elofson 1941, p. 400, lengths only. $K_L = 0.095$.

TABLE 4

Growth stage	Measured means (mm.)	Calculated means (mm.)
	Length	Length
0	0.103	0.100
1	0.114 0.130	0.125
	0.122	
2	0.158	0.155
3	0.200	0.193
4	0.236	0.240
5	0.287	0.299
6	0.361	0.372

Analysis suggests that the two mean lengths 0.114 mm. and 0.130 mm. refer to one instar; the mean 0.122 is close to the calculated length for growth stage 1. Apart from this the correspondence between measured and calculated lengths is close, with a maximum difference of 0.012 mm. The relatively large growth increment suggests the possibility of later instars as yet unidentified.

5. *Hirschmannia viridis* (O. F. Müller). Recent, marine. Data from Elofson 1941, lengths only. $K_L = 0.078$.

TABLE 5

Growth stage	Measured means (mm.)	Calculated means (mm.)
	Length	Length
1	0.130	0.120
2	0.144	0.143
3	0.170	0.171
4	0.195	0.205
5	0.238	0.246
6	0.295	0.294
7	0.350	0.352
8	0.434	0.421

Eight growth stages are recognized, the lengths of which correspond closely to those calculated, the maximum difference being 0.013 mm.

6. *Heterocypris incongruens* (Ramdohr). Recent, marine. Data from Schrieber 1922, lengths only. $K_L = 0.100$.

TABLE 6

Growth stage	Measured means (mm.)	Calculated means (mm.)
	Length	Length
3	0.190	0.200
4	0.250	0.251
5	0.288	0.316
6	0.368	0.398
7	0.496	0.501
8	0.608	0.631
9	0.800	0.794
10	1.008	1.000
11	—	1.260
12	1.600	1.590

The maximum difference between measured and calculated lengths is 0.030 mm. in growth stage 6. It is apparent that the pre-maturation moult, i.e. growth stage 11, has not been recorded.

7. *Macrocypris succinae* (G. W. Müller). Recent, marine. Data from G. W. Müller 1893, lengths only. $K_L = 0.090$.

TABLE 7

Growth stage	Measured means (mm.)	Calculated means (mm.)
	Length	Length
5	0.290	0.282
6	0.370	0.347
7	0.440	0.427
8	0.530	0.525
9	0.630	0.646
10	0.800	0.794
11	0.920	0.977

The correspondence between measured and calculated lengths is reasonably good, except in the last instar, where the difference is 0.057 mm. It is not known, however, how many individuals were measured and therefore how close the figure of 0.977 mm. is to the mean length of this instar.

8a. *Loxoconcha impressa* (Baird). Recent, marine. Data from G. W. Müller 1893, lengths only. $K_L = 0.075$.

TABLE 8

Growth stage	Measured means (mm.)	Calculated means (mm.)
	Length	Length
1	0.100	0.119
2	0.140	0.141
3	—	0.168
4	0.200	0.200
5	0.240	0.237
6	0.280	0.282
7	—	0.335
8	0.370 } 0.400 0.430 }	0.398

As the figures given below (8b, after Elofson) show, the growth in this species is quite normal, so that the irregularities in Müller's record must be due to the fact that some growth stages have been missed, namely stages 3 and 7. Furthermore, it is evident that the lengths 0.370 and 0.430 mm. must refer to the same instar. If this interpretation is correct then the maximum difference between measured and calculated lengths is 0.019 mm.

8b. *Loxoconcha impressa* (Baird). Recent, marine. Data from Elofson 1941, lengths only. $K_L = 0.0825$.

TABLE 9

Growth stage	Measured means ($\mu\text{m.}$)	Calculated means ($\mu\text{m.}$)
	Length	Length
1	0.136	0.121
2	0.144	0.146
3	0.180	0.177
4	0.216	0.214
5	0.260	0.259
6	0.316	0.313
7	0.375	0.378
8	0.463	0.457

Except for the first growth stage the correspondence between measured and calculated lengths is very close. These figures show that, as in *Theriosynoecum fittoni*, the growth rate in *L. impressa* is variable so that, for example, growth stage 7 in the individuals measured by Elofson is intermediate in size between growth stages 7 and 8 in the individuals measured by Müller.

9. *Bairdia serrata* Müller. Recent, marine. Data from G. W. Müller 1893, lengths only. $K_L = 0.102$.

TABLE 10

Growth stages	Measured means (mm.)	Calculated means (mm.)
	Length	Length
3	0.200	0.202
4	0.260	0.256
5	0.320	0.324
6	0.390	0.409
7	0.520	0.518
8	0.660	0.655

Correspondence between measured and calculated lengths is good except for growth stage 6, where the difference is 0.019 mm. This appears to be a rather high growth rate for a species with an adult only 0.660 mm. long. It is possible that later moults have been recorded as a distinct species.

10. *Cythere lutea* (O. F. Müller). Recent, marine. Data from Elofson 1941, lengths only. $K_L = 0.096$.

TABLE 11

Growth stage	Measured means (mm.)	Calculated means (mm.)
	Length	Length
2	0.156	0.156
3	0.188	0.194
4	0.224 0.255	0.240
	0.296	
5	0.296	0.302
6	0.375	0.377
7	0.470	0.470
8	0.578	0.586

Correspondence between measured and calculated lengths is good if, as is suspected, the lengths 0.224 and 0.255 mm. belong to the same instar. As in *B. serrata* the growth increment is large for a species with a maximum recorded length of less than 0.600 mm.

11. *Cyclocypris ovum* (Jurine). Recent, fresh-water. Data from Claus 1872, lengths only. $K_L = 0.070$.

TABLE 12

Growth stage	Measured means (mm.)	Calculated means (mm.)
	Length	Length
2	0.132	0.138
3	0.165	0.162
4	0.190	0.191
5	0.230	0.224
6	0.270	0.263
7	—	0.309
8	0.350	0.363
9	0.450	0.427
10	0.540	0.501
11	0.600	0.589

No length for growth stage 7 was recorded. The difference between measured and calculated lengths in growth stages 9 and 10, i.e. 0.023 and 0.039 mm. respectively, is rather large, otherwise the correspondence is reasonably good.

12. *Dolerocypris fasciata* (O. F. Müller). Recent, fresh-water. Data from Claus 1872, lengths only. $K_L = 0.130$.

TABLE 13

Growth stage	Measured means (mm.)	Calculated means (mm.)
	Length	Length
3	0.270	0.246
4	0.340	0.331
5	0.440	0.447
6	0.600	0.603
7	0.800	0.813
8	1.050	1.096
9	1.450	1.480
10	2.000	2.000

The difference between measured and calculated lengths is rather high in growth stage 8 (0.046 mm.), otherwise the correspondence is reasonably good.

13. *Cythereis simensis* (Le Roy) = *Archicythereis newportensis* Le Roy. 'Middle Pliocene', San Diego formation, California. Data from Spjeldnaes 1951, after Le Roy 1945. $K_L = 0.106$, $K_H = 0.100$, $p = 0.006$, $r = 0.194$.

TABLE 14

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Length	Height	Length	Height
5 (A'')	0.350	0.190	0.339	0.218
6 (A')	0.450	0.270	0.433	0.255
7 (A)	0.540	0.310	0.552	0.321
8 (B)	0.680	0.390	0.705	0.404
9 (C)	0.900	0.510	0.900	0.508
10 (E)	1.180	0.640	1.150	0.640

Le Roy believed that an instar (D) occurred between C and E but this is clearly not the case. The length of growth stage A'' was misquoted by Spjeldnaes as 0.380 mm.

14. *Cythereis holmani* Le Roy. Miocene, marine, east coastal area of Sumatra. Data from Spjeldnaes 1951, after Le Roy 1945. $K_L = 0.119$, $K_H = 0.105$, $r = 0.140$, $p = 0.014$.

TABLE 15

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Length	Height	Length	Height
6 { A B	0.500 } 0.520	0.300 } 0.305	0.518	0.309
7 C	0.670	0.400	0.681	0.394
8 { D♀ D♂	0.850 } 0.895	0.510 } 0.490	0.895	0.501

These figures are difficult to interpret. Presumably the dimensions given for growth stages A and B appertain to one instar. Only the average dimensions of the adult male and female are closely related to those calculated for growth stage 8.

15. *Candona whitei* Scott and Smith. Eocene, fresh-water. Data from Scott and Smith 1951. $K_L = 0.080$, $K_H = 0.074$, $r = 0.180$, $p = 0.006$.

TABLE 16

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Length	Height	Length	Height
1	0.120	0.092	0.120	0.078
2	—	—	0.145	0.093
3	—	—	0.174	0.110
4	0.204	0.146	0.209	0.131
5	0.258	0.159	0.251	0.155
6	0.304	0.187	0.302	0.184
7	0.367	0.218	0.363	0.218
8	0.434	0.258	0.437	0.258
9	0.532	0.306	0.525	0.306
10	—	—	0.631	0.363
11	0.718 } 0.771	0.407 } 0.438	0.759	0.431
12	0.824 } 0.974	0.468 } 0.554	0.912	0.511

The correspondence between measured and calculated dimensions is so close in the earlier growth stages that the figures given for the last three instars need to be critically examined. A possible interpretation is that growth stage 10 has not been recorded, and that for the next growth stage both high and low variants have been given. The graph in Scott and Smith's paper, however, shows no obvious grouping of the length/height ratios. The dimensions given under growth stage 1 are those of the supposed egg.

16. *Cytherella bullata* Alexander. Cretaceous, marine. Prairie Bluff, Pontotoc County, Mississippi. Data from Shaver 1953. $K_L = 0.078$, $K_H = 0.076$, $r = 0.144$, $p = 0.002$.

TABLE 17

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Length	Height	Length	Height
4	0.216	0.139	0.205	0.145
5	0.250	0.163	0.246	0.172
6	0.294	0.192	0.294	0.205
7	0.364	0.243	0.352	0.244
8	0.439	0.291	0.421	0.291
9	0.508	0.337	0.504	0.347
10	0.597	0.400	0.603	0.413
11	0.707	0.473	0.721	0.492
12	0.867	0.588	0.863	0.586

Measured and calculated values correspond very well throughout, the maximum difference in length being 0.018 mm. in growth stage 8, and in height 0.019 mm. in growth stage 11.

17. *Aurikirkbya wardensis* (Hamilton). Permian, Glass Mountains, Texas. Data from Sohn 1950a. $K_{L\text{hinge}} = 0.083$, $K_H = 0.079$.

TABLE 18

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Hinge length	Height	Hinge length	Height
n	0.828	0.414	0.826	0.430
n1	0.999	0.519	1.000	0.515
n2	1.219	0.631	1.211	0.618
n3	1.426	0.730	1.466	0.741
n4	1.768	0.882	1.774	0.889

The data relating to this species have proved most difficult to analyse. Sohn's figures suggest a periodicity which could be mistaken for instar intervals. The author says (p. 36) that it is not possible by examining these figures to recognize growth stages by measurement alone. The obvious periodicity is, however, due to some extraneous factor, most probably the micrometer unit interval. If, for example, the micrometer unit used was 0.049 mm. and the half unit estimated as either 0.02 or 0.03 such a periodicity could be expected. A detailed analysis of Sohn's figures suggests that five growth stages were represented in the material and that their dimensions are approximately as given in the table above.

18. *Pseudobythocypris pediformis* Knight. Pennsylvanian, marine. Exline Shale, Peoria County, Illinois. Data from Shaver 1958. $K_L = 0.091$, $K_H = 0.078$, $r = 0.148$, $p = 0.013$.

TABLE 19

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Length	Height	Length	Height
2	0.155	0.103	0.152	0.102
3	0.193	0.123	0.188	0.122
4	0.230	0.138	0.231	0.146
5	0.286	0.167	0.285	0.175
6	0.358	0.208	0.352	0.209
7	0.440	0.250	0.434	0.250
8	0.542	0.300	0.535	0.299
*9	0.656	0.354	0.659	0.359

* Includes both males and females

Correspondence between measured and calculated values is very close, with a maximum difference of only 0.008 mm.

19. *Cavellina cavellinoidea* (Bradfield). Marine, Pennsylvanian, Lonsdale Zone, Vermillion County, Illinois. Data from Shaver 1951, lengths only. $K_L = 0.078$.

TABLE 20

Growth stage	Measured means (mm.)	Calculated means (mm.)
	Length	Length
5	0.254	0.246
6	0.297	0.294
7	0.352	0.352
8	0.422	0.421
9	0.500	0.504
10	0.592	0.603
11	0.720	0.721
12	0.892	0.863
13	1.038	1.033

The greatest discrepancy between measured and calculated values (0.029 mm.) is in growth stage 12.

20. *Cavellina jejuna* Coryell and Sample. Marine, Pennsylvanian, Exline Shale, Peoria County, Illinois. Data from Shaver 1951, lengths only. $K_L = 0.0815$.

TABLE 21

Growth stage	Measured means (mm.)	Calculated means (mm.)
	Length	Length
5	0.267	0.256
6	0.314	0.308
7	0.375	0.372
8	0.443	0.449
9	0.548	0.541
10	0.646	0.653
11	0.779	0.788
12	0.953	0.951
13	1.098	1.147

Correspondence between measured and calculated lengths is good except for the ultimate stage. This species and *C. cavellinoides* have more than the average number of growth stages.

21. *Ectodemites plummeri* Cooper. Marine, Pennsylvanian, lower Marble Falls formation, Texas. Data from Cooper 1945. $K_L = 0.079$, $K_H = 0.079$, $r = 0.185$, $p = 0$.

TABLE 22

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Length	Height	Length	Height
3	0.169	0.113	0.173	0.113
4	0.206	0.138	0.207	0.135
5	0.253	0.163	0.248	0.162
6	0.300	0.193	0.298	0.195
7	0.369	0.244	0.357	0.233
8	0.447	0.281	0.429	0.280
9	0.531	0.338	0.514	0.336
10	0.619	0.400	0.617	0.403
11	0.725	0.466	0.740	0.481

Correspondence between measured and calculated dimensions is close, the maximum difference being 0.018 mm. in growth stage 8. This is one of those rare cases where $p = 0$, i.e. where the growth rate in length and height is the same, so that the adult is proportionately higher than the juvenile.

Cooper used a method of calculation based on Huxley's (1932) differential growth formula $y = bx^k$, and found that $H = 0.765 L^{0.969}$. This, however, assumes a uniform growth rate ratio, which is not the case in most other species.

22. *Ctenocolina cicatricosa* (Warthin). Middle Devonian, marine, Norway Point formation, Traverse Group, Michigan. Data from Kesling 1951. $K_L = 0.105$, $K_H = 0.100$, $r = 0.233$, $p = 0.005$.

TABLE 23

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Length	Height	Length	Height
5	0.338	0.187	0.335	0.185
6	0.441	0.235	0.427	0.233
7	0.541	0.288	0.543	0.293
8	0.686	0.369	0.692	0.369
9	0.874	0.474	0.881	0.474

Correspondence between measured and calculated dimensions is good with a maximum difference of 0.014 mm. If in fact growth stage 9 is the ultimate one it is apparent that the size attained by the adult is not directly related to the factor K_L . It may be that when K is large the number of moults is fewer, and when K is small more moults are needed to reach maturity. Thus it is possible that neither growth rate, number of instars, nor adult size are constant for the species, but that within certain limits all may vary according to ecological conditions.

23. *Beyrichia* (*Mitrobeyrichia*) *clavata* Kolmodin = *Beyrichia jonesi* Boll. Marine, Silurian, Mülde Marl (Wenlock), Gotland.

(a) Data from Spjeldnaes 1951, lengths only. $K_L = 0.108$.

TABLE 24

Growth stage	Measured means (mm.)	Calculated means (mm.)
	Length	Length
3	0.214	0.211
4	0.269	0.270
5	0.343	0.347
6	0.443	0.445
7	0.571	0.570
8	0.728	0.731
9	0.927	0.938
10	1.185	1.200
11	1.515	1.540
12	1.914 } 2.171 }	2.043

The last two lengths, though recorded as separate instars, are more probably sexual dimorphs. If a further growth stage were present it could be expected to have a length of 2.540 mm. Correspondence between measured and calculated lengths is reasonably good for all growth stages except the last.

(b) Data from Martinsson 1957. $K_{L\text{hinge}} = 0.094$, $K_{L\text{anterior}} = 0.100$.

TABLE 25

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Hinge length	Anterior length	Hinge length	Anterior length
n	0.360	0.250	0.359	0.250
n+1	0.440	0.305	0.446	0.315
n+2	0.540	0.380	0.553	0.396
n+3	0.670	0.480	0.687	0.499
n+4	0.830	0.620	0.853	0.628
n+5	1.060	0.790	1.060	0.791
n+6	1.320	0.990	1.320	0.996
n+7	1.630	1.240	1.630	1.254
n+8	1.950 [♂] 1.0 [♀]	1.375 [♂] 1.240 [♀]	2.030	1.578

The correspondence between measured and calculated dimensions is so close in all but the last instar that this remarkable departure from the normal growth rate at the maturation moult is difficult to explain, unless virtually all the growth in length has taken place in the posterior half of the carapace (see *T. fittoni*, where the posterior growth rate is greater than the anterior).

24. *Primitopsis planifrons* Jones. Marine, Silurian, Mülde Marl (Wenlock), Gotland. Data from Martinsson 1956, means taken from the graph, *not* from the table. $K_L = 0.100$, $K_H = 0.100$, $r = 0.140$, $p = 0$.

TABLE 26

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Length	Height	Length	Height
6	0.390	0.290	0.398	0.289
7	0.520	0.370	0.501	0.363
8	0.635	0.465	0.631	0.457
9	0.805	0.590	0.794	0.576
10	0.995	0.730	1.000	0.725
11	{ 1.200 1.300	0.865	1.291	0.912

Like *Ectodemites plummeri*, *P. planifrons* is unusual in that the length/height ratio does not change during development. Again, as has been noted in many cases, the mature individual is smaller than would have been expected if the growth rate were uniform throughout. Possibly at the maturation moult a part of the growth potential is diverted to the development of the reproductive organs.

25. *Eoleperditia fabulites* (Conrad). Marine, Middle Ordovician, northern Illinois. Data from Scott 1951. $K_L = 0.750$, $K_H = 0.701$, $r = 1.303$, $p = 0.049$.

TABLE 27

Growth stage	Measured means (mm.)		Calculated means (mm.)	
	Length	Height	Length	Height
2	1.325	0.880	1.410	1.023
3	—	—	1.680	1.203
4	—	—	2.000	1.413
5	2.300	1.900	2.370	1.660
6	—	—	2.820	1.951
7	3.175	2.150	3.350	2.290
8	—	—	3.980	2.695
9	4.795	3.145	4.730	3.170
10	—	—	5.620	3.722
11	6.638	4.247	6.680	4.373
12	8.039	5.116	7.940	4.151
13	9.773	6.063	9.440	6.054
14	11.435	7.263	11.200	7.114

Unless this species differs from all other recorded species in its method of growth, then it is apparent that the dimensions of five growth stages have not been recorded. One of the useful applications of the method of analysing growth in ostracods described above is the ease with which missing growth stages can be detected and their approximate dimensions determined.

TABLE 28. Range of growth increments in Ostracods

Species	1	2	3	4	Age	5	6
<i>D. fasciata</i>	0.130	2.000	2.000	10	Recent	200	1.349
<i>C. holmani</i>	0.119	0.895	0.895	8	Tertiary	112	1.315
<i>B. clavata</i>	0.108	2.043	1.980	12	Silurian	165	1.282
<i>C. simensis</i>	0.106	1.180	1.150	10	Tertiary	115	1.276
<i>C. cicatricosa</i>	0.105	0.874	0.881	9	Devonian	98	1.274
<i>B. serrata</i>	0.102	0.660	0.655	8	Recent	82	1.265
<i>T. fittoni</i> (O)	0.100	1.080	1.000	10	Cretaceous	100	1.259
<i>P. planifrons</i>	0.100	1.300	1.291	11	Silurian	117	1.259
<i>H. incongruens</i>	0.100	1.600	1.590	12	Recent	133	1.259
<i>T. fittoni</i> (W, S, B ₂)	0.099	1.060	0.977	10	Cretaceous	98	1.256
<i>T. fittoni</i> (B ₁)	0.096	0.940	0.912	10	Cretaceous	91	1.247
<i>C. lutea</i>	0.096	0.578	0.586	8	Recent	73	1.247
<i>H. nigrescens</i>	0.095	0.361	0.372	6	Recent	62	1.245
<i>N. leioderma</i>	0.092	1.030	1.028	11	Recent	93	1.236
<i>P. pediformis</i>	0.091	0.656	0.659	9	Carboniferous	73	1.233
<i>M. succinae</i>	0.090	0.920	0.977	11	Recent	89	1.230
<i>C. vidua</i>	0.089	0.617	0.639	9	Recent	78	1.229
<i>P. jonesi</i>	0.088	0.938	0.933	11	Recent	85	1.225
<i>L. impressa</i>	0.083	0.463	0.457	8	Recent	57	1.209
<i>C. jejuna</i>	0.082	1.098	1.147	13	Carboniferous	88	1.206
<i>C. whitei</i>	0.080	0.974	0.912	12	Tertiary	76	1.202
<i>E. plummeri</i>	0.079	0.725	0.740	11	Carboniferous	67	1.200
<i>C. bullata</i>	0.078	0.867	0.863	12	Cretaceous	72	1.197
<i>C. cavellinoides</i>	0.078	1.038	1.033	13	Carboniferous	79	1.197
<i>H. viridis</i>	0.078	0.434	0.421	8	Recent	53	1.197
<i>E. fabnilites</i>	0.750	11.44	11.20	14	Ordovician	80	1.189
<i>L. impressa</i>	0.075	0.400	0.398	8	Recent	50	1.189
<i>C. ovum</i>	0.070	0.600	0.589	11	Recent	54	1.175

Column 1, growth factor for length, K_L .

„ 2, mean of measured lengths, adult.

„ 3, calculated length of adult.

„ 4, number of theoretical growth stages.

„ 5, adult length divided by number of growth stages.

„ 6, incremental factor for growth in length.

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SERIAL SECTIONING OF STEINKERNS

by J. W. STANLEY

SERIAL sections have long been used for the investigation of the internal structures of fossil invertebrates, especially brachiopods. Sectioning techniques, originally applied to material which proved difficult to prepare by excavation of the internal matrix, are now commonly used as a routine procedure. With most unsilicified Lower Palaeozoic material sectioning is quicker and more likely to yield accurate information than other methods of preparation.

During a study of the Silurian brachiopod genus *Sphaerirhynchia* a situation arose in which the interiors of some forms were known only from serial sections of recrystallized specimens, and of others only from latex impressions of a small number of natural completely decalcified specimens. To assist comparison of the two forms it seemed desirable to be able to present the information from both in the same manner. Since it was not possible to prepare satisfactory steinkerns from the recrystallized specimens an attempt was made to serially section replicas of the natural steinkerns.

Technically there is no reason why the following procedure (as from stage 3) should not be applied directly to the specimen. However, a plaster replica would normally be prepared as a preliminary to sectioning in any case so that destruction of the original would be to no advantage in terms of time, labour, or the quality of the resulting sections.

TECHNIQUE

1. A latex impression of the steinkern is prepared in the normal way. Special care is taken to ensure penetration of the latex into crural cavities, &c. (Latex used: M. R. Revultex, by Revertex Ltd., Harlow, Essex.)

2. The latex impression is used as a mould for the casting of a plaster replica of the steinkern. (Plaster: dental quality.)

3. The plaster replica is blackened with a thin complete coating of indian ink, allowed to dry, and then embedded in white dental plaster. It is important to ensure penetration of the white plaster into crural cavities, &c., in the replica. This is assisted by using a plaster mix of thin creamy consistency applied by brush.

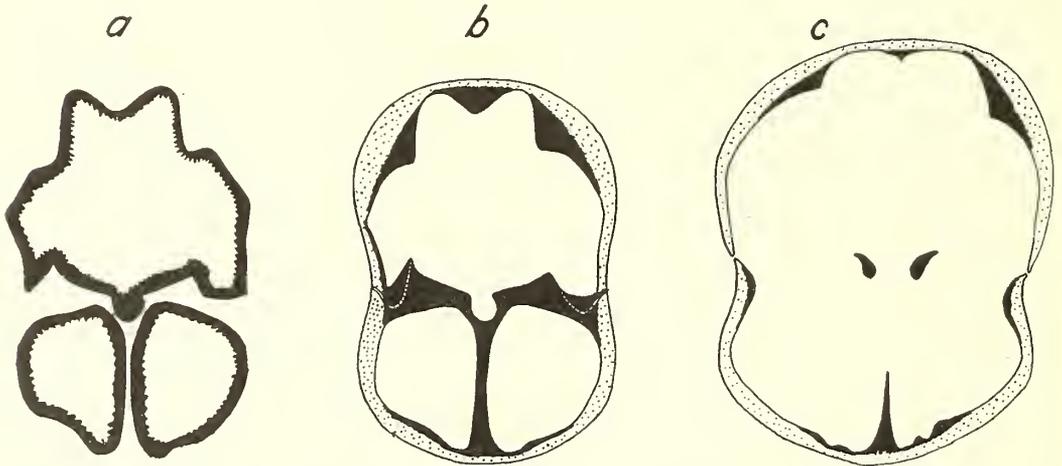
4. The block is sectioned in the normal way using parallel grinding apparatus (e.g. Croft 1950; Jefferies, Adams, and Miller 1962; Hendry, Rowell, and Stanley 1963). For less accurate work, or preliminary investigation in the absence of other equipment, a lap or plate for hand grinding could be used.

The technique has proved successful to a degree governed initially by the quality of the original steinkern and secondly by the care taken in subsequent preparation.

Ground section surfaces (see text-fig. 1*a*) show a black outline of the internal structures and interior shell surface. Section surfaces may easily be photographed as the contrast is high. Structures such as median septum, crura, cruralium, and dental plates

can be clearly seen in section and their shapes compared directly with those revealed in conventional sections.

Reconstruction of the outer shell surface is assisted by examination of the cavity from which the steinkern was obtained. This can only be approximate, although the minimum thickness of shell in certain parts (e.g. at the sides of the ventral and dorsal muscle impressions) may be definitely indicated. Dentition cannot be accurately reconstructed although the amount of variation possible is limited by the shape of the shell material in the appropriate area on the sections.



TEXT-FIG. 1. Section surfaces of a brachiopod steinkern replica, $\times 6$.

a. Section as seen on the block after grinding. The clean edge to the black area represents the junction between the position of the original shell and internal matrix. The blurred edge results from ink soaking into the plaster of the replica.

b. The same section drawn in the conventional manner with shell material in black, or where inferred, in stippled shading. Teeth and sockets reconstructed.

c. A subsequent section showing the accuracy with which fine structures such as crura may be reproduced. Shading as in *b*.

Interesting possibilities emerge for the technique since there is no destruction of the original specimen. Sections of valuable specimens (e.g. rare specimens and types) preserved as steinkerns can be made provided the original will withstand removal of the latex impression.

It is not suggested that sections prepared in this way are superior to photographs of latex impressions of steinkerns which are frequently published; on the contrary, they are subsidiary, enabling a more complete presentation of information and easier comparison with forms whose internal structures are known only from conventional sections.

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THE CORAL GENUS *METRIOPHYLLUM* EDWARDS AND HAIME

by F. J. W. HOLWILL

ABSTRACT. The morphology of the genus *Metriophyllum* has been investigated with the aid of serial sections and the skeletal structure of the coral is described in detail. A review of all recorded species of *Metriophyllum* is made and a revised description is given of *M. bouchardi* and *M. gracile*; in addition a new species is described from the Ilfracombe Beds (Middle/Upper Devonian) of north Devon.

THE genus *Metriophyllum* was established by Edwards and Haime in 1850 with *M. bouchardi* as the type species; they did not, however, publish a full description with figures until the following year (Edwards and Haime 1851). The known range of the genus extends from Middle Devonian to Lower Permian, though the genus is particularly characteristic of the Middle and Upper Devonian. It includes some of the smallest corals yet described—*M. gracile* has an average length of 6–7 mm. and an average maximum diameter of 3–4 mm.

Edwards and Haime (1851) originally placed *Metriophyllum* in the Stauridae, but Hill (1939) proposed a new family—the Metriophyllidae, with *M. bouchardi* as type genus—to contain *Metriophyllum* and allied forms; subsequent writers, notably Stumm (1949) and Lecompte (1952), have accepted the new family though they differ in their opinions as to the genera which should be included.

Possibly because of the small size of most species, the morphology of *Metriophyllum* has not been studied in detail hitherto. Even in the present study, it has been found difficult to discover specimens in which the apical end is completely preserved, and the earliest ontogenetic stages are therefore still not fully known.

In preparing this paper, I have collected extensively from the type locality of *M. bouchardi* at Ferques (Boulogne, France) and also from the Gerolstein area of Germany. In addition, I have studied collections from the British Museum (Nat. Hist.) and the Geologisch-palaeontologisches Institut und Museum at Bonn; I have also had original photographs of type specimens from the New York State Museum available for comparisons.

Techniques. Thin sections were made in the normal way, except that because of the small size of most of the specimens, a dental cutting wheel, making a cut of less than 0.5 mm., was used instead of the normal petrological slicing wheel. For serial sections, the specimens were embedded in a transparent plastic such as 'CEEMAR'; the resulting block was then milled flat on both sides and all subsequent grinding was done by hand. The advantage of this is that the specimen can be kept under constant observation and drawings made at minute intervals to record the rapidly changing arrangement of the septa and the carinae. At convenient intervals, cellulose peels were taken and these were mounted between glass slides and used as photographic negatives. The peels were made by dipping the etched surface of the coral into a 2/1 solution of butyl and amyl acetate

and then pressing the saturated surface on to a piece of transparent cellulose 0.01 in. thick. The advantage of this method over the one described by Butler (1935) is its speed and the ease with which the peel can be removed from the coral. The interval between successive serial sections was found by measuring the total thickness of the specimen plus plastic, before and after grinding, by means of an engineer's micrometer.

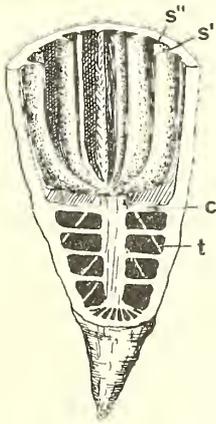
In some specimens there was little or no colour contrast between the coral structure and the infilling calcite. The latter was found to be slightly richer in iron than the coral itself, so that by dipping the polished surface of the coral into a solution of potassium ferricyanide and dilute hydrochloric acid (see Henbest 1931) it was found possible to stain the infilling material differentially. This greatly facilitated both photographic and microscopic examination of such specimens.

Genus *METRIOPHYLLUM* Edwards and Haime 1850

Metriophyllum Edwards and Haime 1850, p. lxxix.

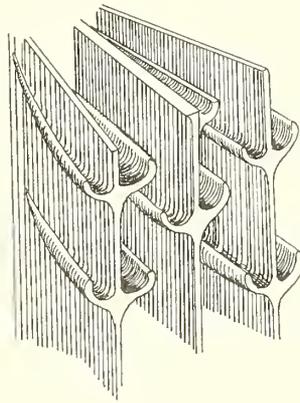
Lopholasma Simpson 1900, p. 206, figs. 19–21.

Type species (by original designation). *Metriophyllum bouchardi* Edwards and Haime 1850, p. lxxix; 1851, p. 318, pl. 7, figs. 1, 1a, 1b, 2, 2b. Upper Devonian, Frasnian (Beaulieu Shales and Ferques Limestone), Ferques, near Boulogne, France.



TEXT-FIG. 1

TEXT-FIG. 1. Exploded diagrammatic view showing the main morphological features of *Metriophyllum*.
s' = major septa; s''—minor septa; t = tabulae; c = carinae.



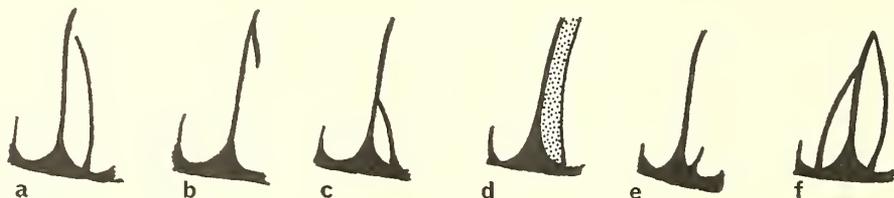
TEXT-FIG. 2

TEXT-FIG. 2. Diagram showing the form of the horizontal trough-shaped carinae developed at alternating levels on adjacent septa.

Description. Small solitary turbinato to ceratoid corals. Calice deep and steep sided with septa projecting as sharp low ridges on the inner side. The floor of the calice is flat or slightly concave and the septa extend across this floor to meet at the axis where they are welded together with sclerenchyme to form a pseudo-columella (text-fig. 1; Pl. 16, fig. 2). The outer walls are also much thickened with sclerenchyme. The sides of the septa below the calice carry horizontal or nearly horizontal carinae which have upturned outer edges (text-fig. 2). The carinae may occur at the same or differing levels on either side of a septum but they always alternate in level with those on the neighbouring septa.

Tabulae are very thin and steeply inclined downwards away from the axis. Rejuvenation is uncommon but has been observed in *M. bouchardi*. It is doubtful whether true dissepiments are present in any species.

Remarks. The genus *Lopholasma* (type species *L. carinatum* Simpson 1900) is regarded as congeneric with *Metriophyllum* since transverse and longitudinal sections (Pl. 16, figs. 2 and 3) clearly show the presence of horizontal carinae so typical of *Metriophyllum*. (The dissepiments which Simpson (1900) described in *L. carinatum* are in fact the steeply sloping tabulae being cut by the transverse section; longitudinal sections confirm this.) I prefer to follow Stumm (1949) and Hill (1956) in regarding *Stereolasma* Simpson 1900 (type species *Streptelasma rectum* Hall 1876 (in part)) as a separate genus and not congeneric with *Metriophyllum* as Smith (1945) suggests; the horizontal carinae appear



TEXT-FIG. 3. Diagram showing some characteristic appearances of the carinae when cut by transverse sections.

to be a well marked and persistent character in the genus *Metriophyllum* and although *Stereolasma* is clearly a related form, the absence of any carinae makes it inadvisable to include it within the genus *Metriophyllum*. The same comments also apply to the specimens in the New York State Museum labelled *M. ungula* (Hall); longitudinal sections of this species clearly show that it lacks horizontal carinae and almost certainly belongs to the genus *Stereolasma*; (compare median longitudinal sections of *M. carinatum*, *S. rectum*, and '*M.*' *ungula*—Pl. 16, figs. 3, 5, and 7).

Range. Middle Devonian–Lower Permian.

Carinae. Edwards and Haime failed to recognize the true nature of the carinae and they interpreted the strong horizontal processes seen in the median section (text-fig. 1; Pl. 16, fig. 1) as tabulae. Barrois (1882) was the first to publish a diagram showing the spur-like appearance of carinae in longitudinal sections and Simpson (1900) recognized the existence of the horizontal carinae, but he did not appreciate the significance of the spur-like processes on the sides of the septa. Soshkina (1928) appears to have been the first to recognize their true significance.

Because of the unusual form of the carinae within the genus *Metriophyllum* much confusion may arise when interpreting their appearance in sections. In transverse sections they may simulate septa or appear as spurs on either side of the true septa (Pl. 18, fig. 2); they may also give the impression that a septum is splitting. Text-fig. 3 shows some of the appearances of carinae in transverse sections. Where the plane of section cuts through the junction between a septum and carinae the septum will appear to be much thickened (text-fig. 3d). In longitudinal sections the carinae commonly appear as lobed hooks or spurs but in median sections they show as strong horizontal bars.

In *M. bouchardi* and *M. gracile* the carinae are very delicate trough-shaped structures (Pl. 18, figs. 6, 10, and Pl. 19), but in *M. carinatum* they are stouter and less upturned at their outer edges (Pl. 16, fig. 3). In all the species which have been examined the outer upturned edges of the carinae tend to be thickened (text-fig. 2) so that they appear lobed in longitudinal sections.

Wang (1950) demonstrated that the carinae are built up of fibrous tissue, as are the septa; the outer wall is made up of lamellar tissue. These skeletal structures are clearly seen in the section of *M. bouchardi* (Pl. 16, fig. 6).

The carinae only start to develop at the base of the calice, and the septa extend across the floor of the calice before any carinae are formed. It is often possible to distinguish a suture between the septum and its attached carinae (see Pl. 16, figs. 3 and 6) where impurities have become trapped.

Tabulae. These are very thin and not always seen even in median sections. They slope at about 45° down from the axis (Pl. 16, fig. 1, and Pl. 19, fig. *a*) and may terminate against the carinae. In longitudinal sections, not passing through the axis, they appear as plates which link the carinae (Pl. 19, fig. *c*, and Pl. 18, fig. 6). Barrois (1882) recognized the true tabulae, though not in median sections; his figure (pl. vii, fig. 2*d*) shows very regularly developed tabulae linking the outer lips of neighbouring carinae and he described them as 'planchers ondulés'. Hill (1939) was the first to note that they are 'steeply domed' when seen in median section.

Plate 19 shows longitudinal serial sections from the axis to the outer wall of *M. bouchardi*. The form of the carinae can be appreciated by tracing them individually through the series from the strong horizontal cross-bar appearance (fig. *a*) to the spur-like appearance seen in off-median sections. The outward sloping tabulae are clearly seen in the median section (fig. *a*) and the way in which they cut the carinae is seen in fig. *b*. Later sections show the way in which tabulae extend between the carinae—very much less regularly than suggested by Barrois's figure in his description of the Asturian specimens.

Metriophyllum bouchardi Edwards and Haime 1850

Plate 16, fig. 6; Plate 17, figs. 1–6, 11; Plate 18, figs. 7, 11; Plate 19; text-fig. 4

1845 *Cyathophyllum mitratum* (Schlotheim); Michelin, p. 183, pl. xlvii, fig. 7 (*non Hyppurites mitratum* Schlotheim 1820, p. 352).

1850 *Metriophyllum Bouchardi* Edwards and Haime, p. lxxix (*nom. nud.*).

1851 *Metriophyllum Bouchardi* Edwards and Haime, p. 318, pl. 7, figs. 1, 1*a–b*, 2, 2*b*.

Description. Small solitary turbinate to ceratoid corals with a maximum diameter of about 10 mm. Overall length rarely exceeds 20 mm. The outer surface usually shows longitudinal striations corresponding to the internal positions of the septa, and about three well-marked transverse constrictions or wrinkles (Pl. 17, fig. 1); more rarely the outer surface is nearly smooth. The calice is deep and steep sided; it may occupy a third of the total length of the coral, but the walls are frequently broken off near the base of the calice (Pl. 19, fig. 11); the floor of the calice is flat or gently concave. Septa within the calice are short and project from the wall as sharp ridges; both major and minor septa are seen in the calice, the latter being slightly less prominent than the major ones (Pl. 17, figs. 3 and 4); subsequently the septa and the wall are thickened with the result

that the minor septa are completely embedded in sclerenchyme; however, it is at these minor septal positions that the carinae join the outer wall. The number of major septa is commonly 18–20, though Edwards and Haime (1851) give 22–24 as characteristic of the species; the septa are straight or only slightly flexed and they extend across the floor of the calice to meet at the axis; the axial ends are slightly swollen and they are cemented together by sclerenchyme to form a pseudocolumella. In some specimens the columella is narrow, while in others it occupies nearly one-third of the lumen (Pl. 16, fig. 6).

The major septa carry horizontal carinae which have upturned outer edges. They are developed at alternate levels on adjacent septa and usually at different levels on opposite sides of the same septum. The carinae are spaced at about 1 mm. intervals. Tabulae are thin discontinuous plates sloping downwards away from the axis; they are irregularly spaced.

Rejuvenation is rare but does occur (Pl. 17, figs. 2 and 5; Pl. 18, fig. 7).

Horizon and locality. Upper Devonian (Frasnian); from the Beaulieu Shales and Ferques Limestone, Ferques, near Boulogne.

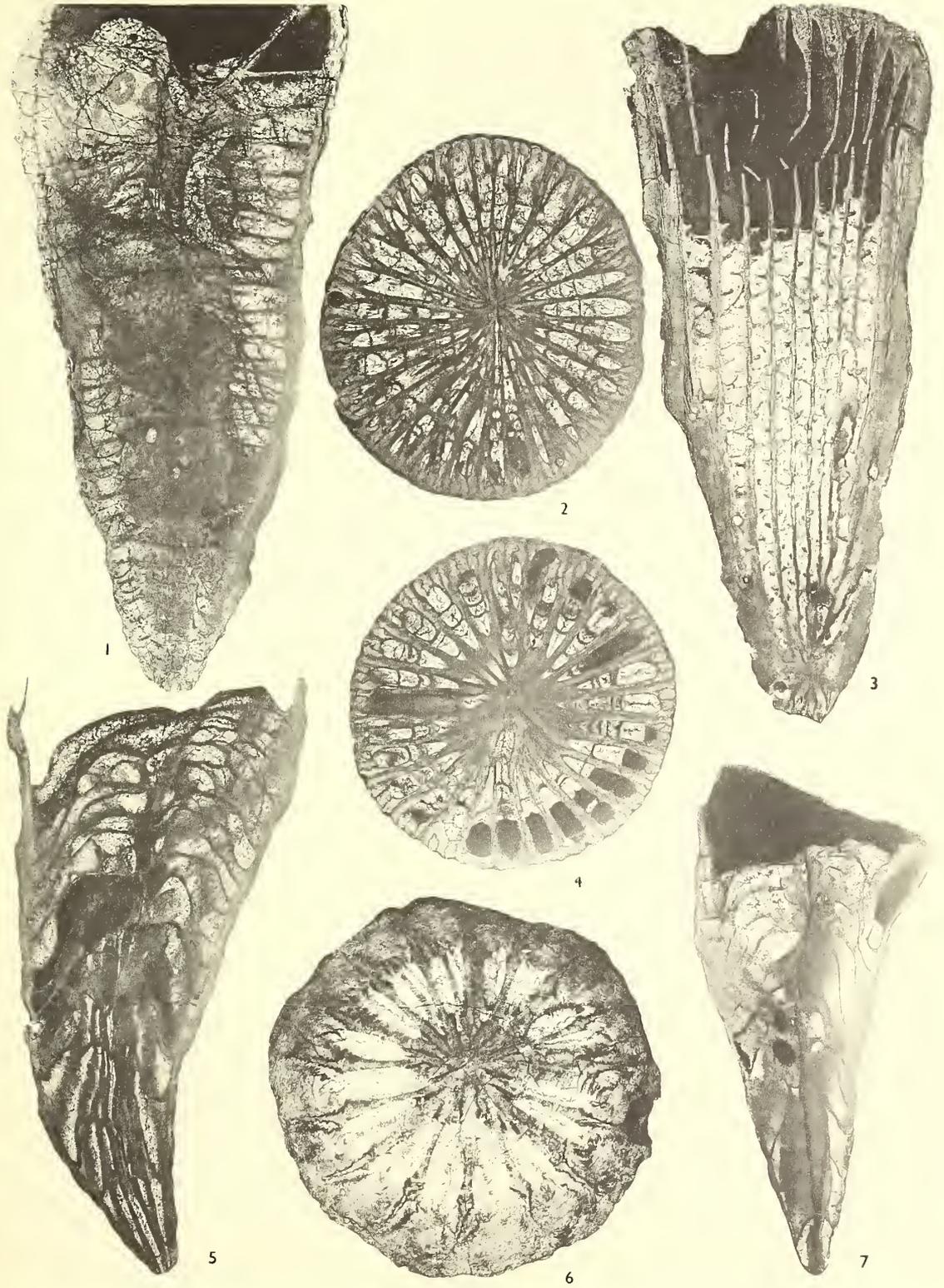
Discussion. Lang, Smith and Thomas (1940) designated the specimen figured by Edwards and Haime (1851, pl. vii, figs. 1, 1a) as lectotype. The original specimen appears to be lost. Their figure shows 22 major septa though Edwards and Haime, in their text, mention 22 to 24 as typical. Topotype specimens have been figured by Smith (1945) and these show 19 septa. Of some 20 specimens from the type area which I have examined, only 2 have more than 20 septa and none has as many as 24; the vast majority have only 18 or 20.

Barrois (1882) described specimens of *M. bouchardi* from Moniello and Arnao (Asturia) in which the calice is very shallow. He suggested that the specimens may have broken before interment and this seems the most probable explanation, since the distal parts of the calice are thin, having no secondary stereoplasmic thickening.

Smith (1945) stated that *Lopholasma carinatum* agrees with *M. bouchardi* in all essential characters and differs from it only in size and unimportant details. His remarks suggest that he regarded them as conspecific. There can be no doubt that *L. carinatum* is a species of *Metriophyllum*, but I cannot agree that they are conspecific, since *M.*

EXPLANATION OF PLATE 16

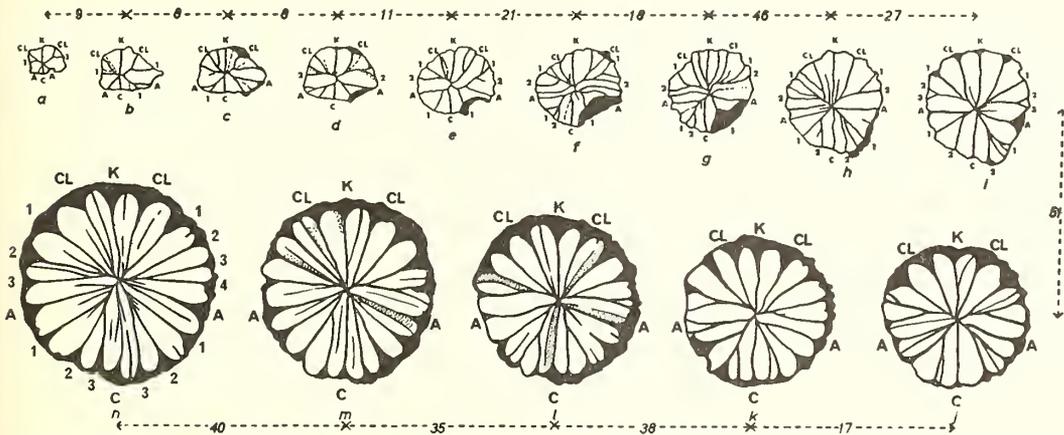
- Figs. 1–3. *Metriophyllum carinatum* (Simpson), Hamilton Beds, Livonia salt shaft, Livingstone Co., N.Y. 1, Longitudinal thin section (median) of a cotype showing the tabulae and horizontal carinae. NYSM 292, $\times 3.3$. 2, Transverse thin section of a cotype; major and minor septa are visible; the skeletal elements between the septa are sections through tabulae; NYSM 291, $\times 3.3$. 3, Longitudinal thin section (off median) showing the carinae appearing as spurs on either side of the septa. NYSM 290, $\times 3.3$.
- Figs. 4, 5. *Stereolasma rectum* (Hall). 4, Transverse thin section of hypotype, NYSM 320, $\times 3.3$. 5, Longitudinal thin section of hypotype, NYSM 322, $\times 3.3$.
- Fig. 6. *Metriophyllum bouchardi* (Edwards and Haime). Transverse thin section showing the lamellar structure of the outer wall and the fibrous structure of the septa and carinae. The suture between septa and carinae is well seen in the upper part of the plate. BMNH R16237, $\times 7$. Middle Devonian, Ferques, Boulonnais, France.
- Fig. 7. *Streptelasma ungulata* (Simpson). Longitudinal thin section of hypotype, NYSM 322, $\times 3.3$. Hamilton Beds, Hamburg-on-the-Lake, Erie Co., N.Y.
(The original photographs of figs. 1–5, 7 were kindly supplied by the New York State Museum.)



HOLWILL, *Metriophyllum*

bouchardi has only about twenty septa while *L. carinatum* shows thirty; also the carinae of *M. bouchardi* are larger and more strongly curved, thus producing deeper troughs; the carinae are also more widely spaced than in *L. carinatum*.

Septal development. Investigation of septal development in *M. bouchardi* presents unusual difficulties because, as has been pointed out above, the carinae simulate septa in transverse sections; in fact new septa and carinae arise in a similar way from the sides of the earlier formed septa. The fundamental difference between the two is that new septa arise only in four positions whereas the carinae may develop within any of the interseptal loculi. In making the present study it was found necessary to record sections at intervals of 0.003–0.005 inches and sixty-eight sections were made in a distance of 0.26 in. The sections were recorded by means of cellulose peels and a selection of critical



TEXT-FIG. 4. Selected serial sections to show the septal development of *M. bouchardi*. The figures indicate the distances between each section in thousandths of an inch. BMNH R16249, $\times 4$.

sections is reproduced in text-fig. 4. The septa in *M. bouchardi* show a radial arrangement in all stages of growth. However, there is a basic bilateral symmetry associated with a pinnate method of septal insertion.

The apical ends of several apparently complete specimens have been sectioned and the most juvenile arrangement of septa observed is that illustrated in text-fig. 4a. Two metasepta (marked 1 on the figure) are present in addition to the six protosepta (C = cardinal septum; K = counter cardinal septum; A = alar septa; CL = counter lateral septa; the septal nomenclature used here is that advocated by Hill (1935). The axial ends of the protosepta are swollen and welded together with sclerenchyme (this is not shown on text-fig. 4 as the sclerenchyme has been omitted for the sake of clarity). There is also thickening along the sides of the septa. The first formed metasepta are those which develop on the cardinal side of the counter lateral septa; those on the cardinal side of the alar septa follow almost simultaneously (text-fig. 4b and c), and this pattern is maintained with only minor exceptions throughout the development of the coral.

The newly formed septa grow until they almost reach the centre and their axial ends are within the central sclerenchyme. However, they always remain attached to the

protosepta from which they originated so that it is possible to distinguish four distinct groups of septa even in the mature corallite (see text-fig. 4*n*).

Within the calice the septa occur as longitudinal ridges; between these are a further series of ridges, usually somewhat less prominent, from which at a later stage of growth the carinae develop. These latter ridges occur in the position of minor septa and the outer surface of the epitheca has grooves which correspond to them. Because of the thickening of the epitheca below the calice, these ridges are not always apparent in sections made through the earlier formed parts of the corallite, but they can sometimes be distinguished embedded in lamellar tissue if the preservation is good. Whether or not these ridges should be regarded as true minor septa is open to question; they are closely linked with the subsequent development of the carinae and this suggests that they are not in fact minor septa. On the other hand, their regular position between the major septa, the septal grooves in the outer wall which correspond to them, and their formation from lamellar tissue would suggest a contrary interpretation. I incline to the view that they are true minor septa, and they are described as such in the systematic part of this paper.

Carinae are present in all but the earliest ontogenetic stages and each septum bears them. In the mature corallite the carinae run closely parallel to their parent septum, but in earlier stages they are more radially disposed and this increases the difficulty of distinguishing them from newly formed septa.

Metriophyllum gracile Schlüter 1884

Plate 17, figs. 7–10, 12, 13; Plate 18, figs. 1, 5, 6, 9, 10, 12–16

Metriophyllum gracile Schlüter 1884, pp. 82, 83.

Metriophyllum gracile Schlüter 1889, pp. 18–20, pl. 2, figs. 5–8.

Metriophyllum laeve Schlüter 1889, p. 18.

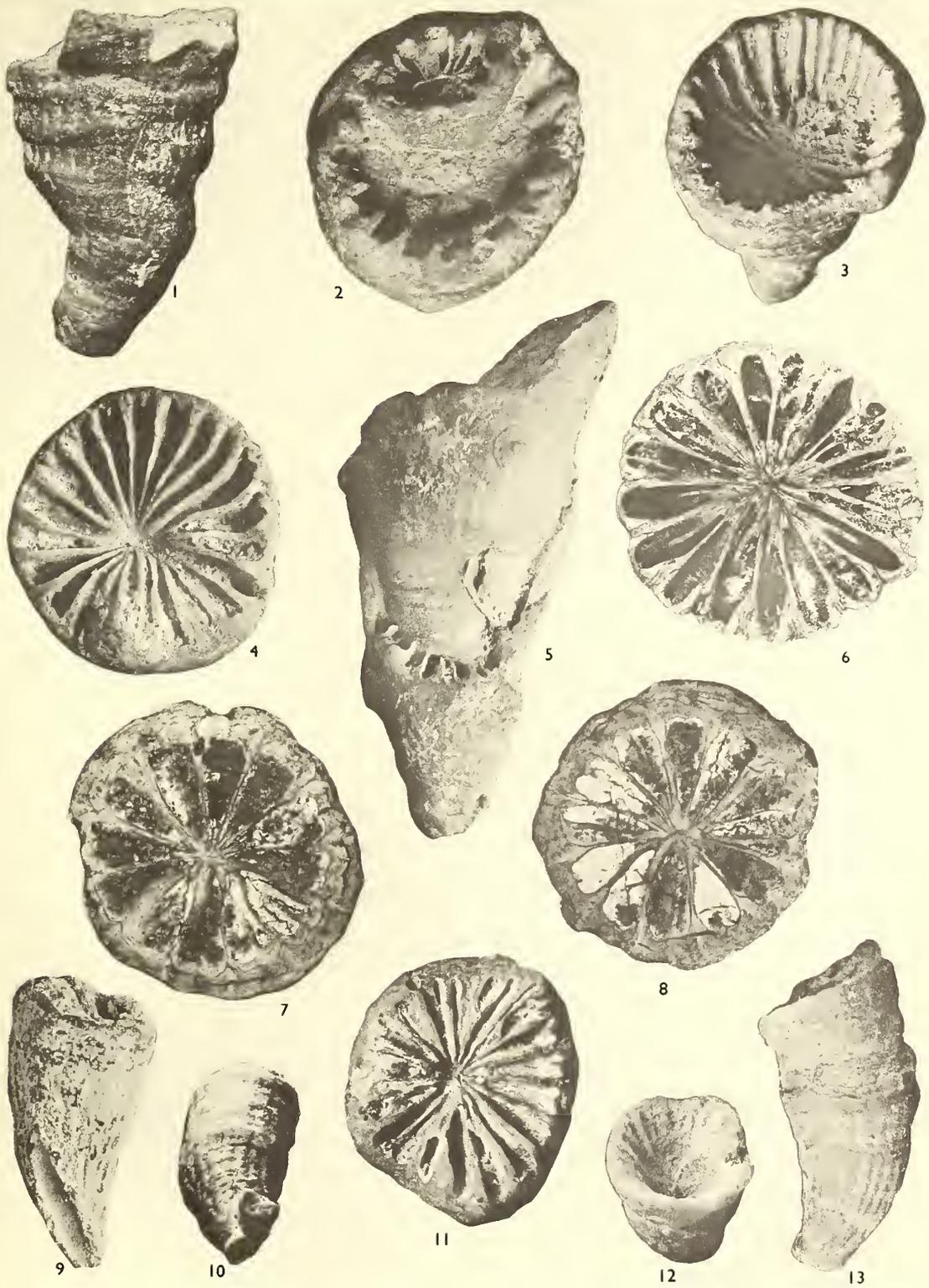
non Lopholasma gracile Soshkina 1928, p. 369.

Lectotype. Schlüter's species is based upon a number of syntypes in the Geologisch-palaeontologisches Institut und Museum at Bonn. From these syntypes the specimen illustrated in Plate 17, fig. 13 is here selected as the lectotype (Bonn, 161c).

EXPLANATION OF PLATE 17

Figs. 1–6, 11. *Metriophyllum bouchardi* (Edwards and Haime). Middle Devonian limestones and shales of Ferques, Boulonnais, France. 1, Exterior showing typical trochoid form and rugae; calicular margin is damaged. BMNH R18517, $\times 5$. 2, Calicular view of a specimen starting to rejuvenate. BMNH R18513, $\times 5.4$. 3, Specimen showing the deep steep-sided calice with major and minor septa appearing as ridges. BMNH R18517, $\times 5.4$. 4, Calicular walls have been broken revealing the form of the major and minor septa across the floor of the calice with carinae not yet formed at this level BMNH R16246, $\times 4.7$. 5, Specimen showing rejuvenation. BMNH R16248, $\times 4.8$. 6, Thin section (transverse) of a typical specimen; the flexure and thickening of the septa at the outer margin is well seen. BMNH R16249, $\times 8$. 11, Specimen in which the calicular walls have been completely abraded revealing the arrangement of septa across the calicular floor; some carinae are visible. BMNH R16231, $\times 5.4$.

Figs. 7–10, 12, 13. *Metriophyllum gracile* (Schlüter). Gerolstein area of Germany. 7, 8, Thin sections (transverse) showing the typical arrangement of the septa meeting at the axis and cemented by sclerenchyme. MM11120, $\times 14$. 9, Specimen showing the attachment groove which typifies individuals from a locality 1 km. south of Gerolstein (472.644). MM11119, $\times 6$. 10, Specimen with prominent root-like processes at the apical end. MM11117, $\times 6$. 12, Paralectotype showing the deep calice. Bonn, $\times 7.7$. 13, The lectotype, Bonn 161c, $\times 6.5$.



HOLWILL, *Metriophyllum*

Description. Small solitary trochoid corals with an average length of 8 mm. and a diameter of 3–4 mm. The calice is deep and steep sided and may occupy as much as half the length of the corallite; the septa project into the calice as low ridges. The outer wall is relatively thick and marked by longitudinal grooves corresponding to the septal positions. There are 14–18 major septa in the average-sized specimen; these are slender and straight or only slightly flexed; at the axis they are welded together, though in ephebic stages they may withdraw slightly from the axis leaving a narrow aulos (compare Pl. 17, figs. 23 and 27). Minor septa are seen only in the calice, where they alternate with the major septa. Horizontal trough-shaped carinae occur on each septum though not within the calice; they are spaced at about 0.8 mm. intervals (Pl. 18, figs. 6 and 10). Tabulae are thin and slope steeply downwards away from the axis.

Range. *Metriophyllum gracile* has only been recorded from the Gerolstein area of Germany in beds which are of Upper Couvinian age. Hill (1939), in her remarks on *M. sp.* from Western Australia, suggests that *M. gracile* may extend up into the lower Givetian.

Remarks. Schlüter's original description records 16–18 septa but a re-examination of the syntypes and other specimens shows that there are not more than 18 septa and commonly only 14. No tabulae were observed in any of Schlüter's original specimens, but topotype material has been sectioned and this shows the thin, steeply inclined tabulae which are characteristic of the genus. The carinae are very delicate structures and they usually occur at the same level on opposite sides of a single septum, though they alternate in height with those on adjacent septa. The outer surface is usually strongly ribbed, though in larger specimens the distal end shows prominent transverse growth striae; this feature and some observations on the mode of attachment of the species have been the subject of a separate paper (Holwill 1963).

The main ways in which this species differs from *M. bouchardi* are in size, in number of septa, and in the positioning of the carinae.

M. sp. cf. gracile was recorded by Wade (1938) from the Rough Range of Western Australia; this record was based on a preliminary determination by Hill, who subsequently described the form (Hill 1939) merely as *M. sp.*, considering it inadvisable to give the form a name based on a single oblique section. Hill's figure of this specimen shows it to have well-developed minor septa, and on this basis alone it is to be distinguished from *gracile*. It is likely to be a new species, but until further material is available Hill is right in refraining from giving it a specific name.

Metriophyllum gracile (Soshkina) 1928

Soshkina recorded this species as *Lopholasma gracile* (Soshkina 1928, p. 368, pl. 12, fig. 14; text-fig. 12). Since *Lopholasma* is here regarded as synonymous with *Metriophyllum*, *M. gracile* Soshkina is a junior secondary homonym and as such the specific name must be rejected; I have communicated with Dr. Soshkina informing her of this and have invited her to publish a replacement name.

The form described by Soshkina is very small, having a maximum diameter of 2 mm. and a length of 5 mm. Only two individuals are recorded, both from the Lower Permian of the eastern Urals (Shchugor River). There are twelve major septa at this diameter and

no minor ones are apparent. The septa and outer walls are much thickened by sclerenchyme. The carinae are stout horizontal ridges developed irregularly from the sides of the septa; there is very little upturning of their outer edges. Tabulae are not seen.

Metriophyllum laeve Schlüter 1889

1889 *Metriophyllum laeve* Schlüter, p. 278(20), no figures.

Schlüter was uncertain whether *M. laeve* should be regarded as a distinct species. In his original description (Schlüter 1889) he describes the species as similar to *M. gracile* but nearly twice as large and with a smooth epitheca; he stated that *M. laeve* characterized a dolomite bed at the same horizon as the marl bed in which *M. gracile* occurs. A study of Schlüter's specimens shows that the smooth epitheca is not a consistent characteristic (compare Pl. 18, figs. 13 and 16); neither is size alone a reliable criterion for distinguishing species. However, thin and polished sections (Pl. 18, figs. 14 and 15) suggest that the septa are stout and slightly withdrawn from the axis leaving a small aulos; the axial ends of the septa are also swollen. At first sight these features would seem to be of specific importance, distinguishing *M. laeve* from *M. gracile*, but having examined several sections of *M. laeve* it was found that (i) the stout septa are caused by a recrystallization of the original calcite to form dolomite (some specimens were only partly recrystallized and these showed slender septa comparable with those typical of *M. gracile*). (ii) The swelling of the septal ends, and their slight withdrawal from the axis to form an aulos, can also be found in the epehebic stages of *M. gracile* (Pl. 18, fig. 5). It is true that the specimens of *M. laeve* are of larger average size than those of *M. gracile*, but it is not difficult to find specimens of *M. gracile* which are of comparable size; since *M. laeve* characterizes a particular lithology it is reasonable to suppose that the slightly different environment which facilitated dolomitization also tended to prolong the life of *Metriophyllum* so that a higher percentage of the individuals attained old age and developed senile characteristics.

Metriophyllum litmm sp. nov.

Plate 18, figs. 2-4, 8

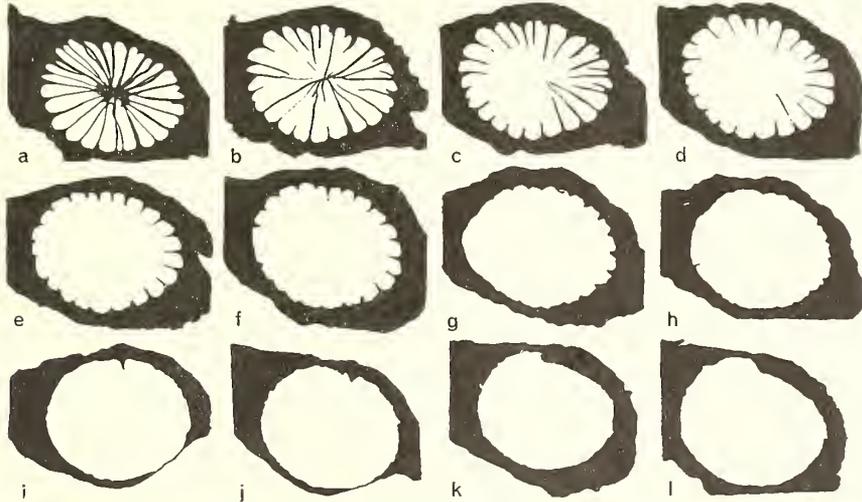
Description. Small solitary corals with a maximum observed diameter of 8 mm. At this diameter there are twenty-two major septa which are slender and usually slightly flexed; they reach the axis (except within the calice) and are welded together at the axis by a small amount of sclerenchyme, thus forming a pseudocolumella. Horizontal trough-shaped carinae are developed regularly up each septum; they are spaced at approximately 1.1 mm. intervals and are the same level on either side of any one septum, but alternate in height with those on adjacent septa. The septa are thickened just before reaching the outer wall, which is moderately thick. The calice is deep and steep sided; its floor is almost flat and the septa project into it as sharp ridges in the lower part; the distal end of the calice shows no evidence of septa on its inner surface (see serial sections, text-fig. 5). Minor septa are absent. The tabulae are steeply inclined downwards away from the axis and are numerous.

Holotype. Specimen MM11113 from the Combe Martin Beach Limestone (Middle/Upper Devonian), Ilfracombe Beds, north Devon.

Material. Much of the material from north Devon is poorly preserved and no complete specimens of *M. lituum* have been obtained; hence the overall length and the form of the corallum are not known with certainty. Altogether eight specimens have been collected (MM11113, 4, 11122, 11125-9).

Locality and horizon. All the specimens have been obtained from the Combe Martin Beach Limestone in the neighbourhood of Newberry Beach, Combe Martin, north Devon. On the basis of the associated fauna the bed is dated as Upper Givetian or Lower Frasnian (see Holwill 1962 for a discussion of the probable age).

Derivation of name. From the Latin *lituus*—a curved staff or wand—referring to the thin flexed septa.



TEXT-FIG. 5. Serial sections through the distal parts of *M. lituum* sp. nov. The sections were taken at approximately equal intervals through a thickness of 0.14 in. MM11114, $\times 4$.

Discussion. *M. lituum* closely resembles *M. bouchardi*, but it differs from the latter both in size and in the number and slenderness of its septa; also in the very regular development of the carinae on either side of each septum. It differs from *M. gracile* in being larger and in having a greater number of septa.

Text-fig. 6 shows serial sections through a small specimen (probably in its nepionic stage, hence the small diameter and few septa). The sections show very clearly the way in which carinae may appear as spurs from the septa and even themselves simulate septa.

Metriophyllum battersbyi Edwards and Haime 1851

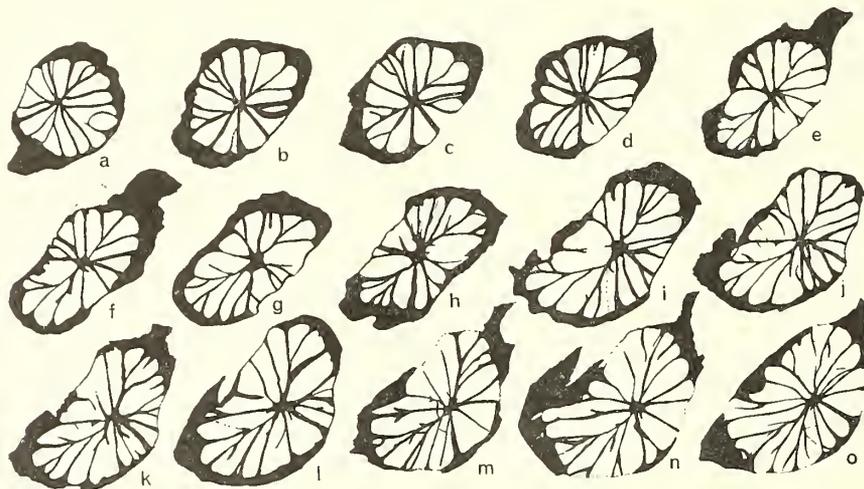
1851 *Metriophyllum Battersbyi* Edwards and Haime, p. 318.

1853 *Metriophyllum Battersbyi* Edwards and Haime, p. 222, pl. 49, fig. 4.

In 1851 Edwards and Haime recorded the coral *M. battersbyi* from the Middle Devonian Limestones of Torquay. They figured this specimen and gave a fuller description of it in their monograph of 1853. Many subsequent workers have referred to this identification and have doubted its validity (e.g. Hill 1939, Smith 1945). Apart from a species of *Metriophyllum* from north Devon (Holwill 1962), and a doubtful identification of *Metriophyllum* by Smith (1953) (see below), it is the only form of *Metriophyllum*

recorded in the British Isles and it differs in so many obvious characters from other known species of this genus that it is not surprising that doubt has been cast on the generic determination.

In describing it in 1853, Edwards and Haime made particular reference to the 'quadri-fascicular mode of arrangement of the septa' of which there were said to be forty-eight major ones, 'somewhat thickened', in a section taken just below the calice. These alternate with minor septa which are thinner. Dissepiments were also recognized. The authors distinguished the species from the type species by the more numerous septa and the fact that they were slightly thickened near the centre.



TEXT-FIG. 6. Serial sections through a juvenile specimen of *M. lituum* sp. nov. The sections were taken at approximately equal intervals through a thickness of 0.14 in. MM11114, $\times 5$.

Unfortunately the original specimen figured by Edwards and Haime has been lost, but their figure (pl. xlix, fig. 4) is closely similar to other specimens labelled *M. battersbyi* which are in the British Museum (Nat. Hist.) and which were obtained from the same area in south Devon as the holotype. A study of these specimens, from which several thin sections have been made, makes it clear that *M. battersbyi* is not a species of *Metriophyllum*; in fact Edwards and Haime's own description of the holotype is sufficient to show that it cannot be included in this genus as defined above. Briefly the chief characters which exclude it from the genus are as follows:

- (a) Absence of horizontal trough-shaped carinae.
- (b) The presence of minor septa extending half-way (or more) to the centre.
- (c) The presence of dissepiments.
- (d) The thickening of the septa in their central parts and their attenuation towards the periphery.
- (e) The presence of numerous inflated tabellae in a central tabularium.
- (f) The presence of an axial whorl.

Other less significant factors are the large size, the numerous septa, and the thin outer wall; none of these features characterizes any known species of *Metriophyllum*. It is

most probable that '*M. battersbyi*' should in fact be referred to the genus *Acanthophyllum* as redefined by Birenheide (1961).

Metriophyllum carbonaria (Grabau 1922)

1922 *Lopholasma carbonaria* Grabau, pp. 43–45, pl. i, figs. 5a–b, 6b, 7b, 7d, 8b, 8d, 9b, 9d, 10b, 10d, 11d, 12; text-figs. 54–56.

This species from the Viséan or Lower Moscovian of China differs from other known species of *Metriophyllum* in having a well-marked fossula and a cardinal septum which does not reach the axis. Grabau describes dissepiments which are 'fairly numerous, thin and for the most part cystiform, i.e. convex upwards', but later he writes: 'between the septa are cystose dissepiments . . . these probably being also in many cases sections of carinae.' His published figures do not support the suggestion that dissepiments are present and I consider that the structures observed by Grabau are either sections through the carinae as he himself suggests, or, even more probably, sections through the outward sloping tabulae. This contention is supported by a later remark of Grabau: 'the dissepiments break up into spines and finally these spines disappear'—this is the behaviour of the carinae in successive serial sections which has been demonstrated above.

Metriophyllum carinatum (Simpson 1900)

Plate 16, figs. 1–3

1900 *Lopholasma carinatum* Simpson, p. 206, figs. 19–22.

Some comments have already been made on this species in the foregoing descriptions and it is illustrated in Plate 16, figs. 1–3. Minor septa are well developed in addition to about thirty major ones which extend to the axis, where they are welded together by sclerenchyme. The minor septa extend slightly beyond the outer thickened wall and usually abut against a major septum (see Pl. 16, fig. 2). The carinae numerous and occur at alternate levels on either side of a septum; they are stouter and less upturned at their outer edges than in *M. bouchardi*.

The species is recorded from the Hamilton Shales (Middle Devonian) of U.S.A.

Metriophyllum deminutivum Easton 1944

1944 *Metriophyllum deminutivum* Easton, pp. 31, 32, pl. 3, figs. 1–3.

This species occurs in the lower part of the Chouteau Limestone (Mississippian) of Missouri, and must unquestionably be included within the genus *Metriophyllum* as defined above. In size and general form of the carinae, *M. deminutivum* resembles *M. gracile*, but at least one marked difference lies in the form of the septa during the middle ephebic stages: Easton describes them as 'grouped somewhat in pairs, five pairs on each side between single thick cardinal septum and thin counter septum with single minors joining it on either side to form tripartite counter system'. The presence of 'not more than three very fine dissepiments' is mentioned and, if true dissepiments are indeed present, this feature alone distinguishes it from other known species.

Metriophyllum erisma Hill 1949

1949 *Metriophyllum erisma* Hill, p. 142, pl. 6, figs. 11, 12.

Hill created this new species for forms in which the septal flanges (carinae) are inclined inwards and downwards and in which the inner tabulae sweep vertically downwards about the axis; there are also occasional outer tabulae. Hill does not indicate whether the carinae are of the trough-shaped variety which are typical of the genus, and unfortunately her figures do not clarify this point; the fact, however, that in the transverse section they 'appear as thickenings of the septa or as slender plates like extra septa running parallel to the septa' suggests that they may have upturned outer edges. The inclination of the carinae downwards towards the axis is exceptional (they make an angle with the horizontal of about 20°), and it has not been noted in any other species. The two sets of tabulae are also unique to this species.

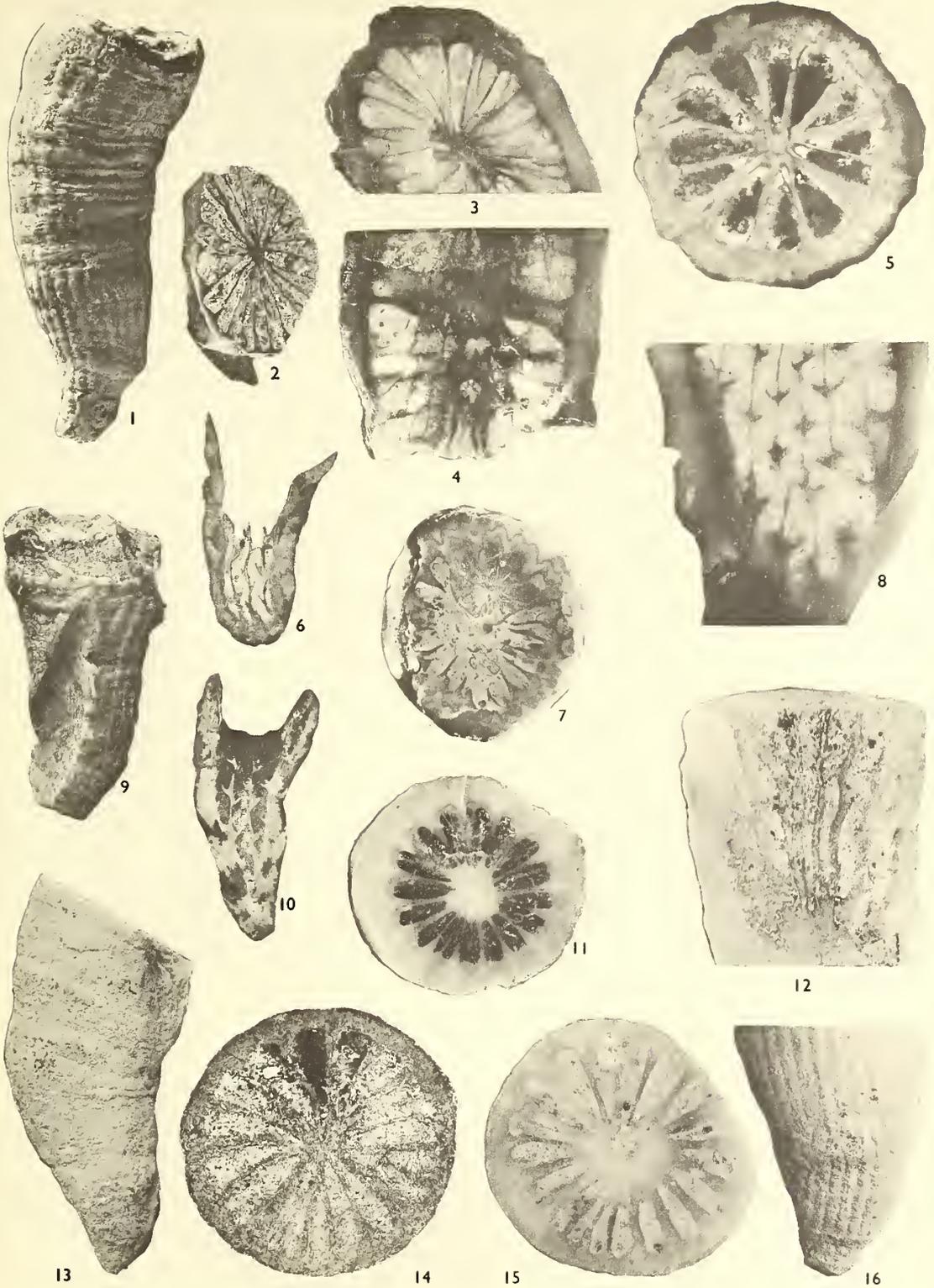
Metriophyllum (Aemulophyllum) exiguum (Billings 1860)

1860 *Heliophyllum exiguum* Billings, p. 261, figs. 9, 10.

M. (Aemulophyllum) was erected as a subgenus of *Metriophyllum* by Oliver (1958) to contain forms of *Metriophyllum* with a calceoloid flattening; to the new subgenus he assigned the form *Heliophyllum exiguum* Billings. In his redescription of this species Oliver mentions the presence of a 'deep fossula on the convex . . . side which is occupied by a short cardinal septum'; he also describes crossbar carinae 'which descend gently

EXPLANATION OF PLATE 18

- Figs. 1, 5, 6, 9, 10. *Metriophyllum gracile* (Schlüter). Gerolstein area of Germany. 1, Typical external appearance with longitudinal ridges prominent at the apical end and concentric growth striae in the distal parts. MM11115, $\times 6.8$. 5, Thin section (transverse) of a specimen in which the septa are slightly withdrawn from the axis leaving a narrow aulos. MM11121, $\times 15$. 6, 10, Thin sections (longitudinal) showing the deep calice with walls thickened near the base and the delicate carinae developed on either side of the septa, MM11124, $\times 5.3$; 11123, $\times 7$. 9, Specimen showing the attachment groove which typifies individuals from a locality 1 km. south of Gerolstein (472.644). MM11116, $\times 7$.
- Figs. 2-4, 8. *Metriophyllum lituum* sp. nov. Combe Martin Beach Limestone (Ilfracombe Beds), Combe Martin, north Devon. 2, Polished section (transverse) of a paratype. Much of the outer wall has been abraded away but the form of the septa and carinae is well shown. MM11122, $\times 6$. Holotype. MM11113. 3, Transverse section, $\times 6.3$. 4, Median longitudinal section showing the horizontal carinae and steeply outward sloping tabulae, $\times 6.3$. 8, Off-median section showing the regular arrangement of the carinae on either side of the septa, $\times 8.8$.
- Figs. 7, 11. *Metriophyllum bouchardi* (Edwards and Haime). Middle Devonian limestones and shales of Ferques, Boulonnais, France. 7, Polished section of a specimen showing the early stages of rejuvenation. BMNH R18513, $\times 4$. 11, Thin section (transverse) of a specimen with a much thickened outer wall and axis. BMNH R16237, $\times 5.3$.
- Figs. 12-16. *Metriophyllum gracile* (Schlüter). Gerolstein area of Germany. All these are original specimens of Schlüter, in the Bonn Museum, which he named *M. laeve*; they are here regarded as conspecific with *M. gracile*. 12, Polished longitudinal section. Bonn 162b, $\times 9$. 13, A large specimen with relatively smooth epitheca. Bonn 162, $\times 7$. 14, Thin section (transverse) of a specimen which has recrystallized, thus destroying the original skeletal structure and creating the impression of much thickened septa. Bonn 162c, $\times 10.75$. 15, Polished transverse section of a specimen showing the septa slightly withdrawn from the axis and laterally in contact, thus forming an aulos. Bonn 162a, $\times 8$. 16, Same specimen, showing longitudinal ridges, $\times 5$.



HOLWILL, *Metriophyllum*

towards the exterior' and are 'apparently limited to the peripheral zone'. These features suggest that the species is incorrectly regarded as a subgenus of *Metriophyllum*, which lacks a fossula, has horizontal carinae developed throughout its length (except in the calice), and has septa all of which reach the axis. Unfortunately I have not had the opportunity to examine the type material which is in the New York State Museum; however, the Museum has kindly sent excellent photographs of the holotypes, and these, together with Oliver's own figures and descriptions, suggest that the form should be regarded as a subgenus of *Heliophyllum* rather than of *Metriophyllum*.

Metriophyllum ilitchense (Soshkina 1928)

1928 *Lopholasma ilitchense* Soshkina, pp. 369–70, fig. 13a, b; pl. 12, figs. 12, 13.

This species is recorded from the Lower Permian of the eastern Urals. Soshkina has compared it with *M. carbonaria* (Grabau) but is reluctant to make the species synonymous because of their wide geographical separation and the fact that they occur in different geological systems. Only one incomplete specimen is recorded which has an elongate conical form and has seventeen major septa at a diameter of 6.5 mm.; there are a corresponding number of minor ones which are short and sinuous. The outer surface is covered by numerous spiny tubercles which are scarcely visible to the naked eye. Horizontal carinae typical of the genus are developed irregularly on either side of each septum. Soshkina specifically states that dissepiments occur running between the septa but that tabulae are absent. It is clear, however, from her figures that the structures she refers to as dissepiments are the same structures as Hill has interpreted as tabulae and which have been described as tabulae in this present paper; they run downwards away from the axis.

Metriophyllum poshiense Mansuy 1912

1912 *Metriophyllum poshiense* Mansuy, pp. 47, 48, pl. 7, fig. 8a–d.

Grabau (1922) doubts the generic identification of this species though his opinion was based only on a study of the published figures. The species, which has a maximum diameter of 7–8 mm., shows two series of septa: the major series meet at the axis and are welded together with sclerenchyme while the minor series are about half as long. The outer wall is thick and some of the septa show a thickening which may be the result of the section cutting through carinae. Unfortunately the reproduction of the plate is not clear enough to be certain on this point. I think Mansuy was probably correct in placing the species in *Metriophyllum*. The species occurs in the Middle Devonian of Indo-China.

? *Metriophyllum* sp. Smith 1953

1953 ? *Metriophyllum* sp. Smith, pp. 305–6, no figures.

Smith described a species of rugose coral from south-west Devonshire and assigned it tentatively to the genus *Metriophyllum*. The slates in which these fossils occur are thought to be of Lower Devonian age. All the specimens are somewhat compressed, and Smith did not feel justified in giving the form a specific name. I have examined the specimens, and I am very doubtful whether they should be referred to the genus *Metriophyllum* since carinae are completely lacking. The septa are much dilated in their axial parts

and laterally contiguous, thus forming a solid structure which fills most of the lumen; tabulae are absent. Smith suggested that the form probably represented an early species of *Metriophyllum* and this may well be, since it has already been noticed above that the Couvinian form, *M. gracile*, often shows septa which are swollen at the axis, sometimes with the development of a narrow aulos. (Such characteristics are also suggestive of *Syringaxon*—a fact which suggests that Lecompte (1952) is correct in placing *Metriophyllum* and *Syringaxon* in the same family (the Metriophyllidae.) However, until better-preserved specimens become available, I prefer not to regard ?*Metriophyllum* Smith as a species of *Metriophyllum* s.s.

Repositories. Corals illustrated in this paper are located in the following museums:

The New York State Museum, Albany 1, U.S.A. (NYSM).

The British Museum (Natural History), London (BMNH).

The Geologisch-palaeontologisches Institut und Museum, Bonn (Schlüter collection) (Bonn).

The Murchison Museum, Dept. of Geology, Imperial College, London (MM).

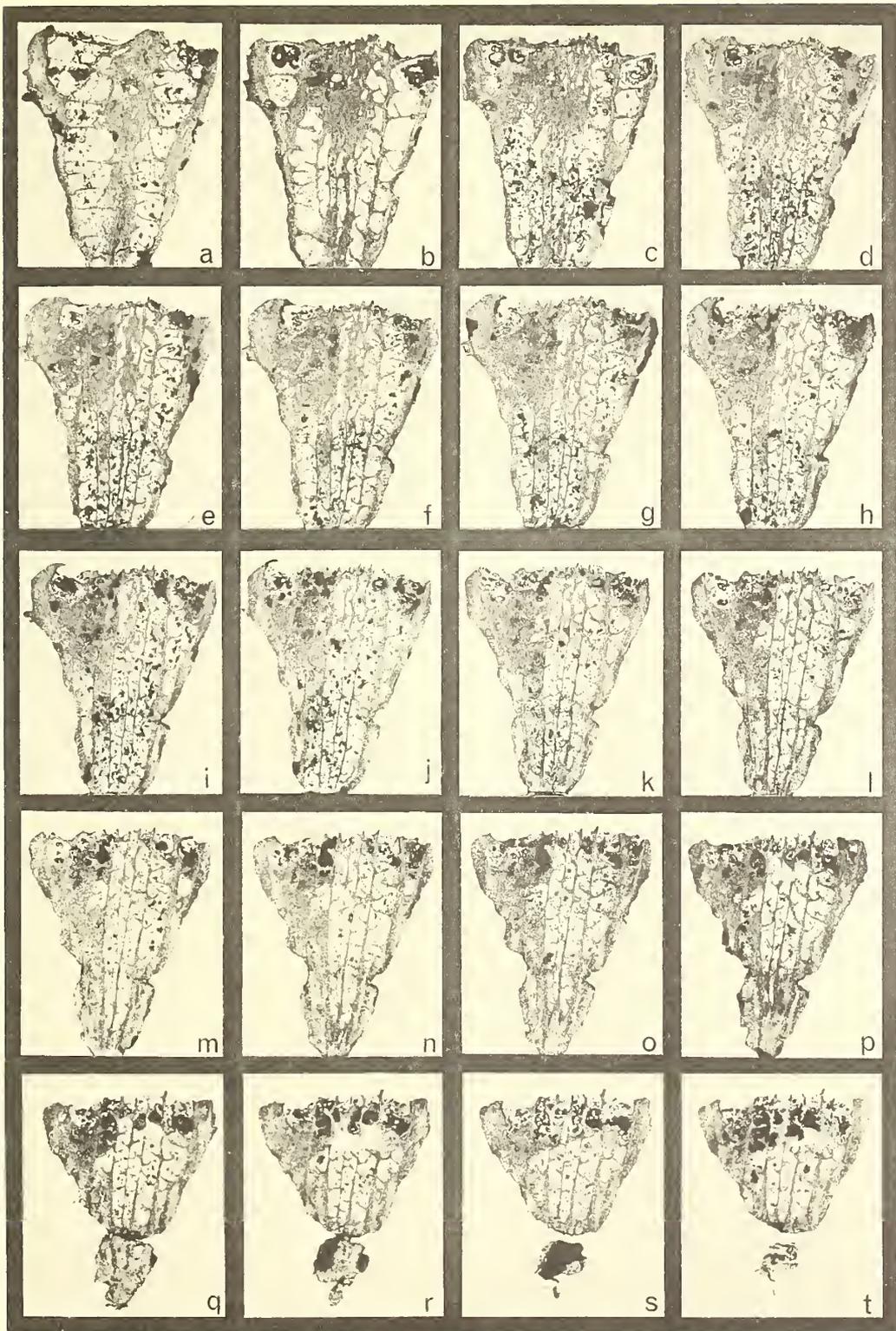
Acknowledgements. I have very much appreciated the co-operation given to me by the staffs of the British Museum (Nat. Hist.) and the Geologisch-palaeontologisches Institut und Museum at Bonn, who have permitted the loan of numerous specimens in their charge; and also the kindness of the New York State Museum in supplying me with excellent photographs of type specimens in that museum. I also express my sincere thanks to Dr. Gwyn Thomas for helpful criticism during the preparation of this paper. The help given by Mrs. J. Creighton and Miss M. Simpson in the preparation of material and by Mr. J. Gee in photographing it, is also gratefully acknowledged.

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EXPLANATION OF PLATE 19

Metriophyllum bouchardi (Edwards and Haime). Sequence of longitudinal sections from the axis (fig. a) to near the outer wall (fig. p). The outward sloping tabulae are well shown in the near axial sections. BMNH R16242, ×4.



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UPPER MIOCENE ANTHROPOIDS FROM THE SIWALIK BEDS OF HARITALYANGAR, HIMACHAL PRADESH, INDIA

by K. N. PRASAD

ABSTRACT. The Nagri beds at Haritalyangar contain a rich mammalian fauna. The present paper deals primarily with the description of the primate fossils collected by the author in 1954 and 1962. A maxillary fragment consisting of three molars is assigned to *Sivapithecus sivalensis*. In addition, a few isolated upper and lower molars, an upper canine, and an upper premolar, belonging to different genera of anthropoid apes, have been briefly outlined. A lower third molar of *Sugrivapithecus gregoryi* has also been recovered for the first time.

The primates collected from Haritalyangar are generally in the form of isolated teeth and broken fragments of mandible, the upper dentition being markedly scarce. This is rather difficult to explain. The total absence of limb bones and skulls, the fragmentary condition of the mandibles and maxillae, and the large concentration of hyaenodonts in the sediments suggest that the hominoids were devoured by these predacious animals.

FOSSIL higher apes, from the Siwalik beds of India, have been described over a long period. Only two specimens were recorded as far back as the year 1910. Pilgrim (1910, 1915, and 1927) recognized several genera and numerous species of fossil apes from the Siwaliks. His researches were based on the detailed study of imperfect jaws, teeth, and fragments of maxilla. The extreme rarity of these fossils and their poor preservation naturally gave rise to a certain amount of splitting, and new genera and species were founded from time to time. The situation has not changed very much in recent years, as no new material of importance has been discovered. Recently (1951, 1954, and 1962) the author made a few attempts towards the systematic collection of these fossils in some of the well-known localities such as Haritalyangar and Chakrana. Eleven more specimens have been found, in addition to the eighty-two finds already recovered from the Siwalik beds.

Re-examination of the higher anthropoid apes by Gregory, Hellman, and Lewis (1938), has thrown much light on the correlation of the individual finds and on their systematic position. Lewis (1937) made an attempt to simplify the taxonomy of the large Siwalik anthropoid fauna, comprising ten genera and twenty species, to four genera and ten species. His contention, that the Siwalik anthropoid fauna could not have been large, being practically restricted to Chinji (Sarmatian) and Nagri (Pontian) formations, does not appear to be tenable. In so far as we are aware, the Upper Miocene formations of Kenya have yielded a relatively large number of fossil hominoids of different groups in recent years. Moreover, remains of *Dryopithecus* (closely resembling *D. punjabicus* of Siwaliks) from Kaiyuan, China, have been reported by Chow (1958). From this evidence, it is reasonable to assume that the Siwaliks of India could have been one of the centres of radiation of these great apes. The time duration from Chinji to Nagri is quite considerable, and it is likely that diverse types existed, showing considerable variation in size and structure adumbrating on their genetic relationship. *Ramapithecus*, for example, is actually one of the latest members of this group showing progressive characters.

The several other higher mammalian forms, including the apes which lived contemporaneously during the period under review, give additional evidence that conditions for their existence were quite favourable. De Terra (1936) has expressed the view that the most favourable conditions existed during early and middle Pliocene. Gregory, Hellman, and Lewis (1936) have postulated that the oncoming glaciers were responsible for the extermination of anthropoids in Europe, India, and China, though a few forms persist in Africa, Burma, and south-eastern Asia. The study of certain fossil wood recovered from the Siwalik beds shows conditions favouring arboreal life, in part at least. It is the ecological conditions, and not the length of the time, that need emphasis. The absence of associated upper and lower dentition in the collections, and the degree of wearing affecting the dimensions and proportions, especially in the lower molars, make it difficult to reduce the different species to the rank of synonyms on the available material.

In the upper dentition, the molars of *Dryopithecus punjabicus* show a number of features which contrast strongly with *S. sivalensis* (Lydekker), and resemble closely the upper molars found in Europe and previously assigned to *Dryopithecus*. This is in accordance with the views expressed earlier by Le Gros Clark and Leakey (1951). *Dryopithecus darwini* has also been assigned to *Sivapithecus darwini* by Lewis. *Palaeosinina rugosidens* Pilgrim contrasts strongly with *S. sivalensis* in a number of characters, especially in the highly wrinkled enamel and in the relatively large paracone. As pointed out earlier, *Dryopithecus* remains closely resembling the Indian form have been reported from China, which gives additional evidence of the existence of these forms in this region. The systematic position of *D. giganteus* is still uncertain and more material is needed for a fuller analysis of this species. The new finds of fossil hominoids from Kenya have been discussed by Frisch (1962). A recent paper by Simons (1961) on the phyletic position of *Ramapithecus* is worthy of note. The author had useful discussions with Dr. Simons of Yale University, who suggested the possibility of one of the upper molars in the author's collection belonging to *Ramapithecus*. It is also now known that *Ramapithecus* was actually recovered from the Nagri beds and not from Tatrots.

MODE OF OCCURRENCE

Numerous fossils, in the form of bones, isolated teeth, fragments of mandible, maxilla, and rarely skulls, have been collected from the Nagri beds of Haritalyangar over a long period. From the faunal list it is apparent that diverse forms of higher mammals such as tragulids, equids, suids, rodents, and even such large forms as rhinoceros, existed along with other groups represented by crocodiles and fishes. The abundance of teeth and dermal scutes of reptiles, as well as crabs, suggests the existence of certain inland lakes, which the mammals frequently visited. The occurrence of hyaenodonts with the hominoids and tragulids suggests that the latter were attacked by the carnivorous beasts and subsequently washed into the lacustrine deposits, a condition similar to that stated by Le Gros Clark and Leakey (1951) on the Miocene deposits of Kenya. Further, the large concentration of fossils including the primates in a restricted area (which was later uplifted) suggests that conditions were very favourable for their growth and existence. The relative abundance of these fossils and their general fragmentary condition show that the soft portions of the skull and limb bones were actually eaten, and only the bones which escaped this treatment subsequently became fossilized.

TABLE 1. Stratigraphical distribution of fossil mammals in the Haritalyangar area

	Lower	Middle		Upper	
	Chinji	Nagri	Dhok-pathan	Tatrot	Pinjor
PRIMATES					
Lorisidae					
<i>Indraloris lulli</i> Lewis, 1933		×			
Pongidae					
<i>Bramapithecus sivalensis</i> Lewis, 1937		×			
<i>Dryopithecis punjabicus</i> Pilgrim, 1910		×			
<i>Ramapithecus brevirostris</i> Lewis, 1934		×			
<i>Sivapithecus sivalensis</i> (Lydekker), 1879		×			
<i>Sivapithecus indicus</i> Pilgrim, 1915		×			
<i>Sivapithecus aiyengari</i> Prasad, 1961		×			
<i>Sugrivapithecus salmontanus</i> Lewis, 1934		×			
<i>Sugrivapithecus gregoryi</i> Lewis, 1936		×			
RODENTIA					
Rhizomyidae					
<i>Rhizomys sivalensis</i> Lydekker, 1878		×			
<i>Rhizomys nagrii</i> Hinton, 1933		×			
<i>Rhizomys lydekkeri</i> Hinton, 1933		?			
<i>Rhizomys pilgrimi</i> Hinton, 1933		×			
<i>Rhizomys harii</i> Prasad, 1963		×			
Hystriidae					
<i>Sivacanthion complicatus</i> Colbert, 1933		×			
Thryonomyidae					
<i>Sayimys perplexus</i> Wood, 1937		×			
Cricetidae					
<i>Kanisanys sivalensis</i> Wood, 1937		×			
<i>Kanisanys nagrii</i> Prasad, 1963		×			
Muridae					
<i>Mastomys colberti</i> Lewis, 1939		×			
CARNIVORA					
Procyonidae					
<i>Sivanasua himalayensis</i> Pilgrim, 1932		×			
<i>Sivanasua nagrii</i> Prasad, 1963		×			
Mustelidae					
<i>Sivaonyx bathygnathus</i> (Lydekker), 1884		×			
<i>Enhydriodon falconeri</i> Pilgrim, 1931		×			
Viverridae					
<i>Viverra nagrii</i> Prasad, 1963		×			
<i>Vishnuictis hariensis</i> Prasad, 1963		×			
Hyaenidae					
<i>Crocuta gigantea</i> (Schlosser) var. <i>latro</i> Pilgrim, 1932		×	×		
<i>Crocuta talyangari</i> Prasad, 1963		×		×	
<i>Crocuta mordax</i> (Pilgrim) var. <i>tatroti</i> Prasad, 1963		×		×	
<i>Lycyaena macrostoma</i> (Lydekker), 1884		×			
<i>Ictitherium nagrii</i> Prasad, 1963		×			
Felidae					
<i>Megantereon praecox</i> Pilgrim, 1932		×			
<i>Vinayakia intermedia</i> Prasad, 1963		×			

TABLE 1 (cont.)

	Lower	Middle		Upper	
	Chinji	Nagri	Dhok-pathan	Tatrot	Pinjor
PERISSODACTYLA					
Equidae					
<i>Hipparion theobaldi</i> (Lydekker), 1877		×	×	×	×
<i>Hipparion antelopinum</i> (Falconer and Cautley), 1849		×	×		
Rhinocerotidae					
<i>Gaundatherium browni</i> Colbert, 1934		×			
<i>Rhinoceros sivalensis</i> (Falconer and Cautley), 1847			×		
ARTIODACTYLA					
Suidae					
<i>Tetraconodon mirabilis</i> Pilgrim, 1926		×			
<i>Lophochoerus nagrii</i> Pilgrim, 1926		×			
<i>Propotamochoerus uliginosus</i> Pilgrim, 1926		×	×		
<i>Dicoryphochoerus robustus</i> Pilgrim, 1926		×			
<i>Dicoryphochoerus titanoides</i> var. <i>jholi</i> Prasad, 1962		×			
<i>Dicoryphochoerus vagus</i> var. <i>nagrii</i> Prasad, 1962		×			
<i>Sus advena</i> Pilgrim, 1926		×			
<i>Sus tatroti</i> Prasad, 1962				×	
Anthracotheriidae					
<i>Anthracotherium punjabiense</i> Lydekker, 1877		×			
<i>Anthracodon hariensis</i> Prasad, 1962		×			
<i>Anthraconema dangari</i> Prasad, 1962		×			
Tragulidae					
<i>Dorcabune nagrii</i> Pilgrim, 1915		×			
<i>Dorcatherium nagrii</i> Prasad, 1963		×			
<i>Dorcatherium minus</i> Lydekker, 1876		×			
Giraffidae					
<i>Giraffokeryx punjabiensis</i> Pilgrim, 1910		×			
<i>Vishnutherium iravaticum</i> Lydekker, 1876		×			
<i>Hyaspitherium megacephalum</i> Lydekker, 1876		×			
Bovidae					
<i>Gazella lydekkeri</i> Pilgrim, 1937		×	×		
<i>Tragocerus punjabicus</i> Pilgrim, 1937		×	×		
<i>Selenoportax vexillarius</i> Pilgrim, 1937		×	×		
<i>Pachyportax nagrii</i> Pilgrim, 1937		×	×		
<i>Pachyportax latidens</i> Pilgrim, 1937		×		×	
PROBOSCIDEA					
<i>Deinotherium indicum</i> Falconer, 1845			×		
<i>Trilophodon hasnotensis</i> Osborn, 1936			×		
<i>Trilophodon macrognathus</i> Pilgrim, 1913	×				
<i>Pentalophodon sivalensis</i> (Cautley), 1836			×		
<i>Tetralophodon falconeri</i> Osborn, 1936			×		
<i>Synconoloplus</i> cf. <i>dhokpathanensis</i> Osborn, 1936		×			
<i>Stegolophodon bombifrons</i> (Falconer and Cautley), 1847			×		
<i>Stegolophodon latidens</i> (Clift), 1828				×	

The fossil hominoids under description were collected by the author from the Nagri beds of Haritalyangar (31° 32" N., 76° 38" E.) during the years 1954 and 1962. The stratigraphy and the descriptions of certain other fossils have already been dealt with by the author (1962, 1963). The geological formations in the Haritalyangar area extend from the Lower to the Upper Siwaliks. The bulk of the fossils come from the Nagri (Sarmatian) and Dhokpathan (Pontian) stages, sections of which are exposed within a band of seven kilometres, east of Haritalyangar.

SYSTEMATIC DESCRIPTIONS

Genus *SIVAPITHECUS* Pilgrim 1910

Genotype S. sivalensis

Diagnosis of the genotype. Lewis (1937) states: 'Jaws and cheek teeth medium large to very large in size. Molars moderately broad; crowns and robust cusps of medium height; labial and lingual cusps converge toward midline, greatest convergence lingual above and labial below. Upper dental arch with incisors separated from highly variable canines by a diastema. No diastemata in the lower dental arch. Horizontal rami of medium depth.'

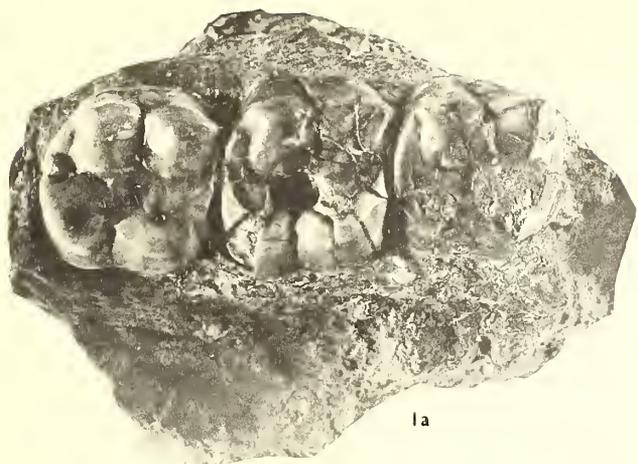
Sivapithecus sivalensis (Lydekker)

Plate 20, figs. 1, 7

Description. The fragment of the maxilla recovered from the Nagri beds of Haritalyangar consists of the lower border of the zygomatic process as well as a portion of the palatal surface. The intermaxillary suture, which is fairly clear, can be estimated. It is about 20 mm. and suggests that the palate was narrow in comparison with the size of the molars. On a reconstructed palate of *Sivapithecus sivalensis*, it has been estimated by Le Gros Clark and Leakey (1951) to be about 25 mm. In *S. indicus* (right maxilla D. 196) the width is about 24 mm. The preserved length of the maxilla anteroposteriorly is 34.5 mm., whereas in *S. indicus* it is about 35 mm.; in *S. sivalensis* it is 32 mm. This emphasizes the wide variation depending on the age and sex of the individual. However, the bone was undoubtedly part of a large specimen considering the general proportions of the molars. The maxillary fragment consists of three molars, of which the third is in

EXPLANATION OF PLATE 20

- Fig. 1. *Sivapithecus sivalensis* (Lydekker). Maxillary fragment (G.S.I. No. 18064), 1a, occlusal view of molars, 1b, side view, $\times 2$.
 Fig. 2. *Sivapithecus indicus* Pilgrim. Upper Canine (G.S.I. No. 18065), 2a, lingual aspect, 2b, labial aspect, $\times 2$.
 Fig. 3. *Sivapithecus indicus* Pilgrim. Upper premolar (G.S.I. No. 18066), 3a, posterior view, 3b, occlusal view, $\times 2$.
 Fig. 4. *Sugrivapithecus gregoryi* Lewis. Lower third molar (G.S.I. No. 18067), occlusal view, $\times 2$.
 Fig. 5. *Dryopithecus punjabicus* Pilgrim. Isolated upper third molar (G.S.I. No. 18068), occlusal view, $\times 2$.
 Fig. 6. *Sivapithecus* sp. Isolated molar (G.S.I. No. 18070), occlusal view, $\times 2$.
 Fig. 7. *Sivapithecus sivalensis* (Lydekker). Last lower premolar (G.S.I. No. 18069), occlusal view, $\times 2$



1a



2b



1b



3a



2a



5



3b



7



4



6

a very good state of preservation. The first and second molars are partly worn, so that the details of the cusps, especially the disposition of the sulci, are not clear.

TABLE 2.

Measurements of upper teeth of various Dryopithecinae, compared with *Sivapithecus sivalensis*

(From Le Gros Clark and Leakey, 1951)

	P 3			P 4			M 1			M 2		
	<i>a.p.</i> <i>mm.</i>	<i>tr.</i> <i>mm.</i>	<i>ind.</i> <i>mm.</i>									
<i>S. africanus</i> Le Gros Clark and Leakey (C.M.H. 6)	8.2	12.3	150	7.5	11.8	157	10.6	11.3	107			
<i>S. africanus</i> Le Gros Clark and Leakey (C.M.H. 26)							10.6	11.1	105			
<i>S. africanus</i> Le Gros Clark and Leakey (C.M.H. 27)										12.0	11.6	97
<i>S. orientalis</i> Pilgrim (D. 196)	7.7			7.3	12.0	164	11.0	12.0	109	12.8	14.2	111
<i>S. sivalensis</i> (Lydekker) (617 and K. 29/466)	8.7	11.0	126	7.6	11.4	150	10.6	12.2	115	11.5	13.7	119
<i>S. sivalensis</i> (Lydekker) (614)							10.3	12.1				
<i>S. indicus</i> Pilgrim (D. 176)							10.9	12.7	117			
<i>S. indicus</i> Pilgrim (D. 191)							10.5	13.5?	129?	12.5	14.0	112
<i>S. indicus</i> Pilgrim (612)							11.3	12.4	109			
<i>S. indicus</i> Pilgrim (613)										12.7	15.5	122
<i>S. indicus</i> Pilgrim (616)										13.3	15.3	115
<i>Palaeopithecus</i> (? <i>Sivapithecus</i>) <i>sivalensis</i> Lydekker	8.9	11.3	127	6.8	11.4	168	10.8	12.0	111	11.3	12.9	114
<i>D. punjabicus</i> Pilgrim	7.0	9.5	136	6.6	9.7	147	10.4	11.3	109	10.6	11.4	108
<i>D. germanicus</i> Abel.							9.6	10.0	104			
<i>D. germanicus</i> Abel.										10.4	11.0	106

First molar: it is more square and smaller than the second molar, and equals the third molar in general proportions. The four main cusps have become swollen, the cusps are higher and blunt. Cingulam is absent. The crown surface shows an advanced degree of wear, and the finer details of the teeth are not clear, though the morphological pattern of the teeth can be made out to some extent. The crests connecting the protocone with the paracone and metacone are not distinct because of wear.

Dimensions *a.p.* *tr.* *index*
12.0 mm. 12.0 mm. 100

Second molar: in the second molar, the cusps are pyramidal in shape, with a broad base. Due to the convergence of the main cusps, the trigon base is relatively small in relation to the size of the crown. The paracone and metacone are subequal, and the protocone has a larger base and is connected by crests with the paracone and metacone. Due to dental decay, the oblique crest connecting the protocone with the metacone cannot be made out. A posterior fovea is slightly developed. The hypocone is comparatively smaller than the protocone. There is no trace of any cingulam.

Dimensions *a.p.* *tr.* *index*
12.0 mm. 13.0 mm. 108

Third molar: the third molar is rather square in shape with four prominent cusps, of

which the protocone is the largest. The metacone and paracone are subequal, whereas the hypocone is very prominent. The enamel does not show any coarse secondary foldings. The crests connecting the protocone with the paracone and metacone can be made out more clearly than in the case of first and second molars. The posterior fovea is slightly developed. There is no trace of any cingulam.

<i>Dimensions</i>	<i>a.p.</i>	<i>tr.</i>	<i>index</i>
	12.0 mm.	12.0 mm.	100

Comparisons with other known maxillary fragments of Siwalik anthropoid apes, which are, however, few in number, suggest that the specimen is attributable to the genus *Sivapithecus*. In the peculiar shape of the molars, especially the third molar, and in the disposition of the cusps, which are almost equal in size, the specimen under description contrasts strongly with *Sivapithecus indicus* and *S. sivalensis* and probably justifies its inclusion under a new species. The specimen differs from *S. africanus* in the absence of an antero-internal cingulam. It is provisionally assigned to *S. sivalensis* as it shows the closest resemblance to that species. The homoetype bears G.S.I. Type No. 18064.

Sivapithecus indicus Pilgrim

Description. Upper right premolar: special importance attaches to this material as well-preserved upper premolars of *Sivapithecus* are rare in the extreme, and the few that have been recovered are invariably fragmentary in nature. This isolated upper premolar, which is unworn and well preserved, was collected from the same beds as the maxillary fragment. Pilgrim (1927), while examining a right maxillary fragment (D. 196), refers to a single external root in P 3. It appears to the author that the lateral portion of P 3 along with the root must have been broken before mineralization. The premolar under consideration, however, has two external roots broken at the base. The cusps are subequal. The anterior and posterior cingula are conspicuous and well-defined crests extending from labial cusps anteriorly and posteriorly separate the two cusps by a fairly deep antero-posterior sulcus.

<i>Dimensions</i>	<i>a.p.</i>	<i>tr.</i>	<i>index</i>
	8.0 mm.	12.0 mm.	150

The large size of the upper premolar teeth is characteristic of the genus *Sivapithecus*. From comparison, it is found that the premolars in *Dryopithecus* were smaller and also exhibit differences in the cusp pattern. It has the closest resemblance to the Indian form *Sivapithecus indicus* and compares favourably with *S. africanus* in so far as the dimensions are concerned. The anterior and posterior cingula in *S. sivalensis* appear to be more well defined than in *S. indicus*. Pilgrim's (1927) measurements of the fourth premolar in D. 196, collected from the same horizon near Haritalyangar, appear more or less assumed as the anterior portion in the specimen is broken off, but his assumption appears to be correct as the P 4 under description compares favourably with his measurements. Accordingly, the isolated premolar is provisionally referred to *Sivapithecus indicus*. It bears the G.S.I. Type No. 18065.

Upper canine: upper canines of *Sivapithecus* have been previously recovered from the Nagri beds of Haritalyangar. The specimen under description was collected by the

author from near the Hari escarpment and is provisionally assigned to *Sivapithecus indicus*. As pointed out by Gregory, Hellman, and Lewis (1938) 'the upper canines of the Indian Anthropoids vary from an almost premolar-like crown, in the supposed female *S. sivalensis*, to a dagger-like crown in the male type of *S. orientalis*'. But *S. orientalis* is now referred to *S. indicus* by Lewis. Material under description is very well preserved, except for the broken portion of the crown. The deep anterior groove and the posterior blade-like ridge are other characteristic features. Coarse wrinkles are preserved on the inner aspect with a fairly well preserved cingulum. The total length of the specimen is 40 mm.; the preserved height of the crown is 17 mm. The antero-posterior diameter of the base of the crown is 15.5 mm. and transverse 13 mm. Pilgrim (1927) refers to an upper left canine of *Sivapithecus* from the Chinji beds of the Lower Siwaliks. The dimensions in centimetres are as follows: length 16.2, breadth 10.6, and height 19.4. However, the specimen under description conforms closely in the general proportions as well as in the morphological pattern to the canine of *S. indicus* and is accordingly assigned to that species. It bears the G.S.I. Type No. 18066.

Sivapithecus sp.

Plate 20, fig. 6

Description. Isolated molar: a further accession to the material is an isolated molar from the same beds. The details of the tooth are not very clear as the occlusal surface is completely worn and the groove pattern is obliterated. It is provisionally assigned to *Sivapithecus*. It bears G.S.I. Type No. 18070.

Last lower premolar: this is well preserved, P 4, G.S.I. Type No. 18069; it was recovered from the clay bands about a kilometre east of Haritalyangar. The buccal and lingual cusps of the main crown are well preserved and permit specific identification. The premolar is small in the general proportions when compared to *S. indicus* and *S. sivalensis*.

	<i>a.p.</i>	<i>tr.</i>	<i>index</i>
<i>Sivapithecus sivalensis</i> (Lydekker) (G.S.I. Type No. D. 177)	8.5 mm.	9.9 mm.	--
<i>Sivapithecus sivalensis</i> (Lydekker) (G.S.I. Type No. 18069)	8.0 mm.	8.0 mm.	100
<i>Proconsul major</i> Le Gros Clark & Leakey	9.0 mm.	9.6 mm.	107

The lingual and buccal cusps of the crown are not worn down to the level of the talonid basin, and the crests connecting the two cusps are well preserved. There is an anterior foveal depression. Except for the variation in size, it closely resembles a fourth premolar of *S. sivalensis*, and it is provisionally referred to that species pending further accession of material.

Genus SUGRIVAPITHECUS Lewis 1934

Sugrivapithecus gregoryi Lewis

Plate 20, fig. 4

Diagnosis. Lewis states: 'Lower molars even narrower than *Sugrivapithecus salmontanus*. Labial side walls of crown show protoconid and hypoconid to be strongly set off from

each other from the occlusal surface to the base of the crown. Metaconid considerably exceeds protoconid in labio-lingual diameter of the cusp base. Antero-posterior diameter of metaconid base relatively longer than in *S. salmontanus*, as compared to the same measurement on the protoconid base. Hypoconid and hypoconulid relatively small. Hypoconulid more labial in position than in *S. salmontanus*. Entoconid located at approximately same antero-posterior latitude as hypoconulid. Main posterior crest nearly perpendicular to midline.'

Description. Lower right molar: in addition to the above material, a practically unworn lower right third molar was recovered from the Nagri beds, east of Haritalyangar, for the first time. The molar is very narrow with low cusps. The enamel is highly wrinkled with a prominent anterior fovea. The relative narrowness of the talonid is also very characteristic. The metaconid and entoconid are subequal, and the hypoconulid is more central in position. There is no trace of any cingula.

<i>Dimensions</i>	<i>a.p.</i>	<i>tr.</i>	<i>index</i>
	12.0 mm.	9.0 mm.	75

The lateral compression and elongation is a common feature in the lower molars of *Sugrivapithecus*. In certain characters the lower molar under description compares favourably to some extent with *Sugrivapithecus gregoryi* Lewis.

Measurements of lower dentition of *Sugrivapithecus*

(From Lewis, 1936)

		<i>S. gregoryi</i>	<i>S. salmontanus</i>
M $\bar{2}$	Antero-posterior	12.6 mm.	12.6 mm.
	Transverse	9.9 mm.	10.4 mm.
	Breadth index	76.7	83.0
M $\bar{1}$	Antero-posterior	11.1 mm.	11.0 mm.
	Transverse	9.0 mm.	9.0 mm.
	Breadth index	81.0	82.0

The pronounced wrinkling of the enamel, the slight crenation of the lingual margin, the low relief of the main cusps, among other things, probably justify inclusion under a new species. However, in view of the fragmentary material, it is provisionally assigned to *S. gregoryi* Lewis. It bears G.S.I. Type No. 18067.

Genus DRYOPITHECUS Lartet
Dryopithecus punjabicus Pilgrim

Plate 20, fig. 5,

Description. Upper third molar: an isolated upper third molar, G.S.I. Type No. 18068, in a fairly good state of preservation, was recovered from below the Hari escarpment. The molar is moderately worn, but the details of the tooth are well preserved. The ridge connecting the protocone and paracone is partly worn out. The metacone and hypocone are very much smaller, the ridge connecting the margin is crenulated, and the fovea posterior, as in the case of *Dryopithecus*, is well developed. The ridge connecting the metacone and hypocone is cleft by two sulci, which unite in the centre to form the valley between the hypocone and connecting protocone-metacone ridge (which is partly worn

out in the specimen). The subsidiary folds in the hypocone are not very clear. The specimen closely resembles the third left upper molar (D. 186) of *Dryopithecus punjabicus* Pilgrim. In the possession of a relatively large trigon, a pronounced paracone, in the presence of coarse secondary foldings (more strongly developed in D. 186) and in the presence of a well-developed posterior fovea, these appear to accord well with the characters of the genus *Dryopithecus* (in contrast to *Sivapithecus*).

Le Gros Clark and Leakey (1951) list the following characteristic features of the upper molars of *Sivapithecus*:

- (1) 'They are larger in general dimensions than those of *Dryopithecus*.
- (2) 'The cusps are of regular pyramidal shape, with a broad base which gives them a massive appearance. In *Dryopithecus*, they are more delicately constructed.
- (3) 'The outer and inner cusps are markedly convergent, so that the trigon basin is relatively constricted in relation to the size of the crown as a whole. The trigon has a regular compact appearance, being bounded by very well defined crests. In *Dryopithecus*, the trigon is relatively larger since the main cusps are more splayed apart.
- (4) 'The base of the hypocone (particularly in M $\underline{2}$) protrudes backwards more than in *Dryopithecus*.
- (5) 'The paracone and metacone are sub-equal, whereas in *Dryopithecus* the paracone is relatively larger.
- (6) 'The enamel is singularly free from coarse secondary foldings. In *Dryopithecus*, these are more strongly developed.
- (7) 'The hypocone is sharply separated by a continuous sulcus from the protocone and metacone, whereas in *Dryopithecus* it is connected with the metacone by a broad ridge, and is also distinctly marked off from the base of the protocone.
- (8) 'The posterior fovea is very slightly developed. In *Dryopithecus*, it is a conspicuous feature.'

Dimensions	a.p.	tr.	index
<i>Dryopithecus punjabicus</i> Pilgrim (G.S.I. Type No. 18068)	9.0 mm.	11.0 mm.	122
<i>Dryopithecus punjabicus</i> Pilgrim (D. 186)	9.6 mm.	11.3 mm.	117

Measurements of upper dentition

(Measurements in millimetres)

	P $\underline{4}$			M $\underline{1}$			M $\underline{2}$			M $\underline{3}$		
	a.p.	tr.	ind.									
<i>Sivapithecus sivalensis</i> (Lydekker) (G.S.I. Type No. 18064)	12.0	12.0	100	12.0	13.0	108	12.0	12.0	100
<i>Sivapithecus indicus</i> Pilgrim (G.S.I. Type No. 18065)	8.0	12.0	150
<i>Dryopithecus punjabicus</i> Pilgrim (G.S.I. Type No. 18068)	9.0	11.0	122
<i>Sivapithecus sp.</i> , (G.S.I. Type No. 18070)	11.5

Measurements of lower dentition

(Measurements in millimetres)

	P 4			M 3		
	a.p.	tr.	ind.	a.p.	tr.	ind.
<i>Sugrивapithecus gregoryi</i> Lewis (G.S.I. Type No. 18067)	12.0	9.0	75
<i>Sivapithecus sivalensis</i> (Lydekker) (G.S.I. Type No. 18069)	8.0	8.0	100

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THE FUNCTION OF ZIGZAG DEFLEXIONS IN THE COMMISSURES OF FOSSIL BRACHIOPODS

by M. J. S. RUDWICK

ABSTRACT. The commissures and valve-edges of many fossil brachiopods are deflected into a zigzag form. During ontogeny, this often produced radial ribs (costae) on the shell. Schmidt's hypothesis, that zigzag valve-edges acted as protective devices by transforming the apertures into narrow zigzag slits, is extended by determining the paradigm for this function. The zigzag deflexions of fossil brachiopods approximate, often very closely, to this paradigm; they are therefore interpreted as protective devices. The nature of the 'protection' conferred is discussed in the light of observations on the physiology of living brachiopods. The gradual development of paradigmatic zigzags during the later stages of ontogeny is interpreted in terms of the increasing degree of protection required as the animal grew in size. The presence of species with zigzag deflexions does not imply any special environmental conditions. The rigid specification of the paradigm, and the existence of closely similar zigzags in fossil and living oysters, suggest the intrinsic probability that zigzags were evolved many times independently. This is confirmed extrinsically by the varied origin and development of zigzags during ontogeny, and by their scattered distribution in geological time and among the major taxonomic groups. Examples are cited from most superfamilies of the Articulata, and from horizons ranging from Middle Ordovician to Eocene.

THE taxonomy of brachiopods is confused, and their evolutionary history difficult to reconstruct. This is partly because many structural features recur in taxa that seem on other criteria to be only distantly related. An analysis of the probable function of these features may help to clarify the nature and patterns of evolutionary change in the Brachiopoda.

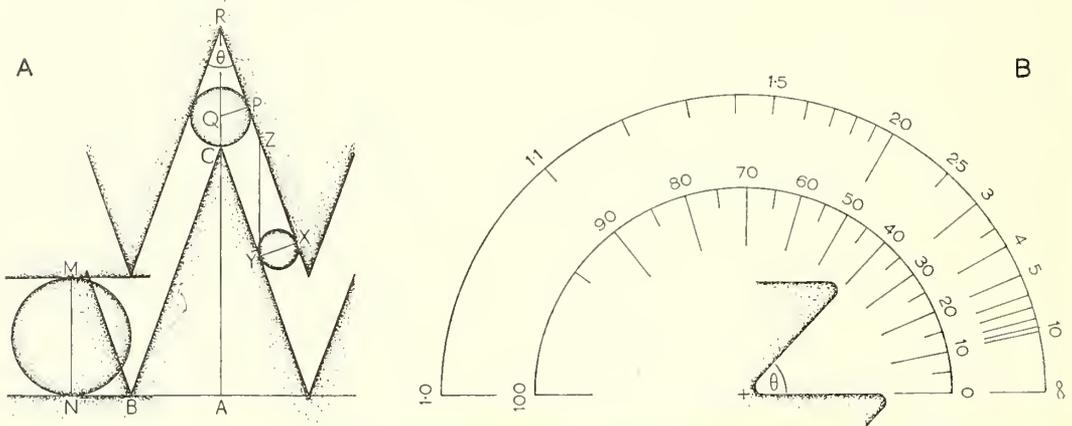
One character which occurs frequently but sporadically throughout the phylum—and indeed outside it—is a sharply angular type of radial ribbing on the surface of the shell. Causally, this is due to a special pattern of accretionary growth rates at the edges of the valves. A series of anomalies in the growth rates, predominantly in their vertical components (Rudwick 1959, p. 4), produces a *zigzag serial deflexion* at the commissure. During the further growth of the shell, a corresponding series of angular radial ribs or *costae* may be formed on the surfaces of the valves. But the prominence of these costae depends not only on the form of the deflexion, but also on the degree of overall convexity in the valves and the point in ontogeny at which the deflexion first appears. Consequently, the primary function of this character must be sought in the zigzag deflexion, rather than in the angular costae that it may or may not produce on the surface of the shell. It has been suggested, for example, that by corrugating the surface of the shell the costae may have served to increase either its mechanical strength (e.g. Cooper 1937, p. 40) or the area of the mantle tissue lining it internally (e.g. Cumings 1903, p. 131). Some costae on some shells may have had these effects, but perhaps only fortuitously; for interpretations of this kind cannot be applied to all zigzag deflexions, since some occur without any appreciable corrugation of the shell (see Pl. 27, figs. 1, 2).

The methodology of functional interpretations of fossils has been analysed elsewhere (Rudwick 1961*a*, p. 450; 1964). This paper follows the same method: first, the demands of a postulated function are analysed; from this analysis is derived a structural specification (the *paradigm*) which would give maximal efficiency for the function;

finally, the functional interpretation is tested by comparing this specification with the observed structure of actual fossil specimens.

THEORY OF PROTECTIVE NARROW SLITS

Many years ago, Dr. Herta Schmidt (1937, pp. 27–30) interpreted the zigzag deflexion of the rhynchonellacean *Sphaerirhynchia* (= *Wilsonia*) as a protective device. (A similar suggestion for the orthocean *Platystrophia* was made by Cumings as early as 1903, p. 131.) If the valves gaped only slightly apart, a narrow zigzag slit would have appeared between them. This slit might have prevented harmfully large particles from entering the mantle cavity. Schmidt analysed the degree of protection which a zigzag slit could

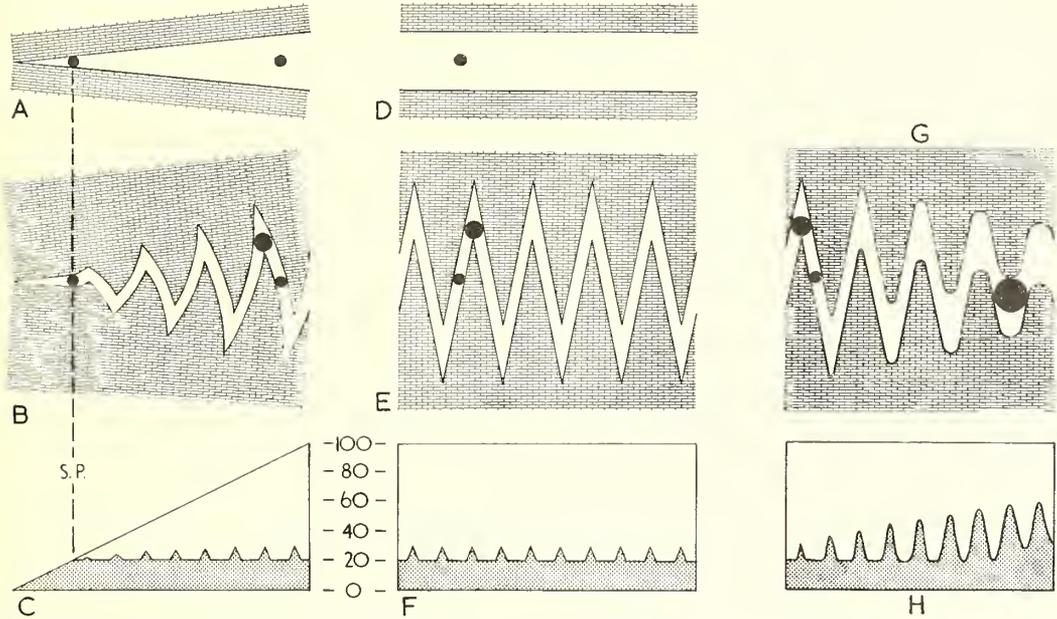


TEXT-FIG. 1. A, Portion of 'ideal' protective zigzag slit, showing spherical 'particles' passing through flanks of slit (diameter XY), crest of slit (diameter PQ), and undeflected slit of same gape (diameter MN). Degree of protection of slit, $P = 3.0$; width of slit = 33 per cent. of gape; crestal angle = 39° . B, Protractor for determining degree of protection (outer circle), and width of slit as percentage of gape (inner circle), from crestal angle of zigzag. A zigzag is shown in position for measurement ($P = 2.5$ or slit = 40 per cent.).

give at three different degrees of opening of the shell, treating the 'harmful particles' under the ideal form of small spheres (Schmidt, Abb. 12). The zigzag deflexion could confer a functional advantage relative to an undeflected commissure, either by increasing the area of the slit without increasing the risk of entry of harmful particles, or by reducing that risk without reducing the area. If the advantage is expressed as a ratio between the deflected and undeflected conditions, Schmidt's three alternatives become identical.

Let the valve edges separate through a vertical distance to be termed the *gape* (text-fig. 1A, $YZ = CR$). For a unit length of the commissure, this determines the area of the slit. Let the *relative amplitude* of the zigzag be the ratio between the length of its *flank* and half the 'wavelength' between adjacent *crests* (i.e. BC/AB). Let the *degree of protection* (P) of the zigzag slit be expressed as the ratio (MN/XY) between the diameters of (a) the largest sphere able to pass through an undeflected slit of the same area (MN), and (b) the largest particle able to pass through the flanks of the zigzag slit (XY). Then the degree of protection is equal to the relative amplitude ($MN/XY = YZ/XY = BC/AB$, by similar triangles XYZ, ABC). Therefore the degree of protection depends only on the

'strength' of the zigzag, and not on the extent to which the valve edges gape apart; it can therefore be determined even for fossil brachiopods. The width of the zigzag slit may be expressed as a fraction of the width of the undeflected slit (XY/MN or $\sin \theta/2$), i.e. the reciprocal of the degree of protection.



TEXT-FIG. 2. Paradigm for protective zigzag slits. A, D, Undeflected valve edges perpendicular and parallel to hinge-axis. B, E, Valve edges with corresponding paradigmatic zigzag deflexions, gaping apart to same degree; S.P., suppression point. C, F, Graphs showing maximum size of particle admitted at each point of zigzags, relative to maximum gape (= 100 per cent.): particles up to 30 per cent. at crests, but uniform at 20 per cent. on flanks; degree of protection $P = 5.0$. G, H, Effect of angular and rounded crests on protective efficiency of zigzag slit ($P = 5.0$); G, slit with crests of varying degrees of angulation; H, corresponding graph showing maximum size of particle admitted at each point.

For any given zigzag there is a constant ratio between the diameters of the largest particles able to pass through the crests and the flanks of the slit (by similar triangles PQR , XYZ). The particles passing through the crests are in fact localized anomalies in an otherwise uniform degree of protection, represented by the particles passing through the flanks (text-fig. 2F). This justifies using the latter, i.e. the width of the slit, for defining the 'degree of protection'.

An ideal deflexion must give a zigzag slit which is uniformly narrow at all points, and in which the deleterious effect of the crests (in allowing the passage of particles larger than the rest of the slit) is reduced as much as possible. This is ensured by a deflexion of uniformly high relative amplitude and large wavelength, with uniformly inclined flanks (text-fig. 2D, E), and sharp crests (text-fig. 2G, H).

But this specification presupposes portions of the valve edges which, when gapping apart, are equidistant from one another at all points (text-fig. 2D, E). In an actual brachiopod this condition would be approached most closely on an arc parallel to the hinge-axis (i.e. usually the antero-median arc). But even here, since the valve edges separate, not on a linear course, but by rotation around the hinge-axis, the zigzag

deflexion must be an *axial deflexion* (Rudwick 1959, p. 13), lying in a cylindrical surface centred on the hinge-axis (text-fig. 3A).

For a zigzag slit which lies in a plane perpendicular to the hinge-axis, the relative amplitude must decrease in a definite 'graded' way towards the hinge-axis ($\sin \theta/2 \propto 1/a$, where a is the distance from the hinge-axis). At one particular *suppression point* (S.P.), the relative amplitude will fall to unity ($\theta = 180^\circ$), and the zigzag deflexion will therefore die away (text-fig. 2A-C). Between the suppression point and the hinge-axis the commissure will be undeflected, and the slit necessarily less than the standard width. The flanks of the zigzag will be curved, with the concave side of each flank facing the hinge-axis (text-fig. 2B); this is due partly to the continuously changing angle of inclination required for a slit of uniform width, and partly to the fact that the valve edges move apart by rotation. As in a deflexion parallel to the hinge-axis, the deleterious effect of the crests will be reduced by a zigzag that is sharp-crested and of large wavelength.

In actual brachiopods, since most of the commissure is curved in plan and inclined obliquely to the hinge-axis, the paradigm for a protective zigzag deflexion will combine these specifications. It will be (a) axial, (b) sharp-crested, (c) of large relative wavelength, i.e. of low *crestal number* (N , the total number of crests distinguishable around the commissure), (d) of high relative amplitude and straight flanks anteriorly, and (e) of appropriately graded relative amplitude and flank-curvature laterally and posteriorly. Such a deflexion will produce a *graded zigzag slit* (text-fig. 3B, C) of uniform width all round the commissure, from one suppression point round to the other. It can be shown graphically by plotting the relative width of the slit at each point. The relative gape (directly proportional to the relative distance from the hinge-axis) gives a *gape curve*. The width of the slit (derived from the relative amplitude and gape at each point) gives a *slit curve*. If the zigzag is perfectly graded, the slit curve will be a horizontal straight line, intersecting the gape curve at the suppression points. The proximity of the slit curve to the base line indicates the degree of protection given by the zigzag. (Each point on a slit curve represents the mean between the widths of the slit on either side of each crest, though intermediate points can be determined if necessary; the slit curve does not show the effect of the crests themselves.)

Grading ensures that the slit on all arcs of the commissure is as wide as possible, without detracting from the degree of protection given. This would minimize the extra resistance to the flow of water through the gape, caused by drag against the lengthened edges of the valves. Any zigzag must be a compromise between protection and rate of flow.

ZIGZAG DEFLEXIONS IN FOSSIL BRACHIOPODS

Material studied. In this section, the interpretation of zigzag slits as protective devices is tested by comparing the functional paradigm with the actual deflexions of fossil brachiopods.

Although I have searched several large collections, the species cited or figured here (see list in Appendix) are not an accurately representative sample of all species with zigzags. The faunas of some periods, particularly the Triassic and Upper Carboniferous, are certainly under-represented; and in some instances I have had to rely on published figures. The available faunas of some other periods, particularly the Jurassic, have been so abundant that the sample is probably overweighted at these points. Moreover, the

faunas of different periods have received very unequal attention from modern systematists; as Cooper and Williams (1952) showed in another context, quantitative conclusions cannot safely be drawn from data of this kind (see also Williams 1957). But I believe that the coverage has been complete enough to show qualitatively the pattern of distribution of zigzag deflexions.

The repositories of the figured specimens are shown by the following abbreviations: A.M.N.H., American Museum of Natural History, New York; C.M.Z., Cambridge University, Museum of Zoology; M.C.Z., Museum of Comparative Zoology, Harvard University; S.M., Sedgwick Museum, Cambridge University; U.S.N.M., United States National Museum, Washington; U.W.I.P., Universität von Wien, Institut für Paläontologie.

Techniques for the analysis of zigzag deflexions. The presence of grading is shown by the regular reduction in amplitude towards the hinge, and the curvature of the flanks of the zigzag. The degree of grading can be estimated fairly simply: if a comparison with a chart of zigzags of known amplitude shows that the width of the slit anteriorly is 20 per cent. of the gape, then the suppression points for perfect grading will be 20 per cent. of the distance between the hinge-axis and the front of the shell (text-fig. 3A, C). (Determinations from published figures are obviously less reliable, since it cannot be assumed that 'lateral views' are in fact strictly lateral.) A more accurate analysis of the grading can be made by constructing a slit curve. Though somewhat laborious, this is greatly simplified in practice by the use of a specially calibrated protractor (text-fig. 1B), which gives the width of the slit or the degree of protection directly from the crestal angle; and by the use of other graphical devices which convert the positions of the crests directly into percentage distances, and allow the points on the slit curve to be plotted without any actual numerical calculation.

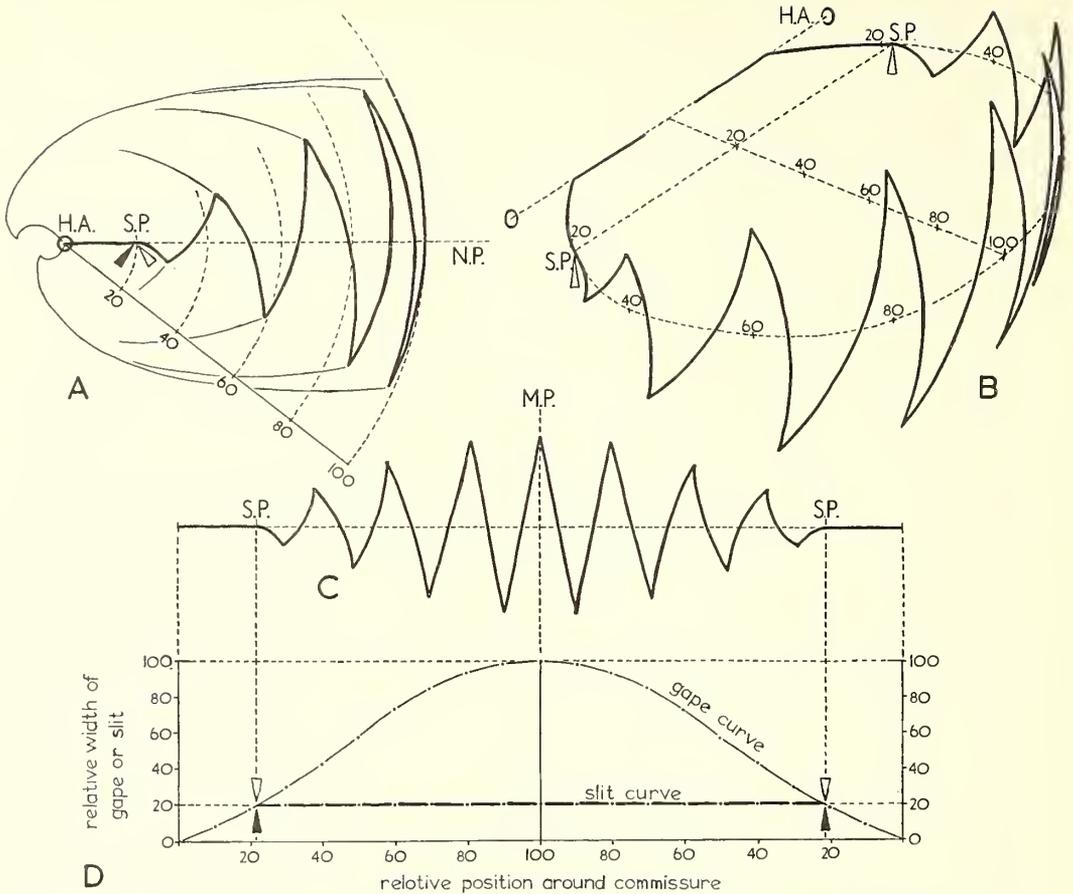
Note on illustrations. Most zigzag deflexions are illustrated in the text-figures by standard anterior and lateral views of the shell, traced from photographs. The dorsal valve is always shown uppermost. The lines marked on the valve surfaces are the loci of crests of the zigzag. In the *lateral view*, the normal plane (where distinguishable) is indicated by a small arrow pointing towards the shell; the orientation of the median deflexion (if present) is shown by a small arrow pointing away from the shell; a small circle marks the hinge-axis. An open and a black isosceles triangle point to the actual and ideal suppression points respectively. On the *anterior view*, a vertical line indicates the median plane; a horizontal line ending in two small circles shows the position of the hinge-axis projected into the plane of the drawing. *Commissure traces* and *slit curves* may also be given, but they are not drawn to scale. All the photographs reproduced here were taken after coating thinly with ammonium chloride. They are oriented with the dorsal or adapical direction (as appropriate) uppermost.

Classification of zigzag deflexions

Since brachiopod shells grow by accretion and leave traces (in the growth-lines) of the stages of their growth, the genesis of a zigzag deflexion can be described from any well-preserved specimen. This provides the basis for a classification of the deflexions, for their origin and development during ontogeny are remarkably diverse. In the ontogenetic descriptions which follow, terms such as 'early', 'late', 'slow', and 'rapid' refer not to the absolute time-scale of growth (which is of course unknown in fossil species), but to the relative time-scale provided by the growth in the overall size of the shell. The reference throughout is to ontogeny, not to phylogeny.

In distinguishing different types of zigzag, an attempt is made to translate the definitions into 'cumulative' terms of description; but since the cumulative expression of the deflexions (i.e. in costae, folds, sulci, &c.) depends on the individual shell form, these 'translations' can only be approximate.

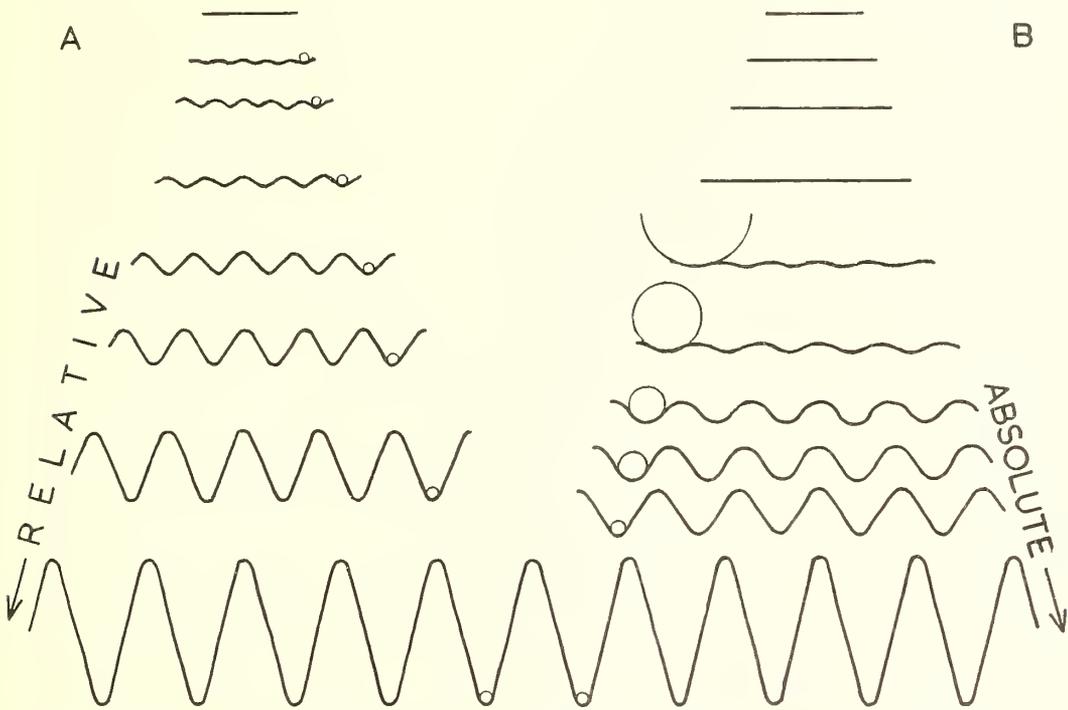
All zigzag deflexions were formed during ontogeny by the modification of an earlier



TEXT-FIG. 3. Paradigm for protective zigzag deflexion ($P = 5.0$) on commissure of subcircular plan. A, Lateral view of shell; note curvature of anterior commissure in arc centred on hinge-axis (H.A.)—definitive of an *axial* deflexion; note suppression point (S.P.) at 20 per cent. of distance from hinge-axis—since deflexion is paradigmatic, actual suppression point (white pointer) coincides with ideal (black pointer); N.P., normal plane; (N.B. this is only one possible form of shell on which this commissure could occur). B, Perspective view of commissure; numerals show (i) percentage perpendicular distances from hinge-axis towards anterior side, and (ii) percentage distances from hinge-line around projection of commissure into normal plane; note curvature of flanks of zigzag. C, Commisure trace, reduced. M.P., median plane; compare median and lateral arcs with text-fig. 2E, B, respectively. D, Gape curve and slit curve for the commissure; vertical and horizontal axes calibrated from B with numerals (i) and (ii) respectively; horizontal slit curve, at 20 per cent. on vertical axis, implies perfect grading with degree of protection = 5.0; compare median and lateral portions with text-fig. 2F, C, respectively.

serial deflexion of more rounded or *undulate* form. This *angulation* (text-fig. 4) may be either relative or absolute. In *relative angulation*, the undulate deflexion arose early in ontogeny, and thereafter became gradually more angulate: as the wavelength increased the flanks became longer and straighter; but the crests, although becoming relatively sharper, maintained a constant absolute degree of rounding (text-fig. 4A). In *absolute angulation* the deflexion remained undulate until a fairly late stage; the crests then became sharper absolutely (i.e. their minimum radius of curvature decreased) while the

flanks were becoming straighter (text-fig. 4B). The final zigzags produced by these two processes may be indistinguishable. In most shells the angulation can be confidently assigned to one class or the other by simple inspection of the growth-lines; in a few the evidence is more ambiguous, so that this distinction cannot be regarded as entirely rigid.



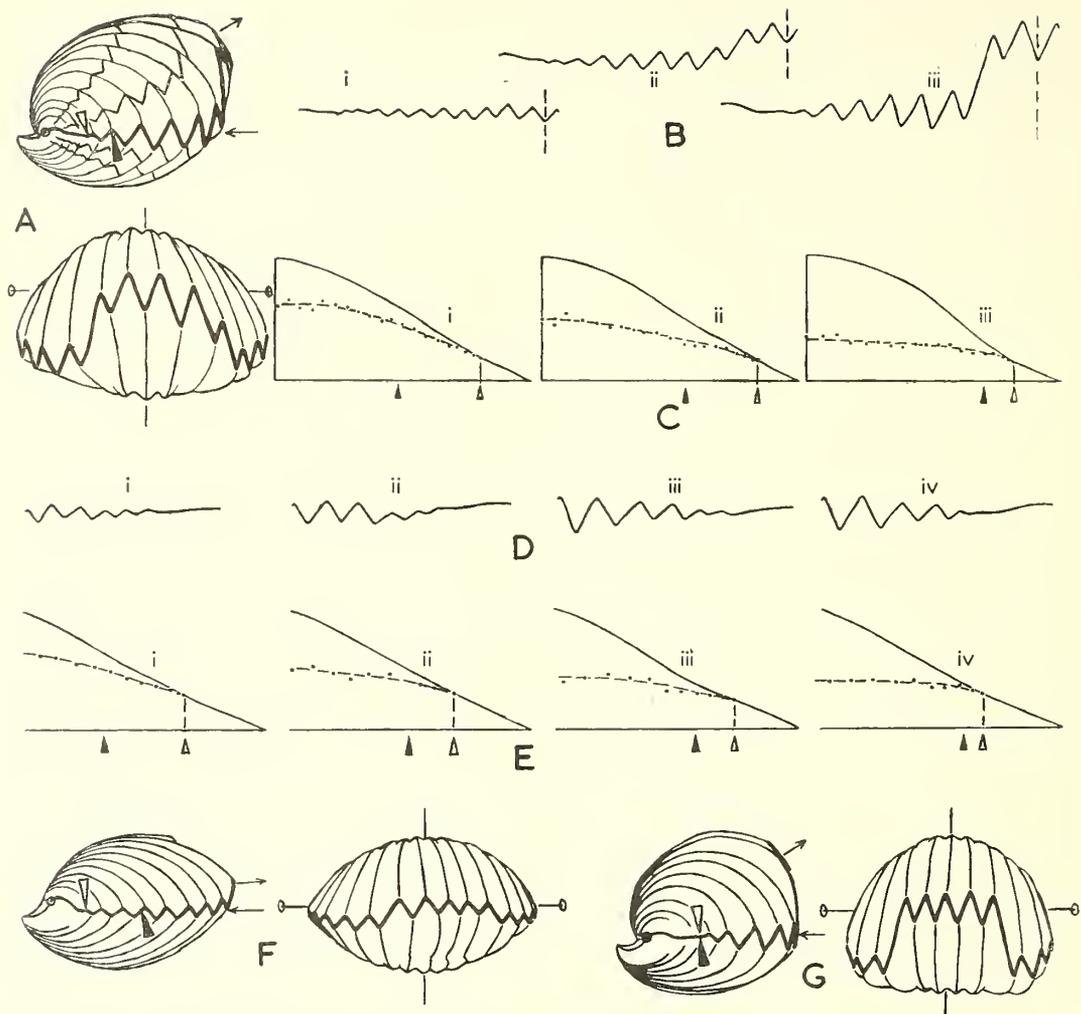
TEXT-FIG. 4. Diagram to show formation of zigzag deflexion during ontogeny by relative (A) or absolute (B) angulation of a pre-existing undulate serial deflexion. Each line represents the same (anterior) arc of the commissure, growing in length during ontogeny. The circles fitted into certain crests show the radius of curvature of the crests—almost constant during relative angulation, rapidly reduced during absolute angulation.

Group A

The serial deflexion from which the zigzag was ultimately produced arose very early in ontogeny, and appeared almost simultaneously on all arcs of the commissure. (In cumulative terms, all the costae arise close to the umbo of each valve.)

Subgroup A. 1 (text-figs. 5-7; Pls. 21-24): The crestal number remained almost constant after an early stage in ontogeny, and the zigzag was produced by relative angulation. (In cumulative terms, most of the costae extend without interruption from near the umbo to the commissure, becoming gradually broader and relatively more sharply ridged.)

This subgroup contains a wide variety of shells: *Globirhynchia* may be taken as an example (text-fig. 5; Pl. 21, figs. 6, 7; Pl. 22, figs. 3-5). Relative angulation gave the deflexion a zigzag form at a fairly early stage; but its relative amplitude was low, and



TEXT-FIG. 5. Zigzags of Subgroup A. I: Rhynchonellacea: *Globirhynchia*. A, 'Adult' shell of *G. subobsoleta* (Davidson): right lateral and anterior views; $P = 3.0$; $N = 32$; grading good; median deflexion slightly asymmetrical. S.M. J. 48763, $\times 1.5$. B, Three stages in growth of right half of commissure of same shell; note progressive suppression of crests. C, Slit curves for same growth stages; note approach towards perfect grading; final degree of protection = 3.0. D, Four stages in growth of lateral arc of commissure of another shell; note progressive suppression of crests. S.M. J. 48766. E, Slit curves for same growth stages; note approach towards perfect grading; final degree of protection = 2.5. F, 'Young' shell with poor grading and weak median deflexion; $P = 2.0$; $N = 38$. S.M. J. 48767, $\times 3$. G, 'Adult' shell of *G. tatei* (Davidson): $P = 3.0$; $N = 28$; grading perfect; deep median deflexion with steepened flanks. S.M. J. 48761, $\times 3$. All from Oolite Marl, Inferior Oolite (M. Jurassic); Notgrove Station (A-F) and The Frith quarry, Painswick (G), Gloucestershire, England.

also fairly uniform on all arcs of the commissure. Consequently the degree of protection was low and the grading poor (text-fig. 5F; Pl. 21, fig. 7). In later stages the relative amplitude on the more anterior arcs rose rapidly. This not only increased the overall degree of protection, but also, by shifting the ideal suppression point towards the hinge, tended to improve the grading. Moreover, at the same time the crests nearest the hinge were gradually and progressively suppressed, so that the actual suppression point was shifted forwards towards the ideal. This *crestal suppression* can easily be detected in the growth-lines on the postero-lateral sectors of the valve-surfaces (Pl. 22, figs. 3, 5); and its effects can be determined by tracing successive growth-lines and analysing their slit-curves (text-fig. 5B-E). Thus the final commissure of a 'mature' specimen may have a moderately high degree of protection and good grading (text-fig. 5A; Pl. 21, fig. 6). A complication is introduced by the development of a dorsal median deflexion, which was superimposed on the much earlier serial deflexion. At first the median deflexion was very weak; it merely shifted the antero-median arc of the zigzag very slightly in a dorsal direction, and lengthened two of its flanks (text-fig. 5F). As the median deflexion increased in height, its lateral flanks either coincided with a single flank of the zigzag (text-fig. 5B; Pl. 22, fig. 4) or else were 'shared' by more than one flank of the zigzag. Since the median deflexion was often slightly asymmetrical, both these conditions may be found in a single shell (text-fig. 5A). The median deflexion did not affect the degree of protection of the zigzag, and is therefore not apparent in the slit-curves (text-fig. 5C).

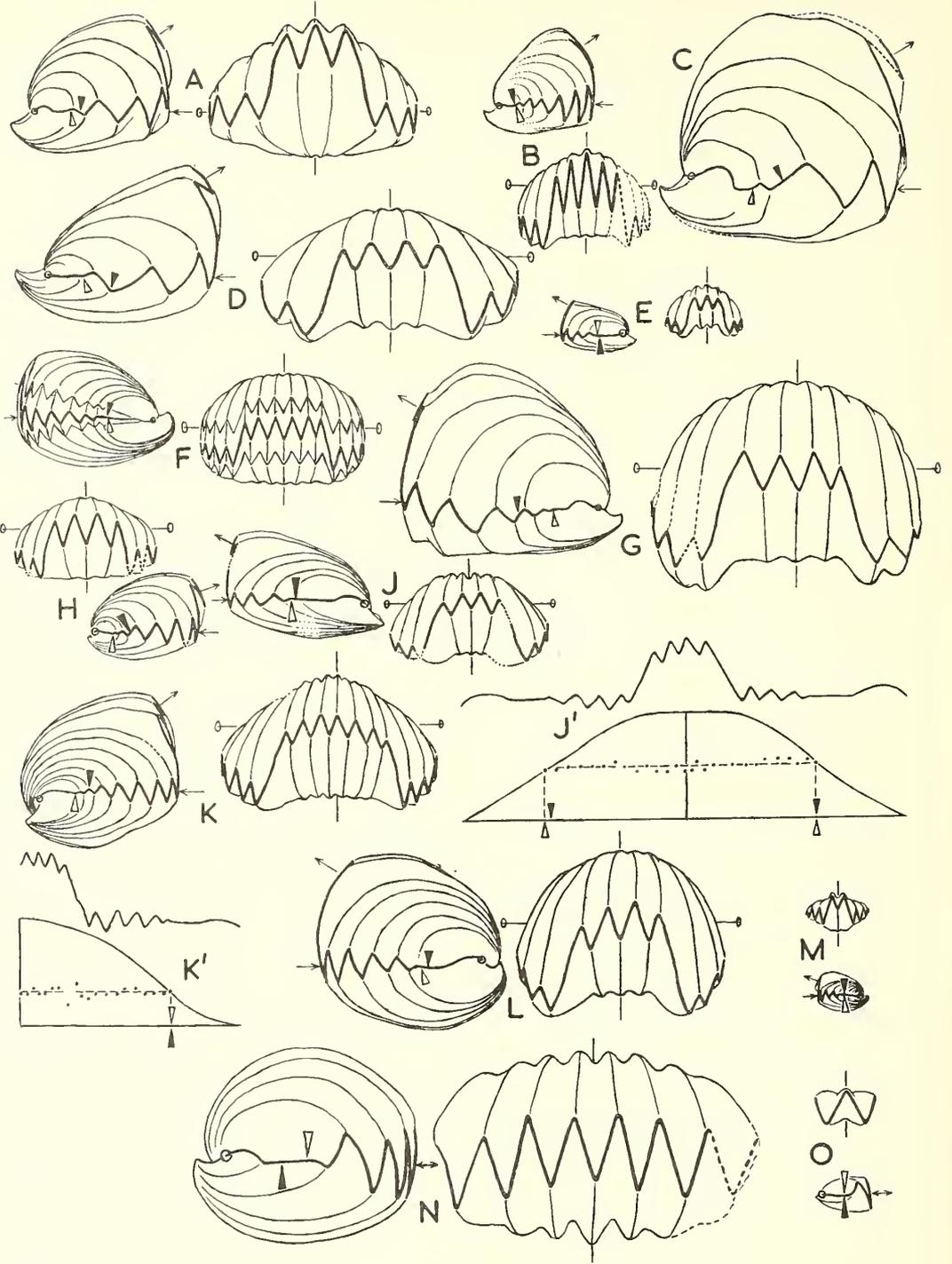
Even within the single genus *Globirhynchia*, there is great variation in the absolute size at which a zigzag with a given degree of protection may be found. Thus a typical mature specimen of *G. tatei* (text-fig. 5G) has a well-graded zigzag similar in form to that of a typical specimen of *G. subobsoleta* (text-fig. 5A), although it is only half as large in linear dimensions.

Similar zigzags are abundant among the rhynchonellaceans of every period from the Ordovician (in which the superfamily first appeared) until the Cretaceous (text-fig. 6; Pls. 21-23), and they also occur sporadically in several other superfamilies (text-fig. 7; Pls. 23-24).

The serial deflexion always arose early in ontogeny. Its crestal number was usually fairly high, but very exceptionally as low as five (text-fig. 6O). Occasionally its initial crestal number was increased at an early stage by the production of new crests (i.e. new costae appear near the umbo: Pl. 24, fig. 4). The ridges of the costae show that the angulation was predominantly relative (Pl. 21, figs. 4, 5; Pl. 23, figs. 1, 4, 6, 8; Pl. 24, figs. 4, 5).

The zigzag might at first be poorly graded (text-fig. 7H), but was generally improved in the final stages by posterior crestal suppression (text-fig. 7J; Pl. 23, fig. 6; see also Pl. 23, figs. 2, 7; Pl. 24, figs. 3, 5). Where such suppression failed to occur, the posterior part of the deflexion, behind the ideal suppression point, sometimes retained its much earlier undulate form (Pl. 23, fig. 3). On 'mature' shells the zigzags often approximated closely to the paradigm: anteriorly they had straight flanks and uniform amplitude (Pl. 22, figs. 1, 6; Pl. 24, fig. 8) and the degree of protection was sometimes very high (Pl. 21, fig. 2); while laterally the flanks were appropriately curved and graded in amplitude (Pl. 21, fig. 2; Pl. 23, figs. 1, 4).

Usually there is a dorsal median deflexion. It invariably appeared later than the serial deflexion, and merely shifted the antero-median arc of the commissure in a dorsal

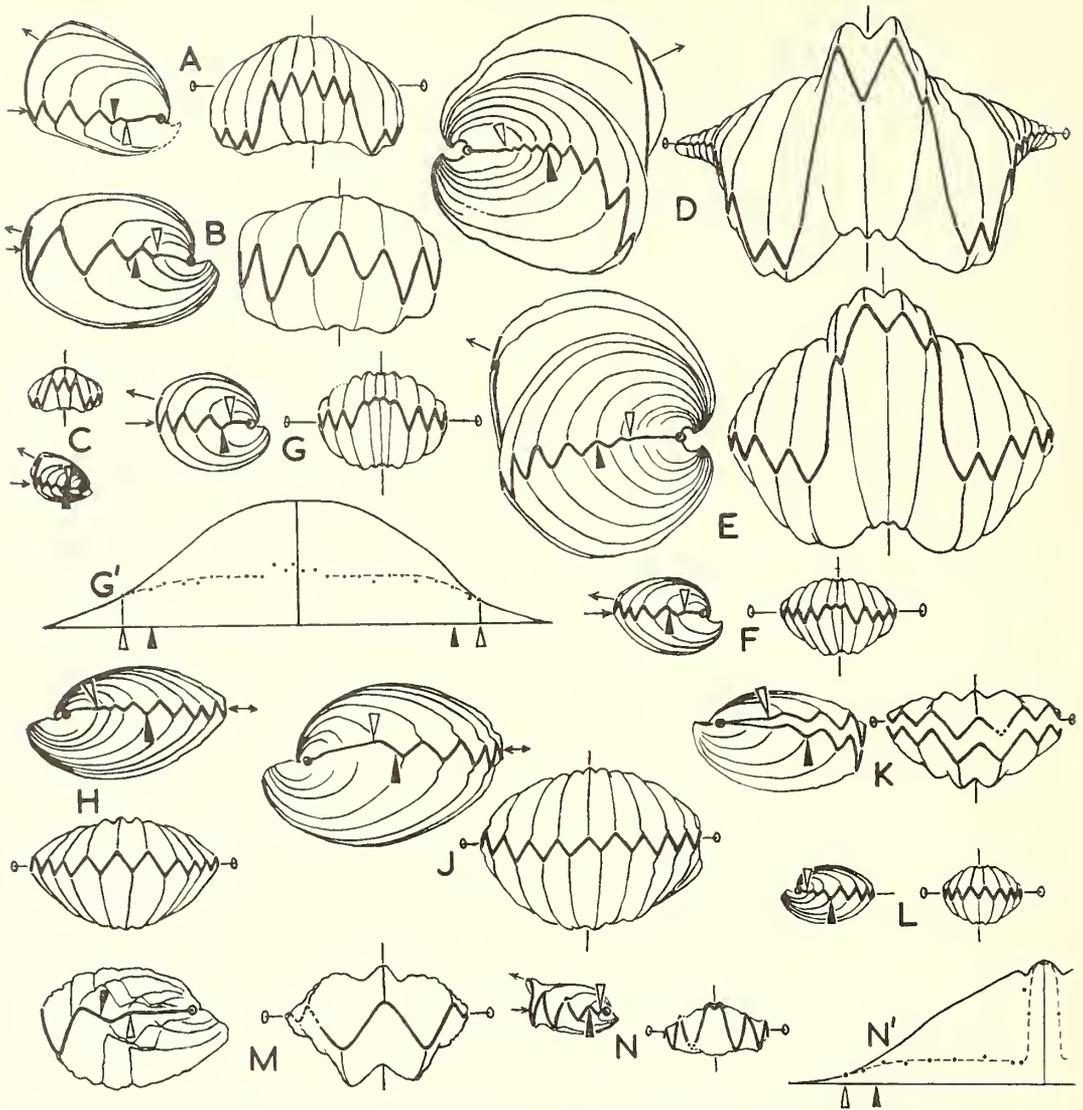


TEXT-FIG. 6

direction. Occasionally this arc was distinguished from the lateral arcs, even at an early stage, by the production of new crests of the serial deflexion (in cumulative terms, there is some 'branching' of the costae in the median sector near the umbo, Pl. 21, fig. 1). The number of crests of the serial deflexion incorporated in the median deflexion is highly variable, even, sometimes, within a single species: in some species there were as few as three crests there (text-figs. 6M, 7N; in cumulative terms, there are only two costae on the fold and one in the sulcus). The quality of the putative protection of the median deflexion is generally exactly the same as that of the lateral arcs, so that the presence of the median deflexion is not apparent on the slit-curves (text-fig. 6J', K'). But in some shells the protection of the antero-median arc was distinctly poorer than that of the lateral arcs, for example, by having a lower amplitude or lower wavelength or poorer angulation of the crests (text-figs. 6D, 7B, F, G, N; Pl. 24, fig. 1). Even on the flanks of the median deflexion the width of the slit was either unaltered or only reduced in the final growth stages by a relative steepening (text-figs. 6A-M, 7A-G). Occasionally this steepening involved the reduction or even elimination of some flanks and crests of the zigzag (in cumulative terms, costae on the flanks of the median fold or sulcus may be reduced or even die out towards the commissure: Pl. 21, fig. 3; pl. 22, fig. 1; Pl. 23, fig. 5; Pl. 24, fig. 2). In a few shells the zigzag deflexion was unaffected by any median deflexion whatever (text-figs. 6N, O; 7H-M).

Occasional specimens are preserved with the valves gaping slightly apart; these demonstrate clearly the zigzag slits that the deflexions would have produced (Pl. 21, figs. 8, 9, 12).

TEXT-FIG. 6. Zigzags of Subgroup A. I (except B, Subgroup B. I): Rhynchonellacea. All $\times 1.5$ (except N, $\times 1$). A, '*Rhynchonella walkeri* Davidson. P = 3.0; N = 20; grading almost perfect. Claxby Ironstone (L. Cretaceous); Claxby, Lincolnshire, England. S.M. B. 11401 (figured Davidson 1874, pl. viii, fig. 33). B, '*Rhynchonella personata* von Buch (?). P = 7.5; N = c. 35; grading perfect. 'M. Callovien' (U. Jurassic); 'Elatma, gouv. de Tambow' [Tambov], Russia. S.M. F. 9722. C, *Russirhynchia fischeri* (d'Orbigny). P = 2.5; N = 19; grading fair. 'L. Portlandien' (U. Jurassic); Mniovniki, near Moscow, Russia. S.M. F. 9671. D, '*Rhynchonella subvariabilis* Davidson. P = 2.5 (less in median deflexion); N = 20; grading fair on lateral arcs. Kimeridge Clay (U. Jurassic); Wheatley, Oxfordshire, England. S.M. J. 1506. E, '*Rhynchonella decurtata* Girard. P = 2.5; N = c. 17; grading perfect (?). 'Muschelkalk' (M. Trias); Recoaro, Vicenza, Italy. (After Bittner 1890, Taf. 32, fig. 3.) F, *Uncinunellina jabiensis* (Waagen). P = 3.0; N = 35; grading perfect; note vertical zones between marked growth-line and final commissure. U. Permian; Basleo, Timor. S.M. A. 11512. G, *Camarotoechia pleurodon* (Phillips). P = 2.5; N = 33; grading fair. Gastropod beds, Carboniferous Limestone (L. Carboniferous); Ashfell Edge, Westmorland, England. S.M. E. 10425. H, *Stegerhynchus daphne* (Barrande). P = 3.2; N = 29; grading fair. Kopanina limestone (U. Silurian); 'Jarow', Czechoslovakia. S.M. A. 50252. I, J, *Rhynchotrete cuneata* (Dalman). P = 2.0; N = 22; grading perfect. M. Silurian; Klinte, Gotland, Sweden. S.M. A. 8779 (figured St. Joseph 1937, text-fig. 6). K, K', *Camarotoechia borealis* (Schlotheim). P = 3.0; N = 40; grading good. Wenlock limestone (M. Silurian); Dudley, Worcestershire, England. K, S.M. A. 8709; K', S.M. A. 8682. L, *Lepidocyclus capax* (Conrad). P = 3.0; N = 25; grading perfect. 'Hudson River group' (U. Ordovician); Ohio. S.M. A. 47252. M, *Rostricellula ? minuta* Cooper. P = 3.0; N = 23; grading perfect. L. Hermitage formation (M. Ordovician); near Woodbury, Tennessee. (After Cooper 1956, pl. 137, figs. 1, 3.) N, *Halorella amphitoma* (Bronn) var. *crisagalli* Bittner. P = 3.6; N = c. 21; grading good. Kalke der Hohen Wand (U. Trias); Wiener Neustadt, Austria. (After Bittner 1890, Taf. 20, fig. 15.) $\times 1$. O, *Oligorhynchia angulata* Cooper. P = 2.0; N = 5; grading perfect. Hogskin member, Lincolnshire formation (M. Ordovician); Luttrell, Tennessee. (After Cooper 1956, pl. 125, figs. 42, 44.)



TEXT-FIG. 7. Zygags of Subgroup A. I: Other than Rhynchonellacea. All $\times 1.5$ (except D, $\times 2$). A, Rhynchoporacea: *Rhynchopora nikitini* Tschernyschew. $P = 3.0$; $N = 27$; grading good. Goniatite bed (U. Carboniferous); Pariñas Quebrada, Amotape Mts., Peru. S.M. A. 14825. B, Punctospiracea: *Hustedia hessensis* King. $P = 2.7$; grading good; crests less angulate in median deflexion. Bone Spring formation (L. Permian); Victorio Canyon, Sierra Diablo, Texas. A.M.N.H. 27328/1:1 (figured Stehli 1954, pl. 27, figs. 10, 11). C, Syntrophiacea: *Plectocamara costata* Cooper. $P = 2.5$; $N = c. 21$; grading good (?). Hogskin member, Lincolnshire formation (M. Ordovician); near Washburn, Tennessee. (After Cooper 1956, pl. 122, figs. 9, 10.) D, Orthacea *Platystrophia cypha* (James). $P = 2.5$; $N = c. 37$; grading fair; waves on flanks of median deflexion almost or completely eliminated from final commissure. Arnheim formation (U. Ordovician); Summit, Mason Co., Kentucky. U.S.N.M. 78670, $\times 2$. E, Orthacea: *Platystrophia crassa* (James). $P = 2.3$; $N = 32$; grading fair—some posterior suppression; 'Hudson River group' (U. Ordovician); Cincinnati, Ohio. S.M. A. 47092. F, Athyracea: *Rhynchospirina baylei* (Davidson). $P = 2.5$; $N = 24$; grading fair; wavelength low in

Subgroup A. II (text-fig. 8; Pl. 25): The crestal number was radically reduced at a fairly late stage in ontogeny, the reconstituted deflexion undergoing relative angulation. (In cumulative terms, the fine costae which extend radially from near the umbo of each valve are replaced near the commissure by a much smaller number of broader costae.)

This is a small, but highly distinctive, group. The serial deflexion arose very early, and generally had a high crestal number (Pl. 25, figs. 1, 2, 3, 6). At a fairly later stage, after it had begun to be affected by a dorsal median deflexion, but while it was still low in relative amplitude, *crestal reduction* began to occur. This involved the rapid coalescence of groups of adjacent crests, or the suppression of some crests and the retention of others. The angularity of the initial crests was usually carried over without a break into the surviving reconstituted crests; and the new deflexion, thereafter, became a zigzag by relative angulation. Crestal reduction sometimes affected all arcs of the commissure simultaneously; but, more commonly, it occurred first on the antero-lateral arcs, just outside the median deflexion, and then spread both laterally and medially. Posterolaterally, it spread at least as far as the ideal suppression point; beyond this point a few 'unreduced' crests might persist (Pl. 25, figs. 2, 4) or might ultimately be suppressed in the usual way to give perfect grading. Occasionally the reduction failed to spread into the median deflexion, so that the median arc of the final zigzag remained anomalously low in wavelength (text-fig. 8D; Pl. 25, fig. 3). The distinctive shell-form produced by this sequence of events is confined to the rhynchonellaceans, but occurred sporadically in the Devonian, the Jurassic, and the Cretaceous.

Group B

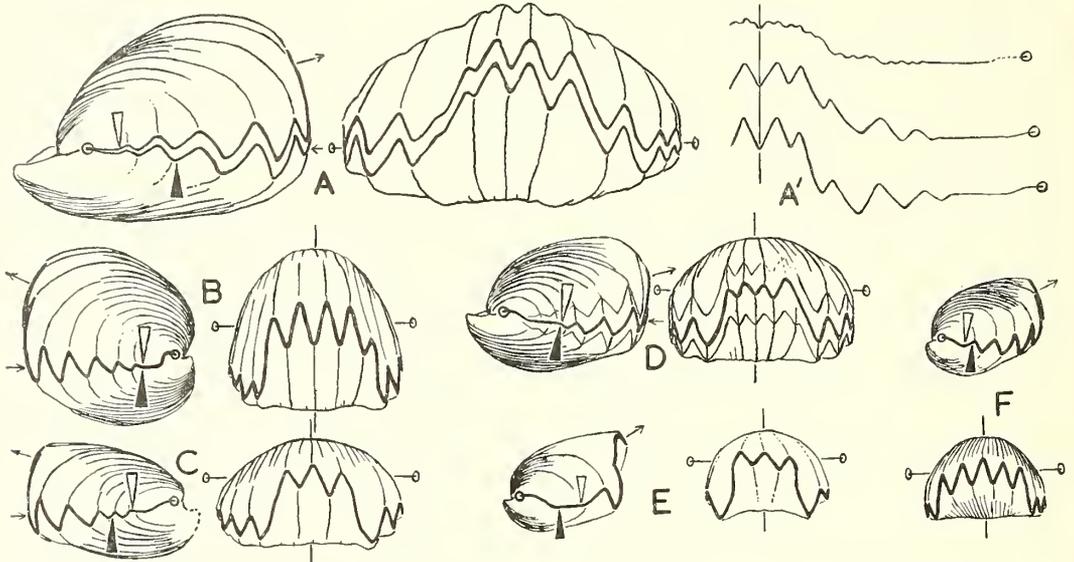
The serial deflexion from which the zigzag was ultimately produced arose progressively throughout ontogeny, spreading gradually from the anterior on to the lateral arcs of the commissure. (In cumulative terms, the medial costae arise nearer the umbo than the more lateral costae.)

Subgroup B. I (text-figs. 9, 10; Pls. 26, 27): The serial deflexion arose moderately late in ontogeny, and on the final commissure had a moderately large crestal number; it was transformed into a zigzag by predominantly absolute angulation at a late stage.

median deflexion. 'Gothland limestone series' (Silurian); Gotland, Sweden. S.M. A. 48786. G, G', Athyracea: *Trematospira salteri* (Davidson). P = 3.0; N = 23; grading good laterally; wavelength and amplitude lower in median deflexion. Wenlock Limestone (M. Silurian); Dudley, Worcestershire, England. G, S.M. A. 27189; G', S.M. A. 27182. H, J, Terebratellacea: *Eudesia cardiium* (Lamarck). H, Immature specimen; P = 2.0; N = 33; grading poor. J, Mature specimen; P = 2.0; N = 24; grading good (but with slightly lower degree of protection in median arc). Great Oolite (M. Jurassic); Minchinhampton, Gloucestershire, England. H, S.M. J. 22427; J, S.M. J. 22433. K, Terebratellacea: *Choristothyris plicata* (Say). P = 1.6; N = 13; grading fair. Navesink Marl (?) (U. Cretaceous); New Egypt, New Jersey, S.M. F. 8033. L, Punctospiracea: *Hustedia mormoni* (Marcou). P = 2.2 N = 27; grading fair. Osage group (L. Carboniferous); Howard, Kansas. S.M. E. 14947. M, Terebratellacea: *Ismenia pectunculoides* (Schlotheim). P = 1.7; N = 9; grading good. 'Jurakalk' (U. Jurassic); Nattheim, Baden, W. Germany. S.M. F. 15993. N, N', Athyracea: *Plectospira ferita* (von Buch). P = 3.5; N = 17; grading good; median deflexion not angulate; the very prominent crests are simply due to the strong zigzag developed on valves of weak overall convexity. Devonian; Eifel, W. Germany. S.M. H. 5263.

(In cumulative terms, the costae arise some distance from the umbo of each valve; near the commissure there is a moderately large number of sharply ridged costae.)

This subgroup, like Subgroup A. I, contains a wide variety of shells: *Pugnax pugnax* may be taken as an example (text-fig. 9A; Pl. 26, fig. 1). In the early stages of growth the valves were smooth (apart from very fine costellae) and the commissure rectimarginate.



TEXT-FIG. 8. Zigzags of Subgroup A. II: Rhynchonellacea. All $\times 1.5$. A, A', *Cyclothyris antidichotoma* (Buvignier). A: $P = 2.5$; $N = 29$; grading fair; shell preserved gaping. Lower Greensand (L. Cretaceous); Upware, Cambridgeshire, England. S.M. B. 25761. A': commissure traces from three successive stages. S.M. B. 25764. B, *Rimirhynchia anglica* (Rollier). $P = 4.5$; $N = 31$; grading perfect. Middle Lias (L. Jurassic); West Tynning, near Radstock, Somerset, England. S.M. J. 36345. C, *R. anglica*. $P = 2.3$; $N = 28$; grading fair; note that waves between ideal and actual S.P. are those still unaffected by crestal reduction. Middle Lias (L. Jurassic); Cheltenham, Gloucestershire, England. S.M. J. 36867. D, *R. anglica*. $P = 2.4$; $N = 24$; grading perfect; note median arc unaffected by crestal reduction, and posterior suppression between marked growth line and final commissure. Locality as C. S.M. J. 36871. E, *Furcirhynchia cotteswoldiae* (Upton). $P = 2.4$ laterally, only 1.5 in median deflexion; $N = 11$; grading fair. Cephalopod Bed, Upper Lias (L. Jurassic); Haresfield Beacon, Stroud, Gloucestershire, England. S.M. J. 48668. F, *Nayunella schmuri* (de Verneuil). $P = 3.3$; $N = 25$; grading good. M. Devonian; Eifel, W. Germany. S.M. H. 7607.

A weak dorsal median deflexion then appeared. Soon afterwards the antero-median arc (within the median deflexion) was affected by a weak undulate serial deflexion, which later spread on to the antero-lateral arcs and eventually round on to the postero-lateral arcs. Meanwhile it increased in amplitude. At a fairly late stage it underwent absolute angulation, the crests becoming sharper and the flanks straighter. The final commissure is a zigzag with sharp crests throughout, straight flanks and high relative amplitude anteriorly, curved flanks and well-graded amplitude laterally. It thus resembles the final commissure of many shells in subgroup A. I, although it was derived by a significantly different sequence of events in ontogeny.

Similar zigzags are abundant among the rhynchonellaceans, from at least the Silurian

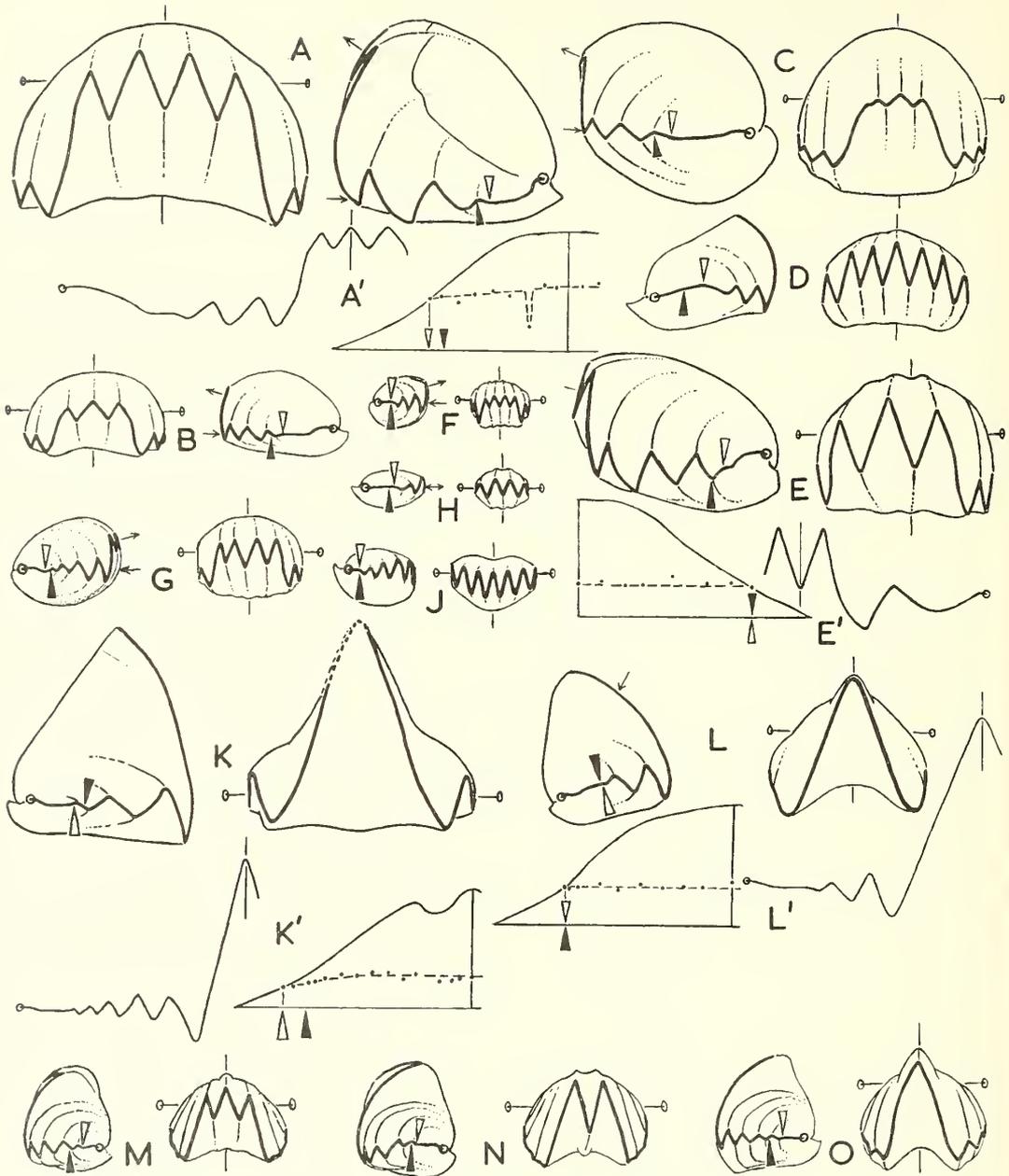
to the Jurassic inclusive (text-fig. 9; Pl. 26; Pl. 27, figs. 1–4), and also occur sporadically in several other superfamilies (text-fig. 10; Pl. 27). The serial deflexion never arose very early in ontogeny, and in some species its appearance was so late that it scarcely produced any clear costae on the valve surfaces (text-fig. 9J; Pl. 27, figs. 1, 2). Its gradual spread on to the lateral arcs can often be seen clearly in the growth-lines (Pl. 26, figs. 1, 3; Pl. 27, figs. 8, 9). On the final commissure, the relative amplitude on the anterior arc may be very high, with angulate crests and straight flanks (Pl. 26, fig. 6); and the zigzag on the lateral arcs may have appropriately curved flanks and graded amplitude (Pl. 26, fig. 5). The grading is often very good or even perfect (text-figs. 9, 10).

Usually there is a dorsal median deflexion, which contains several crests of the zigzag (text-figs. 9A–F, M; 10A, B, D, J; Pl. 26, figs. 1, 2, 6). Rarely there is a similar, but ventral, deflexion (text-fig. 10C, H). In some shells the number of crests within the median deflexion is only three (text-figs. 9N; 10C; Pl. 26, fig. 7). It may even be as low as one, i.e. the median deflexion itself underwent angulation (text-figs. 9K, L, O; 10E, F; Pl. 26, fig. 4). It is interesting to note that one species shows intraspecific variation in this character around a mode of three, with rarer variants with five crests or only one crest in the median deflexion (text-fig. 9M–O). The putative degree of protection within the median deflexion is generally identical with that of the lateral arcs, so that the median deflexion is not apparent on the slit curves (text-figs. 9K', L'; 10A'); but in some shells the zigzag within the median deflexion is distinctly further from the paradigm, having a lower relative amplitude or lower wavelength (text-figs. 9C, F; 10H, J). In a few shells of this subgroup there is no median deflexion (text-figs. 9H; 10G).

In some shells of this subgroup, the costae produced by the zigzag serial deflexion are superimposed on a finer pattern of costellae (Pl. 26, figs. 1, 2; Pl. 27, figs. 5–7). These costellae arose very early in ontogeny, and their early stages may have a close resemblance to the early stages of costae of Group A (compare Pl. 27, fig. 5 with Pl. 21, fig. 4). But unlike those costae, the costellae increased in number (by 'branching' or intercalation), not merely during the earlier stages of growth (Pl. 24, fig. 4), but throughout ontogeny. This suggests that the deflexions which produced the zigzags of Group A may be homologous, not to the deflexions which produced the zigzags of Group B, but to those that produced the costellae on which some of the zigzags of Group B were superimposed.

Subgroup B. II (text-fig. 11; Pl. 28, figs. 1–3): The serial deflexion first arose early in ontogeny, though the crestal number increased throughout ontogeny by the erection of new crests laterally. The earliest crests underwent gradual relative angulation, but all the later (lateral) crests show absolute angulation. A dorsal median deflexion was produced by the relative enlargement of a dorsal median crest of the serial deflexion. (In cumulative terms, the medial costae arise near the umbo of each valve, the lateral costae further away; the median dorsal costa is enlarged anteriorly into a median fold.)

This subgroup is confined to spiriferoids, though it occurs both in the impunctate spiriferaceans of the Silurian and Devonian and in the punctate punctospiraceans at many horizons from the Devonian until the extinction of the group in the Jurassic. The deflection is always conspicuously symmetrical. The progressive erection of new crests throughout ontogeny can easily be seen on the lateral flanks of the valves (Pl. 28, fig. 2). Most of the crests underwent absolute angulation, until on the final commissure a



TEXT-FIG. 9. Zigzags of Subgroup B. I: Rhynchonellacea. All $\times 1.5$. A, A', *Pugnax pugnus* (Martin). A, $P = 2.7$; $N = 19$; grading good; marked growth line shows early median deflexion with very early undulate serial deflexion on anterior arc only. Carboniferous Limestone (L. Carboniferous); Derbyshire, England. S.M. E. 8483. A', commissure trace and slit curve; $P = 1.9$; S.M. E. 8479. B, *Curtirhynchia oolitica* (Davidson). $P = 1.9$; $N = 17$; grading good. Pea Grit, Inferior Oolite (M. Jurassic); Leckhampton Hill, Cheltenham, Gloucestershire, England. S.M. J. 48760. C, *Piarrorhynchia cf. juvenis* (Quenstedt). $P = 1.8$ (but only 1.4 in median deflexion); $N = 19$; grading good. Lower Lias (L.

moderately angulate zigzag was formed (text-fig. 11; Pl. 28, figs. 1, 3). Often the grading is rather poor posteriorly (text-fig. 11A, C, E) though it may be good or even perfect (text-fig. 11D, G). Likewise the relative amplitude is usually only moderate, though occasionally it is high (text-fig. 11C). The median crest, which is always dorsal, underwent relative enlargement during ontogeny and became the median deflexion; generally it failed to become angulate and remained unprotected, though occasionally it is fairly angulate (text-fig. 11B, C).

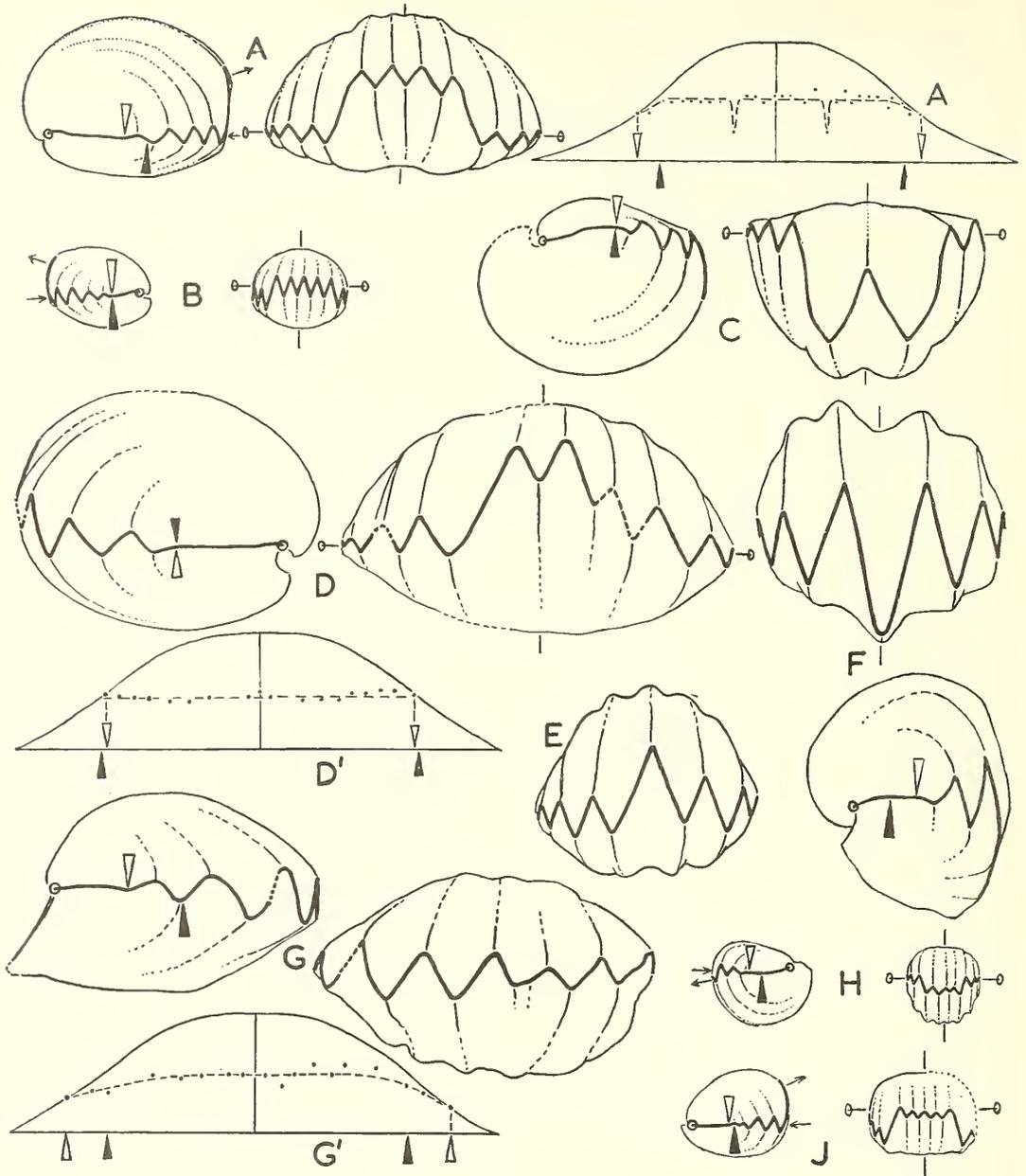
Subgroup B. III (text-fig. 12; Pl. 28, figs. 4, 5): The serial deflexion arose late in ontogeny, and always had a low crestal number (seven or less); it underwent absolute angulation at a late stage. (In cumulative terms, there are only a few broad plicae near the commissure).

This subgroup contains a few miscellaneous species, in all of which the zigzag was produced by the very late absolute angulation of a complex 'fold' incorporating a median deflexion (Pl. 28, figs. 4, 5). The final zigzag is near the paradigm, except that the crests are not highly angulate; the grading is good or even perfect (text-fig. 12).

Accessory crestal protection

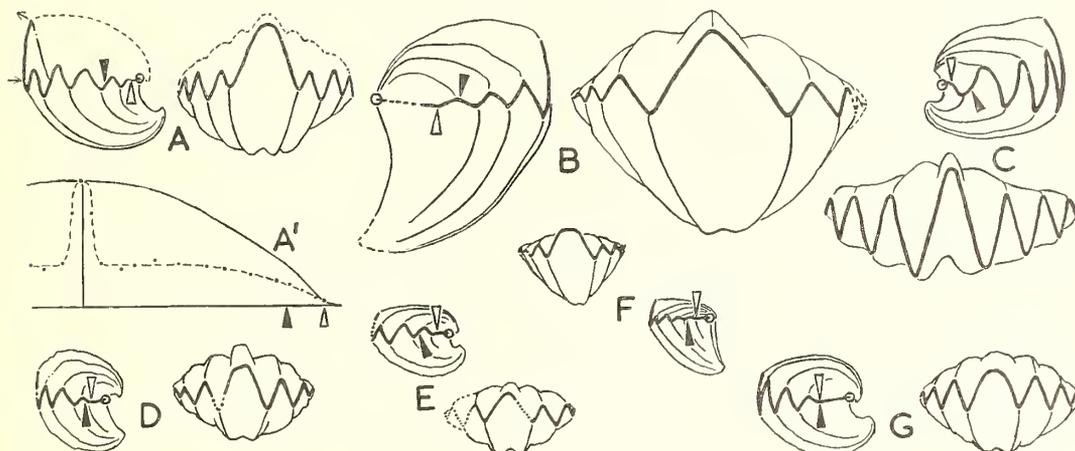
Even in the paradigm, the crests of the zigzag are a deleterious anomaly; however angular they may be, they still allow the passage of 'particles' larger than those passed by the flanks of the slit (text-fig. 2). This anomaly could only be eliminated by placing some accessory structures in these positions. Unless extinct brachiopods possessed organs or tissues entirely unrepresented among living species, only two materials would have been available for this purpose, namely the chitinous *setae* which project from the mantle edge, and the tissue of the mantle edge itself. Both these materials were probably utilized by some brachiopods with zigzag deflexions; but many other zigzag slits probably had no crestal protection.

Jurassic); Tilly-sur-Seulles, Calvados, France. S.M. F. 15992. D, '*Rhynchonella corneliana* Bittner. P = 4; N = c. 19; grading fair. St. Cassianer Schichten (U. Trias); St. Cassian, Bolzano, Italy. (After Bittner 1890, Taf. 3, fig. 18.) E, E', *Rhynchotetra angulata* (Linnaeus). E: P = 3.3; N = 13; grading good; median deflexion slightly asymmetrical. Carboniferous Limestone (L. Carboniferous); Isle of Man. S.M. E. 10186. E', commissure trace and slit curve; P = 3.6. S.M. E. 10165. F, *Monadotoechia monadina* Havlíček. P = 3.5 (2.5 in median deflexion); grading perfect. 'Étage F.f.2' (L. Devonian); Koněprusy, Czechoslovakia. S.M. H. 8453. G, *Sphaerirhynchia davidsoni* (M'Coy). P = 3.3; N = 25; grading good. Wenlock Shale (M. Silurian); Daw End, Walsall, Staffordshire, England. S.M. A. 35248. H, '*Rhynchonella atilina* Bittner. P = 2.5; N = c. 9; grading fair. 'Recoarokalk' (M. Triassic); Felsőörs, Királykút, Hungary. (After Bittner 1890. Taf. 37, fig. 1.) I, *Gnathorhynchia liostraca* (Buckman). P = 5.0; N = 23; grading perfect. Inferior Oolite (M. Jurassic); Corton Denham, Somerset, England. S.M. J. 6177 (figured Davidson 1884, pl. 19, fig. 19). K, K', *Homoeorhynchia acuta* (J. Sowerby). K: P = 3.5; N = 13; grading good. Middle Lias (L. Jurassic); South Petherton, Somerset, England. S.M. J. 35553. K', Commissure trace and slit curve; P = 4.0. S.M. J. 36233. L, L', *Rhynchonella loxiae* Fischer. P = 2.0; N = 9; grading perfect. 'Portlandien' [= Volgian] (U. Jurassic); Khoroshevo, near Moscow, Russia. S.M. F. 9680. M, N, O, *Homoeorhynchia cynomorpha* (Buckman). M, rare variant with five crests in median deflexion; P = 3.0; N = 22. N, Normal form with three crests in median deflexion; P = 3.0; N = 21. O, Rare variant with one crest in median deflexion; P = 2.5; N = 20. Grading good in all. Upper Freestone, Inferior Oolite (M. Jurassic); the Frith quarry, near Painswick, Gloucestershire, England. S.M. J. 6129-31 (figured Buckman 1895, pl. 14, figs. 2-4).



TEXT-FIG. 10. Zigzags of Subgroup B. I: other than Rhynchonellacea. All $\times 1.5$ (except E, F, $\times 1$). A, A', Syntrophiacea: *Parastrophinella reversa* (Billings). P = 2.0; N = 25; grading good. Ellis Bay formation (U. Ordovician); near Junction Cliff, Anticosti Island, Canada. S.M. A. 9393. B, Syntrophiacea: *Camerella pulchra* Cooper. P = 3.5; N = c. 25; grading perfect. Wardell formation (M. Ordovician); near Indian Creek, Tennessee. (After Cooper 1956, pl. 114, figs. 30, 31.) C, Pentameracea: *Gypidula acutilobata* (Sandberger). P = 2.2; N = 15; grading perfect. 'Étage F.f.2' (L. Devonian); Koněprusy, Czechoslovakia. S.M. H. 5278. D, D', Dalmanellacea: *Enteletes lamarki* (Fischer). P = 2.5; N = 19; grading perfect. Fusulina Limestone (U. Carboniferous); Miatchkovo, Moscow, Russia.

If the mantle tissue was thin and non-erectile (as in living articulate brachiopods) any extensions would have to be supported on extensions of the valves, i.e. on *internal marginal spines*. Such spines could only be accommodated within shells with vertical zones. To reduce to a minimum the drag on the flow of water through the slit, the spines



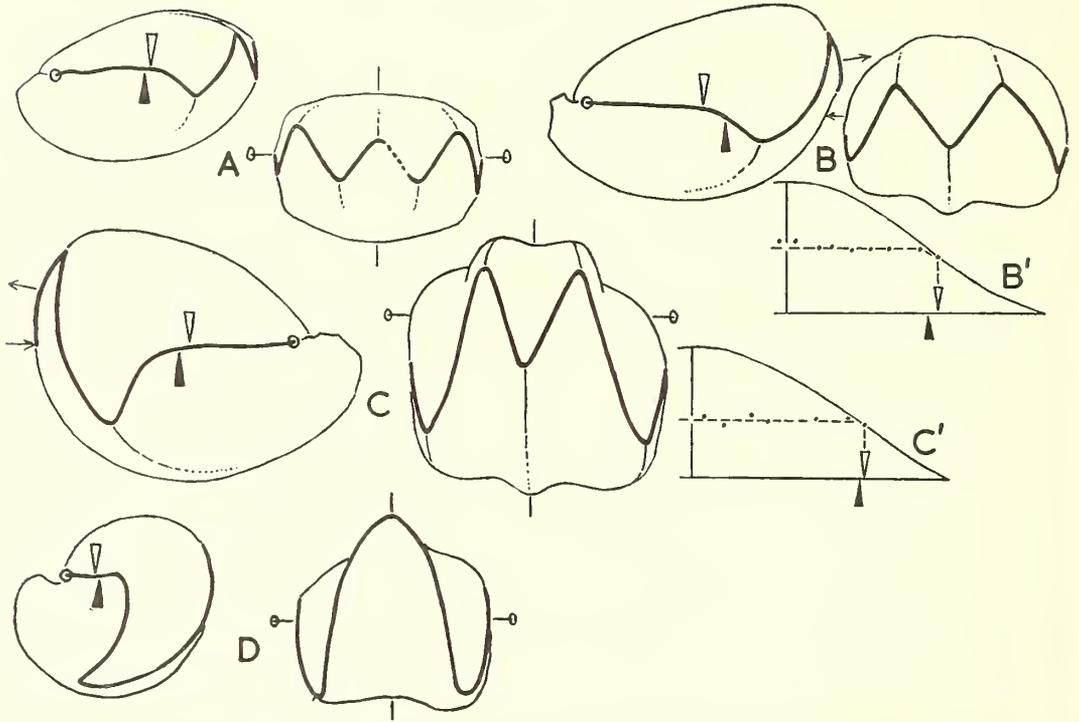
TEXT-FIG. 11. Zigzags of Subgroup B. II: Spiriferoidea. All $\times 1.5$. A, A'. *Spiriferina münsteri* (Davidson): ventral valve only. P = 3.0; N = 21; grading fair. Middle Lias (L. Jurassic); South Petherton, Somerset, England. S.M. J. 36756a. B, *Cyrtina uncinata* (Schafhaeutl). P = 2.0 (less in median deflexion); N = 15; grading good. Kössener Schichten, Rhaetic (U. Trias); Eiseler, Hindelang, W. Germany. S.M. F. 16004. C, *Crenispirifer angulatus* (King). P = 4.0; N = 15; grading fair. Bone Spring formation (L. Permian); Victorio Canyon, Sierra Diablo, Texas. A.M.N.H. 27327/1:2 (figured Stehli 1954, pl. 27, figs. 5, 7). D, *Spiriferellina cristata* (Schlotheim). P = 3.0; N = 15; grading good. Zechstein (U. Permian); Glucksbrunnen, Thuringia, Germany. S.M. E. 16232. E, *Spiriferellina octoplicata* (Sowerby). P = 2.5; N = 15; grading fair. Carboniferous Limestone (L. Carboniferous); Settle, Yorkshire, England. S.M. E. 7241. F, *Cyrtina heteroclita* (Defrance). P = 2.5; N = 17; grading good. 'Étage F.f.2' (L. Devonian); Koněprusy, Czechoslovakia. S.M. H. 5283. G, *Howellella elegans* (Muir-Wood) (= *Crispella crista* auctt.). P = 3.0; N = 13; grading perfect. Wenlock Limestone (M. Silurian); Dudley, Worcestershire, England. S.M. A. 26799.

and their sheaths of tissue would need to be as slender as would be consistent with strength: in paradigmatic form their cross-section would be elongated in the direction of flow, i.e. perpendicular to the line of the commissure. To straddle the gape at every crest, the length of the spines would have to be directly proportional to their distance from the hinge-axis. Spines approximating to this paradigm are known in the Silurian

S.M. A. 45955. E, Dalmanellacea: *Euteletes dumblei* (Girty). P = 2.5; N = c. 17; grading good. Bone Spring formation (L. Permian); Victorio Canyon, Sierra Diablo, Texas. A.M.N.H. 27284/1:1 (figured Stehli 1954, pl. 17, fig. 18). $\times 1$. F, Dalmanellacea: *Parenteletes cooperi* King. P = 4.0; grading fair. Gaptank formation (U. Carboniferous); near Gaptank, Glass Mountains, W. Texas. (After Schuchert & Cooper 1932, pl. 24, figs. 11, 13.) $\times 1$. G, G', Orthotetacea: *Meekella striatocostata* (Cox.) P = 2.0; N = 17; grading fair (some anomalies in median arc). U. Carboniferous; Elk County, Kansas. S.M. A. 45954. H, Terebratulacea: *Notothyris minuta* Waagen. P = 2.5 (only 1.7 in median deflexion); N = 17; grading fair. U. Permian; Basleo, Timor. S.M. A. 11548. J, Stenocismatacea: *Stenocisma gregeri* (Branson). P = 2.0 (only 1.5 in median deflexion); N = c. 25; grading good. Coralville formation (M. Devonian); Dodges Creek, Scott Co., Iowa. U.S.N.M.

rhynchonellacean *Sphaerirhynchia wilsoni* (text-fig. 13C, F; Pl. 28, fig. 11; cf. Schmidt 1937), and they reappeared in the Upper Carboniferous rhynchoporacean *Rhynchopora nikitini* (Pl. 24, figs. 6–8).

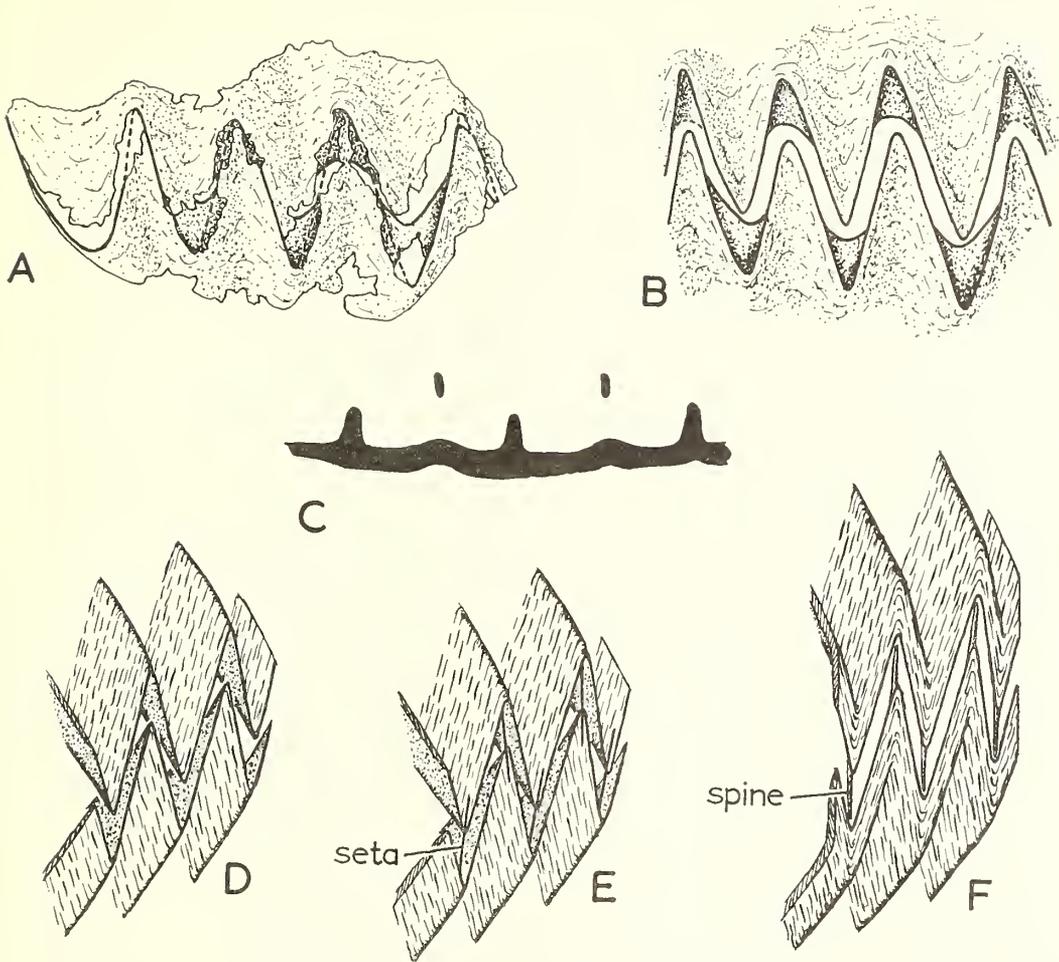
In living articulate, the setae are very slender, and are able to project between the valve edges, even when the valves appear to be tightly closed; and they leave no direct trace in the external form of the shell. Fine setae may therefore have been present in



TEXT-FIG. 12. Zigzags of Subgroup B. III. All $\times 1.5$ (except D, $\times 1$). A, Terebratulacea: *Antiptychina antiplecta* (von Buch). $P = 2.0$ (only 1.7 medially); $N = 7$; grading perfect. 'Jurakalk' [? Vilsen Schichten] (U. Jurassic); [? Vils], Tirol, Austria. S.M. F. 15998. B, B', Terebratulacea: *Heimia hollandae* (Buckman). $P = 1.8$; $N = 5$; grading good. Inferior Oolite (M. Jurassic); Bradford Abbas, Dorset, England. S.M. J. 6168 (figured Davidson 1884, pl. xviii, fig. 22). C, C', Terebratulacea: *Sellithyris upwarensis* (Walker). $P = 2.5$; $N = 5$; grading good. Lower Greensand (L. Cretaceous); Upware, Cambridgeshire, England. S.M. B. 25442. D, Punctospiracea: *Cyrtiopsis davidsoni* Grabau. $P = c.$ 5; $N = 5$; grading probably good. U. Devonian; S. China. (After Grabau 1931–3, pl. 46, fig. 5.) $\times 1$.

many fossil articulate. Stouter and less fragile setae would require special openings at the valve edges. In a few fossil brachiopods, such as the Permian rhynchonellacean *Uncinunellina jabiensis*, small foramina occur at the crests of a zigzag deflexion (Pl. 21, fig. 10). These may be interpreted as the points of emergence of relatively stout setae, which would have provided effective protection at the crests of the zigzag slit.

The setae of living articulate are not erectile. Each lies embedded in the mantle edge, parallel to the inner surface of the valve edge: the orientation of the valve surface thus determines the orientation of the setae. Setae would have been most effective for crestal



TEXT-FIG. 13. Accessory crestal protection of zigzag slits. A, *Parallelelasma pentagonum* Cooper. Fragment of silicified shell showing zigzag on anterior commissure, with internal marginal 'diaphragms' visible where valve-edges are broken. Pratt Ferry formation (M. Ordovician); Pratt Ferry, Alabama. U.S.N.M. 117156f (figured Cooper 1956, pl. 119, fig. 25), $\times 5$. B, The same, with valve-edges restored and gaping narrowly. C, *Sphaerirhynchia wilsoni* (Sowerby). Section of valve-edge parallel to commissure; internal ridges are bases of internal marginal spines; between them the spines from the opposite valve are cut in section. Aymestry limestone (U. Silurian); Sedgley, Staffordshire, England. S.M. A. 30623, $\times 18$. D-F, Diagrams of zigzag valve-edges gaping narrowly, to show zigzag slit unprotected at crests (D), with crestal protection by setae raised on internal 'platforms' (E), and with crestal protection by internal spines (F).

protection if they straddled the gape when the valves opened to the normal extent. But they would not usually have had the correct orientation for this purpose unless the valve edges had a nearly vertical inclination (e.g. on valves with vertical zones). But appropriate thickening of the internal surface of the valves could have changed the orientation of the setae. When the valves closed the setae would have been bent; but when they reopened the setae (which in living species are highly elastic) would have straightened

out and straddled the gape at every crest of the zigzag slit. The amount of thickening required at each crest would depend on the distance from the hinge-axis, but also on the initial inclination of the valve edge. Localized thickenings or *platforms* conforming to this specification are very common in rhynchonellaceans with zigzags of Group A. They occur adjacent to the re-entrants of the zigzag valve edges, and are most readily detected on internal moulds. They are not found on shells of 'immature' form, and were probably secreted once and for all in the final stages of growth. The degree of thickening is conspicuously dependent on the inclination of the valve edges: if the platforms bore setae as postulated, then at one particular degree of opening of the valves each crest of the zigzag slit would have been straddled by one of the setae (text-fig. 13E; Pl. 28, figs. 6, 7, 10). Since these platforms seem to be confined to shells of Group A, it is possible that in this group the crests of the deflexion may have had a one-to-one correspondence with the positions of the setae (as in the serial deflexion of the living *Terebratulina*); and that no such correspondence may have existed in the zigzag deflexions of Group B (as in the serial deflexion of the living *Notosaria*).

Parallelelasma pentagonum is a small pentameracean, with a zigzag of sub-group B. I, found at one horizon and locality in the Middle Ordovician of Alabama. Its most remarkable, and indeed unique, feature is the presence of shelly diaphragms just within the re-entrants of the zigzag valve edges (text-fig. 13A). Each diaphragm is attached near

EXPLANATION OF PLATE 21

Zigzags of Subgroup A. I: Rhynchonellacea.

Fig. 1. *Camarotoechia borealis* (Schlotheim). Postero-dorsal view, showing increase in crestal number during early growth of median arc of serial deflexion. Same specimen as text-fig. 6K, $\times 4.5$.

Fig. 2. *Quadratirhynchia crassimedia* Buckman. Antero-dorsal view of anterior commissure in median deflexion; P = 8. [Middle?] Lias (L. Jurassic); Lyme Regis, Dorset, England. S.M. J. 36893, $\times 3$.

Fig. 3. *Gibbirhynchia gibbosa* Buckman. Left lateral view of median fold, showing gradual loss of crests of serial deflexion on flank of median deflexion. Middle Lias (L. Jurassic); South Petherton, Somerset, England. S.M. J. 35493, $\times 4$.

Fig. 4. *Rhynchotreta cmeata* (Dalman). Right latero-ventral view, showing uniform angularity of crests during ontogeny (relative angulation) and very early origin of serial deflexion. Same specimen as text-fig. 6J, $\times 3$.

Fig. 5. *Stegerhynchus whitii* (Hall). Left lateral view; P = 2.5; N = 23; grading good. Niagara Group (M. Silurian); Waldron, Indiana. S.M. A. 48491, $\times 6$.

Fig. 6. *Globirhynchia subobsoleta* (Davidson). Left postero-lateral view, showing posterior suppression of crests, N reduced from c. 40 to 30; P = 2.7 on final commissure; grading perfect. Oolite Marl, Inferior Oolite (M. Jurassic); Notgrove Station, Gloucestershire, England. S.M. J. 48764, $\times 3$.

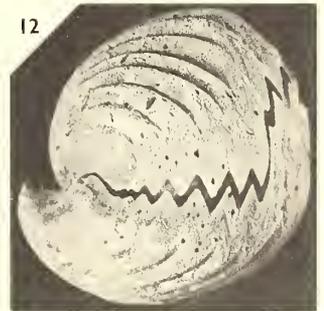
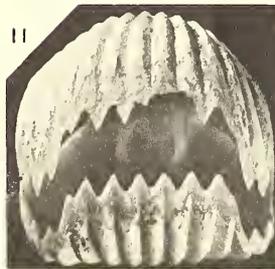
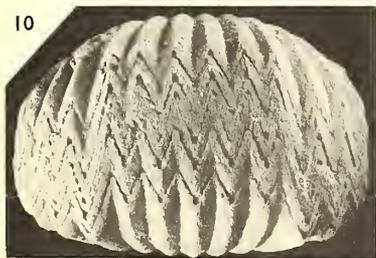
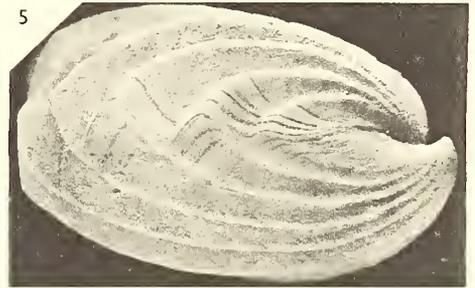
Fig. 7. *Globirhynchia subobsoleta* (Davidson). Right lateral view of 'young' shell, showing poorly graded zigzag. Same specimen as text-fig. 5F, $\times 6$.

Figs. 8, 9. *Russirhynchia fischeri* (d'Orbigny). Right and left antero-lateral views of shell preserved gaping slightly, to show zigzag slit. P = 2.5; N = 20; grading fair. 'Oxfordian' (U. Jurassic); Moscow, Russia. M.C.Z. 6162, $\times 1$.

Fig. 10. *Uncinunellina jabiensis* (Waagen). Anterior view, showing possible setal foramina at crests of zigzag. U. Permian; Basleo, Timor. S.M. A. 11512, $\times 3$.

Fig. 11. Unnamed rhynchonellid. Anterior view of silicified shell, preserved with gape much greater than amplitude of zigzag (crura visible internally). L. Callovien (U. Jurassic); Chatillon-sur-Seine, Côte d'Or, France. U.S.N.M. acc. 195551, $\times 3$.

Fig. 12. Rhynchonellid as fig. 11. Right lateral view of silicified shell, preserved gaping with narrow zigzag slit; note vertical zone, on which serial deflexion has no cumulative expression (i.e. no costae). Locality as fig. 11, $\times 3$.



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the edge of the inner surface of the valve; growth-lines on the diaphragms (see Cooper 1956, pl. 121, fig. 1) indicate that they were built up by accretion at the free edges, presumably by secretion by the mantle cells at or just within the mantle edge. Cooper terms this structure 'a very efficient straining device for the food-bearing currents' (1956, p. 612), but does not explain this interpretation in detail. But if the valves gaped apart giving a zigzag slit, the diaphragms would have straddled the crests of the slit immediately inside the edges of the valves (text-fig. 13B), and thus would have provided effective protection at the crests—but only at the expense of a considerable reduction in the total area of the slit. The inherent inefficiency of this variety of crestal protection may account for its extreme rarity.

Zigzag deflexions in oysters

By far the closest analogues to zigzag deflexions in fossil brachiopods are found in certain oysters (Pl. 29). Although they belong to a different phylum, oysters possess in common with brachiopods a hinged bivalved shell which, on gaping open, reveals inhalant and exhalant apertures bordered by sensitive mantle edges. Zigzag deflexions have probably arisen many times independently in the history of the oysters, and are known at several horizons from the Triassic onwards. Zigzags of highly paradigmatic form can often be found: they have a high degree of protection and sharply angulate crests; the amplitude is well graded, with straight flanks on arcs parallel to the hinge-axis (Pl. 29, figs. 2, 4, 5) and curved flanks towards the hinge-axis (Pl. 29, figs. 1, 3, 7); and the grading is progressively improved in the final stages of ontogeny by posterior crestal suppression (Pl. 29, fig. 1: strictly speaking, in lamellibranch orientation, the crestal suppression should be termed *dorsal*). Even when the commissure plan became crescentic during ontogeny, the grading was clearly correlated with perpendicular distance from the hinge-axis, thus ensuring a slit of uniform width.

THE INTERPRETATION OF ZIGZAG DEFLEXIONS

Zigzag deflexions and the protective paradigm. The foregoing survey shows that zigzag deflexions in brachiopods—and oysters—approximate to the paradigm for protective devices. The approximation may be very close or only moderate; but all these deflexions show an unambiguous *approach* towards the paradigm, which justifies the assertion that they would have been capable of functioning as moderately efficient or even (in some instances) highly efficient protective devices. Indeed zigzag deflexions must *necessarily* have had this function; for whenever the valves gaped apart the zigzag slit must necessarily—by virtue of its form—have conferred relative protection on the gape. Any interpretation of zigzags that questions their adaptive status (e.g. a 'phylogerontic' explanation) is therefore inadmissible.

The specification of the paradigm is rather rigidly determined by the geometry of a zigzag and of a hinged bivalved shell. Any efficient protective zigzag must conform to this specification, in whatever brachiopod (or oyster) species it occurs. Consequently it is *inherently* probable that zigzags were evolved many times in the history of the Brachiopoda. This is probably a factor contributing to the complex evolutionary history of the phylum.

Nature of the 'harmful particles'. All roughly equidimensional particles would have an effect similar to perfect spheres. But this assumes (following Schmidt) that the zigzag slit would have been 'protective' by being a straining device: i.e. that while the valves remained open, the zigzag slit would sort approaching particles into two classes on the basis of their size, rejecting one class and accepting the other. Some analogous straining devices are known in other animals. The inhalant apertures of the lamellibranch *Tivela stultorum* Mawe and the gastropod *Turritella communis* Risso are covered by meshes (formed from pinnate tentacles), which fulfil a straining function by excluding sand grains and admitting the smaller food particles (Weymouth 1923, p. 11; Graham 1938, p. 454). As an example from an entirely different animal, the slit between the jaws of the filter-feeding flamingo *Phoenicaias minor* (Geoffroy) is protected by a row of regularly spaced 'marginal hooks' which act as a straining device (Jenkin 1957). But much closer

EXPLANATION OF PLATE 22

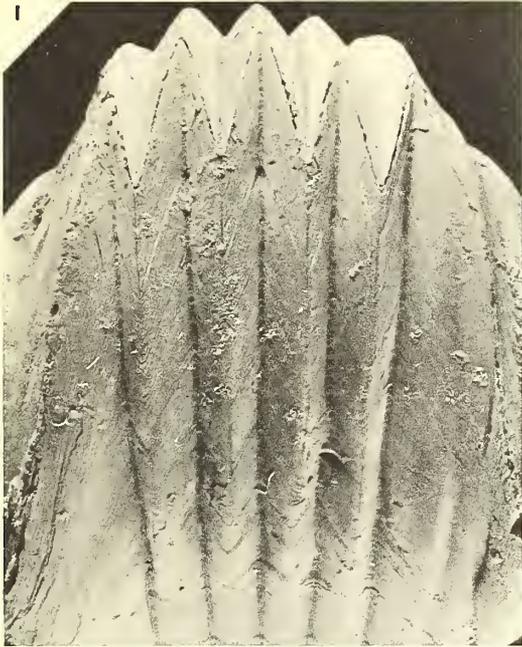
Zigzags of Subgroup A. 1: Rhynchonellacea.

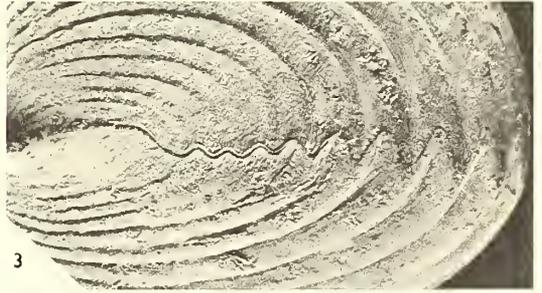
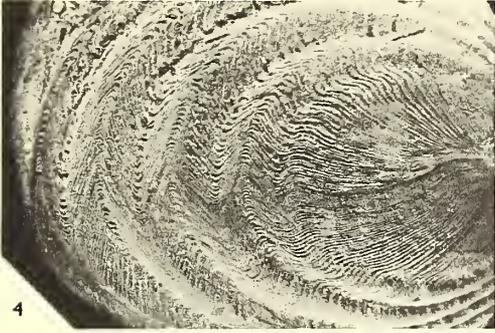
- Fig. 1. *Tetrarhynchia tetrahedra* (Sowerby). Anterior view, showing development of zigzag within median deflexion; angulation predominantly relative, but absolute at first. $P = 4.0$ on final commissure (foreshortened). Middle Lias (L. Jurassic); King's Sutton, Oxfordshire, England. S.M. J. 46810, $\times 4.5$.
- Fig. 2. *Tetrarhynchia tetrahedra* (Sowerby). Right lateral view, showing development of graded zigzag; angulation predominantly relative, but absolute at first. Locality as fig. 1. S.M. J. 46808, $\times 4.5$.
- Fig. 3. *Globirhynchia subobsoleta* (Davidson). Left postero-lateral sectors, showing gradual posterior suppression of crests and consequent improvement of grading. Same specimen as Plate 21, fig. 6, $\times 9$.
- Fig. 4. *Globirhynchia subobsoleta* (Davidson). Right antero-lateral arc, showing flank of zigzag lengthened to form flank of median deflexion, without significant change in orientation. Same specimen as text-fig. 5A-C, $\times 6$.
- Fig. 5. *Globirhynchia subobsoleta* (Davidson). Right lateral view, to show relative angulation of zigzag and posterior suppression of crests from $N = 39$ to $N = 29$; $P = 2.5$; grading good on final commissure. Locality as text-fig. 5A-F. S.M. J. 48765, $\times 6$.
- Fig. 6. *Prionorhynchia serrata* (Sowerby). Anterior arc of commissure, $P = 3.0$. [Middle] Lias; Ilminster, Somerset, England. S.M. J. 35742, $\times 4.5$.

EXPLANATION OF PLATE 23

Zigzags of Subgroup A. 1: figs. 1-4 Rhynchonellacea; figs. 5-8 other superfamilies.

- Fig. 1. *Quadratrhynchia crassimedia* Buckman. Left postero-lateral view, to show graded zigzag developed from early serial deflexion; $P = 8$; $N = 53$. Locality as Plate 21, fig. 2. S.M. J. 36892, $\times 3$.
- Fig. 2. *Gibbirhynchia gibbosa* Buckman. Left lateral view, to show graded zigzag ($P = 5.0$) developed from early serial deflexion, with crestal suppression (N reduced from c. 63 to 37). Same specimen as Plate 21, fig. 3, $\times 6$.
- Fig. 3. *Gibbirhynchia gibbosa* Buckman. Right postero-lateral view, to show undulate crests persisting posterior to ideal suppression point. Locality as Plate 21, fig. 3. S.M. J. 35487, $\times 6$.
- Fig. 4. *Lepidocyclus capax* (Conrad). Left lateral view, to show development of graded zigzag by relative angulation. Same specimen as text-fig. 6L, $\times 4.5$.
- Fig. 5. Orthacea: *Platystrophia crassa* (James). Right antero-lateral view, to show zigzag modified by strong median deflexion. Same specimen as text-fig. 7E, $\times 3$.
- Fig. 6. Terebratulacea: *Eudesia cardium* (Lamarck). Left postero-lateral sectors, to show development of graded zigzag by posterior crestal suppression (note punctate shell-structure). Same specimen as text-fig. 7J, $\times 6$.
- Fig. 7. Terebratulacea: *Ismenia pectunculoides* (Schlotheim). Left lateral view, to show posterior crestal suppression. Same specimen as text-fig. 7M, $\times 3$.
- Fig. 8. Punctospiracea: *Hustedia mormoni* (Marcou). Left postero-lateral view, to show development of zigzag from very early serial deflexion (note strophic hinge). Same specimen as text-fig. 7L, $\times 9$.





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analogues are provided by the oysters with zigzag deflexions; and these suggest a significantly different conception of the 'protection' that might be given by a zigzag slit in a fossil brachiopod. *Ostrea crista-galli* Linnaeus and *Pycnodontes lyotis* (Linnaeus) both occur in tropical waters of the Indo-Pacific region (Thomson 1954). *O. crista-galli* often has a highly developed zigzag deflexion (Pl. 29, figs. 6, 7). *P. lyotis* has a rather less perfect zigzag, but is relatively accessible on the Great Barrier Reef. When feeding normally the valves do not gape far apart, so that a relatively narrow zigzag slit is formed (especially on the inhalant aperture: on the exhalant the deflexion generally remains undulate). The mantle edges lining the slit are sensitive (in this species, unlike many others, they are not modified into sensitive tentacles to guard the gape). If a swimming animal or other object touches the side of the slit, the valves immediately snap shut, by a rapid contraction of the 'quick' portion of the adductor muscle. Thus the zigzag slit is not a passive straining device, but protects the animal with an active and highly sensitive *warning device*.

Although no living brachiopods possess zigzag deflexions, their physiology suggests a similar interpretation. The mantle edge is highly sensitive both to tactile and to chemical stimuli. All the nerve fibres that radiate outwards across the mantle from the central ganglia terminate within the extreme marginal zone of the mantle, and the sensitivity of the mantle is limited to this narrow zone. When the mantle edge is stimulated, the valves are immediately snapped shut by a very rapid contraction of the 'quick' striated posterior adductor muscles (Rudwick 1961*b*). If, as it is reasonable to assume, all articulate brachiopods have possessed mantle edges with similar properties, the acquisition of a zigzag deflexion could represent the further development of this warning device.

This means that a zigzag slit could protect a brachiopod from much smaller 'harmful particles' than Schmidt's hypothesis implied. One such particle might penetrate the slit without touching or stimulating the mantle edge on either side; but a suspension of many small particles would be more likely to be detected, since at least a few of them might touch the mantle edges (or at least approach closely enough to be detected chemically). This would accord well with the rejection mechanisms of living brachiopods: occasional isolated particles are ejected with scarcely any disturbance of the filter-feeding, but a thick suspension (e.g. of sand grains or mud) brings a more radical rejection mechanism into operation, and may seriously interrupt the filter-feeding on part or all of the lophophore (see Rudwick 1962*b*, pp. 609–11). The efficiency of a zigzag slit for detecting small suspended particles could be expressed by the same 'degree of protection' as that defined in the original specification (text-fig. 1A, *MN/XY*). Thus whatever the exact nature of the 'harmful particles' that a fossil brachiopod might have encountered, a zigzag slit could have provided effective protection against them; the paradigmatic specification remains the same, and can be expressed in terms of idealized spherical particles, even though no such particles may ever have existed.

There is some doubt, however, whether in fact a narrow zigzag slit represents the normal degree of opening of the valves. For example, in one rhynchonellacean species (preserved by silicification) some specimens show a good zigzag slit between the valves (Pl. 21, fig. 12), but others show that the valves could gape much more widely without breaking the hinge (Pl. 21, fig. 11). In this and many other species, especially those with a rather high crestral number, it is clear that the zigzag deflexion would not have

produced a zigzag slit unless the valves opened only very slightly (Pl. 28, figs. 6–9). This is unlikely to have been the normal degree of opening: such narrow apertures would have created great resistance to the flow of water, and would have been much smaller than those in living brachiopods, in which the valves normally gape apart almost as widely as the hinge-structure allows.

But, as a warning device, a zigzag slit would have been most important in the early stages of reopening of the shell. During the slow reopening of the shell, living brachiopods appear to ‘test’ the environment to determine whether the factor that provoked the original closure still persists. (If it does persist, the shell may be snapped shut again at once, long before the normal degree of opening has been attained.) Thus any brachiopod with zigzag valve-edges would have had a heightened ‘degree of protection’ at least during this crucial early phase in the reopening of the shell; and the nearer the paradigm (i.e. the higher the value of P and the lower the value of N), the longer the period of reopening during which the zigzag would have been effective. In some shells with highly paradigmatic zigzags, the apertures may have retained their form as zigzag slits even when the valves were gaping apart to the fullest extent.

Zigzag deflexions and current-systems. The protection conferred by a zigzag slit is commonly uniform all round the commissure (apart from imperfect grading in the

EXPLANATION OF PLATE 24

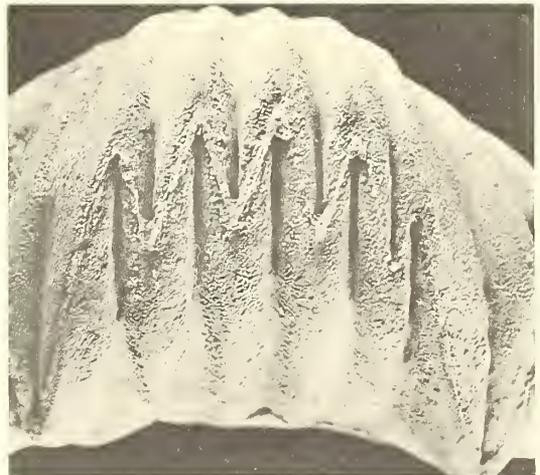
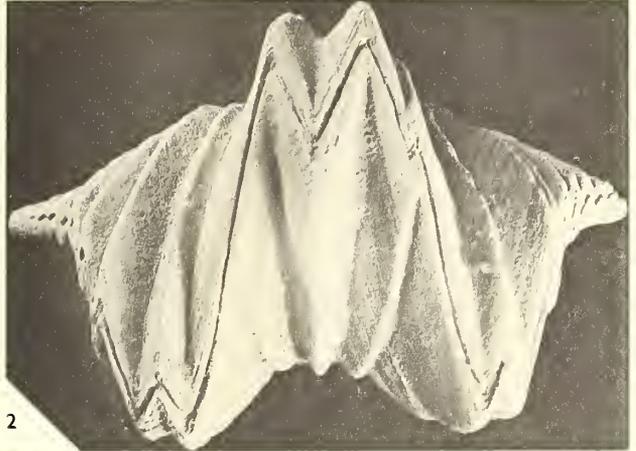
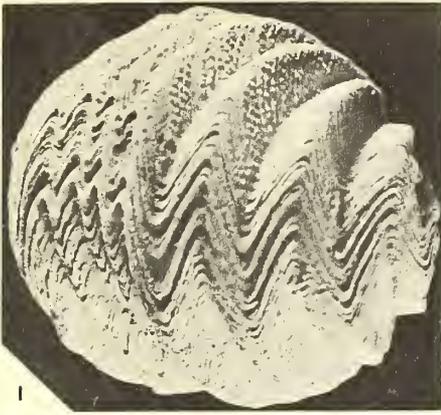
Zigzags of Subgroup A. I: other than Rhynchonellacea.

- Fig. 1. Athyracea: *Trematospira salteri* (Davidson). Left antero-lateral view, to show graded zigzag in lateral arc, with poorer zigzag of low wavelength in median deflexion. Same specimen as text-fig. 7G, ×6.
- Fig. 2. Orthacea: *Platystrophia cypha* (James). Anterior view, to show suppression of crests on flanks of median deflexion. Same specimen as text-fig. 7D, ×3.
- Fig. 3. Orthacea: *Platystrophia ponderosa* Foerste. Right postero-lateral view, to show crestal suppression. ‘Hudson River Group’ (U. Ordovician); Cincinnati, Ohio. S.M. 45745, ×2.
- Fig. 4. Terebratulacea: *Eudesia cardium* (Lamarck). Postero-dorsal view, to show early increase in crestal number of serial deflexion. Same specimen as text-fig. 7J, ×6.
- Fig. 5. Terebratulacea: *Choristothyris plicata* (Say). Right postero-latero-dorsal view, to show early origin of serial deflexion, relative angulation, and posterior crestal suppression. Same specimen as text-fig. 7K, ×4.5.
- Figs. 6–8. Rhynchoporacea: *Rhynchopora nikitini* Tschernyschew. Left lateral, right lateral, and anterior views of an internal mould, showing graded zigzag with internal spines (showing as grooves on mould) at every crest; note also moulds of punctae. Same specimen as text-fig. 7A, ×6.

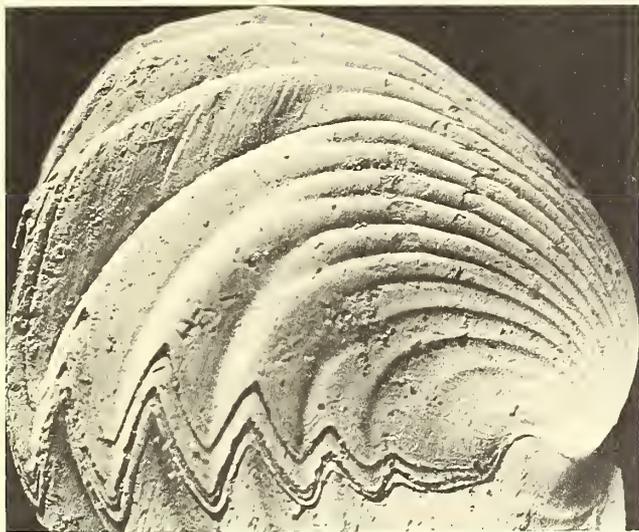
EXPLANATION OF PLATE 25

Zigzags of Subgroup A. II: Rhynchonellacea.

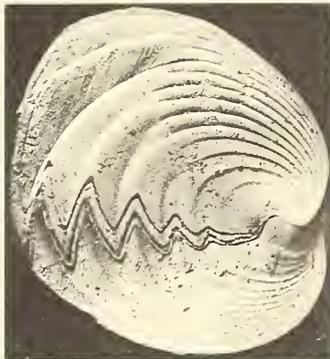
- Figs. 1, 2. *Rimrhynchia anglica* (Rollier). Left lateral views, to show early serial deflexion of large crestal number, crestal reduction initiated antero-laterally and spreading medially and laterally, and final production of graded zigzag. Same specimen as text-fig. 8B. Fig. 1, ×3; fig. 2, ×6.
- Fig. 3. *Rimrhynchia anglica* (Rollier). Right antero-latero-ventral view, to show crestal reduction on antero-lateral arc, failing to spread into median deflexion. Same specimen as text-fig. 8D, ×6.
- Fig. 4. *Rimrhynchia anglica* (Rollier). Right postero-latero-dorsal view, to show crestal reduction on antero-lateral arc, failing to spread to postero-lateral arc. Same specimen as text-fig. 8D, ×6.
- Fig. 5. *Cyclothyris antidichotoma* (Buvignier). Antero-dorsal view, to show fairly early crestal reduction. Same specimen as text-fig. 8A, ×3.
- Fig. 6. *Naynella schmri* (de Verneuil). Antero-ventral view, to show late crestal reduction. Same specimen as text-fig. 8E, ×4.5.



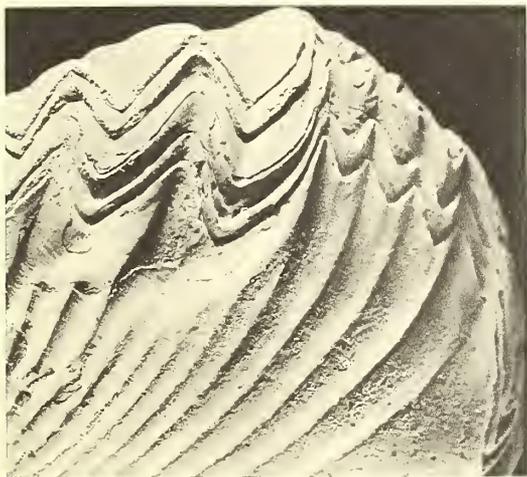
RUDWICK, Zig-zags in brachiopods



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posterior arcs). Therefore the inhalant and exhalant apertures must have shared the same degree of protection, wherever they were situated. This cannot be explained by assuming that the apertures were variable or interchangeable in position: for in living species they are constant in position, apart from slow ontogenetic changes (Rudwick 1962*b*); and reversal of the current-system, and hence of the nature of the apertures, occurs only as a rare and exceptional rejection mechanism (Atkins 1960, p. 470; Rudwick 1962*b*, p. 611). But, in at least some living species, the valves habitually gape apart even when the lophophore is inactive and no currents are flowing (Atkins 1959, p. 130). For species with this habit, an equal degree of protection on all the apertures might be advantageous.

But in a number of zigzags it has been noted that the degree of protection is distinctly poorer on the median arc—whether or not that arc is modified by a median deflexion—than on the lateral arcs. A similar poorly zigzagged arc on the living oyster *Pycnodonia hyotis* represents the position of the exhalant aperture. By analogy, the poorly protected median arc of a brachiopod may represent the site of a median exhalant aperture, which was often deflected dorsally or ventrally away from a pair of lateral inhalant apertures. This system of apertures is almost universal in living articulate brachiopods, apart from early growth-stages and a few very small species (Rudwick 1962*b*). If this inference is correct, it gives evidence for the reconstruction of the current-system, independently from that given by the structure and orientation of the lophophore and its skeletal supports. For example, if a poorly protected median deflexion in a spiriferoid represents a median exhalant aperture, the exhalant current must have emerged medially from the interior of the spiralia (Rudwick 1960), not laterally from the exterior of the spiralia (Williams and Wright 1961). A lower degree of protection on the exhalant aperture would not have been disadvantageous to a species in which the valves never gaped apart except when the lophophore was operative: this habit, like the converse, is known in some living species (Rudwick 1962*b*, p. 607).

A possible anomaly in this interpretation is the existence of a few shells, of which the Carboniferous rhynchonellacean *Pugnax acuminatus* (Martin) is perhaps best known, in which the median deflexion alone underwent absolute angulation, leaving the lateral arcs apparently unprotected. It is possible, though unlikely, that the apertures were reversed in these species. It is more probable that the lateral apertures were equipped with more effective rejection mechanisms than the median aperture (viz. the cilia on the filaments, rather than the mantle cilia), so that protection by a narrowed slit was more necessary on the median than on the lateral apertures.

Ontogeny of zigzag deflexions. All zigzag deflexions developed gradually during ontogeny, showing a progressively closer approximation to the protective paradigm. On most shells, the zigzag was close to the paradigm only in the later growth stages and, above all, on the final commissure of the 'mature' shell. Since the rate of growth of living brachiopods seems to decrease progressively throughout life (Rudwick 1962*a*), the 'final' stages of growth may actually represent a large part of the total life-span. But whatever the proportion of time involved, it is clear that good protective zigzags were in general confined to the later part of the life-span. But this does not imply that the protection developed suddenly *ex nihilo* at some point in ontogeny, since the protection given by a zigzag slit is only an extension and improvement of that given by valve edges of any form (if they are lined with sensitive mantle edges). Protection as such would have existed throughout life, but would not have reached a high degree until the later

part of the life-span, when the shell reached its greatest size. This suggests that the acquisition of a zigzag may be related quite simply to the growth of the organism.

As a brachiopod grows in size during ontogeny, its apertures increase in gape and in overall area. This must heighten the importance of the sensory mechanisms (sensitive mantle edges and setae) and rejection mechanisms (lophophoral and mantle cilia, and 'quick' adductor muscles). For unless their combined efficacy increased in proportion to the activity of the lophophore, the net degree of protection would fall steadily. (Since their efficacy depends in part on properties at the cellular level—sensitivity of individual sensory cells, transporting power of individual cilia—such a development is not improbable.) This could only be avoided by increasing the efficacy of the protective mechanisms, which is precisely what the gradual development of a paradigmatic zigzag could achieve. It would enable the apertures to be increased in area without involving a corresponding increase in the distance between the mantle edges. Hence the overall degree of protection could remain constant.

EXPLANATION OF PLATE 26

Zigzags of Subgroup B. I: Rhynchonellacea.

Fig. 1. *Pugnax pugnax* (Martin). Right antero-latero-dorsal view, to show gradual lateral spread of serial deflexion, and production of zigzag by absolute angulation. Note fine radial costellae. Locality as text-fig. 9A. S.M. E. 8484, $\times 3$.

Fig. 2. *Rhynchotetra angulata* (Linnaeus). Right antero-latero-ventral view, to show rather early serial deflexion, superimposed on fine costellae. Same specimen as text-fig. 9E, $\times 4.5$.

Fig. 3. *Homoeorhynchia acuta* (Sowerby). Left latero-dorsal view, to show gradual lateral spread of serial deflexion, and production of zigzag by absolute angulation. Same specimen as text-fig. 9K, $\times 4.5$.

Fig. 4. *Homoeorhynchia acuta* (Sowerby). Anterior view, to show development of high angulate median deflexion. Same specimen as text-fig. 9K', $\times 3$.

Figs. 5, 6. '*Rhynchonella*' *personata* von Buch (?). Right antero-lateral and antero-dorsal views, to show graded zigzag with high degree of protection. Same specimen as text-fig. 6B, $\times 6$.

Fig. 7. *Homoeorhynchia cynocephala* (Richard). Anterior view, to show high median deflexion incorporated in graded zigzag; P = 3.5; N = 19; grading good. Cephalopod Bed, Upper Lias (L. Jurassic); Frocester Hill, Gloucestershire, England. S.M. J. 48762, $\times 3$.

EXPLANATION OF PLATE 27

Zigzags of Subgroup B. I: various superfamilies.

Figs. 1, 2. Rhynchonellacea: *Gnathorhynchia liostraca* (Buckman). Right lateral and anterior views, to show very late serial deflection with scarcely any cumulative expression (i.e. costae). Same specimen as text-fig. 9I, $\times 6$.

Fig. 3. Rhynchonellacea: '*Rhynchonella*' *funiculata* Deslongchamps. Anterior view, to show zigzag produced by absolute angulation of late serial deflexion. Callovien (U. Jurassic); Montreuil-Bellay, Maine-et-Loire, France. S.M. F. 10462, $\times 6$.

Fig. 4. Orthotetacea: *Meekella striatocostata* (Cox). Antero-dorsal view, to show late absolute angulation of serial deflexion superimposed on costellae. Same specimen as text-fig. 10G, $\times 3$.

Fig. 5. Orthotetacea: *Meekella striatocostata* (Cox). Left latero-ventral view, to show graded zigzag and costellae. Florena shale (L. Permian); Grand Summit, Kansas. S.M. A. 45754, $\times 3$.

Figs. 6, 7. Dalmanellacea: *Enteletes waageni* Gemmellaro. Left lateral and antero-lateral views, to show graded zigzag produced by absolute angulation of serial deflexion superimposed on costellae. Sosio limestone (U. Permian); Pietra di Salomone, Sicily. U.W.I.P., $\times 3$.

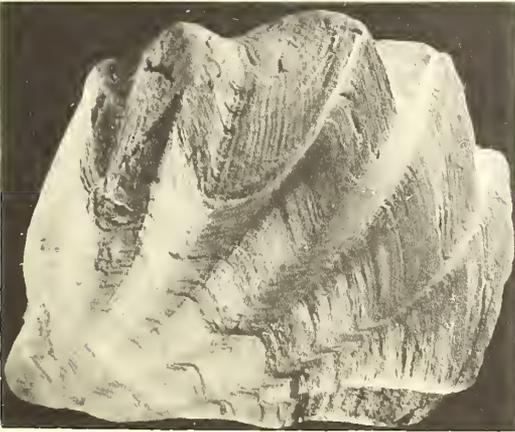
Figs. 8, 9. Syntrophicea: *Parastrophinella reversa* (Billings). Right antero-latero-dorsal and ventral views, to show gradual lateral spread of serial deflexion and its absolute angulation. Same specimen as text-fig. 10A, $\times 4.5$.



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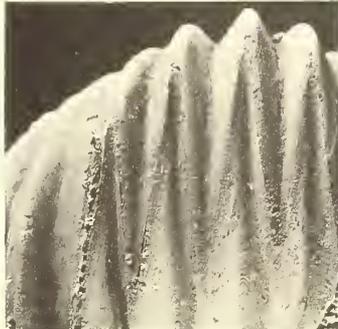
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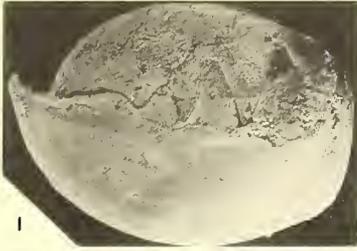
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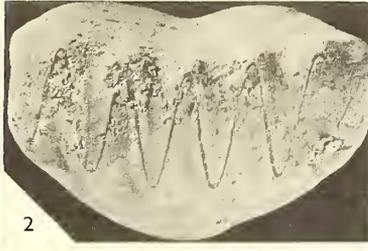
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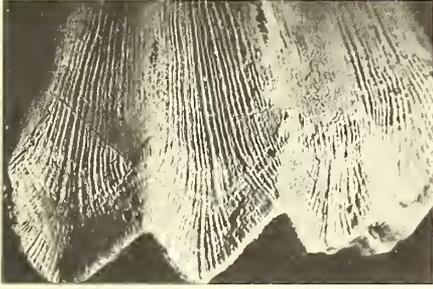
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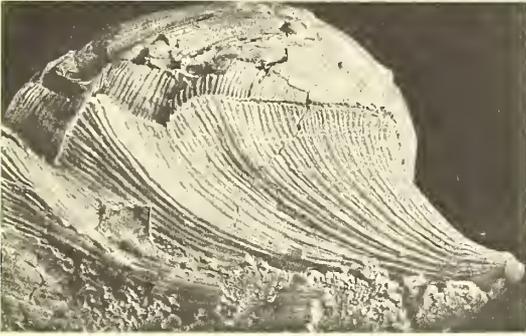
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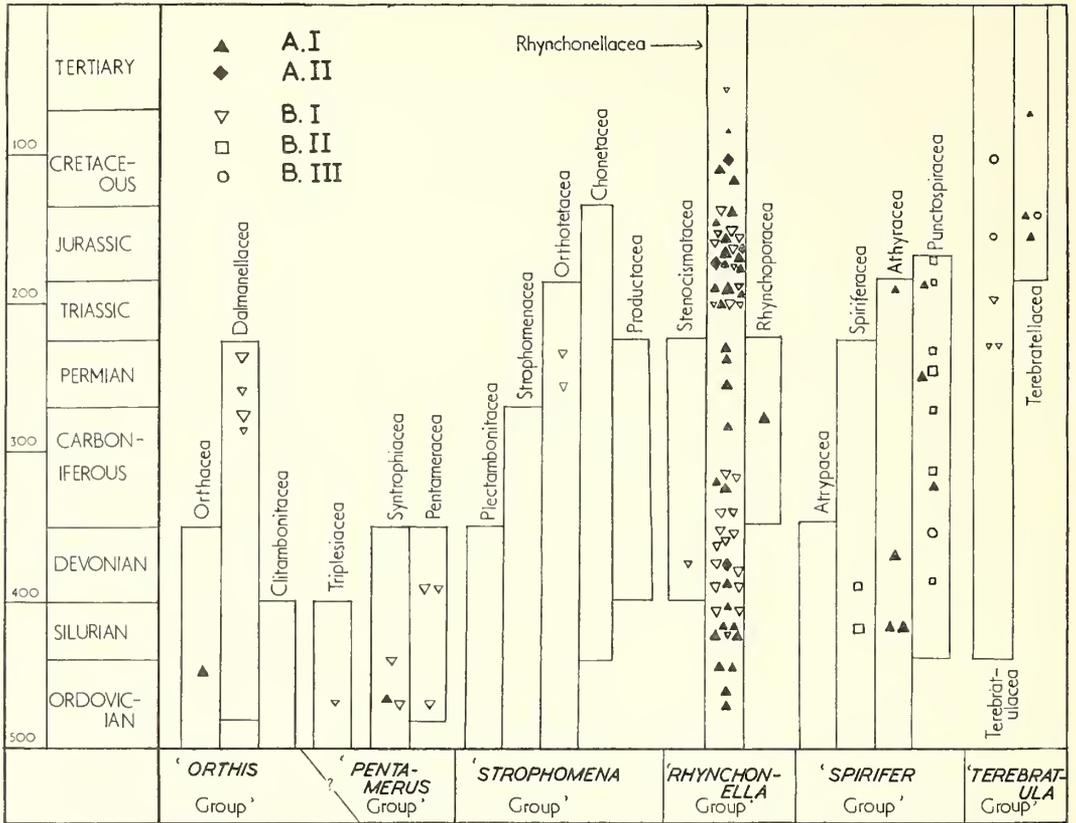


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Ecology of zigzag deflexions. Zigzag deflexions are interpreted here as adaptations to the internal organization of the animals, rather than to any specific feature of the external environment. Thus no reliable inference about the nature of the environment can be made from the mere presence of zigzagged species in a fossil assemblage. There seems to be no good reason for attributing the evolution of zigzags in many Permian stocks to unfavourable, perhaps hypersaline, conditions (Cooper 1937). It is to be expected that species with zigzags may often have lived in close association with species lacking zigzags, and that their fossil shells will often occur together in undrifted assemblages, e.g. the zigzagged rhynchonellacean *Tetrahynchia tetrahedra* (Pl. 27, figs. 1, 2) and the rectimarginate terebratulacean *Lobothyris punctata* in the Middle Lias Marlstone (L. Jurassic) of the English Midlands (see Hallam 1962). Both groups of species would presumably have been subject to the same dangers from 'harmful particles': but it does not follow that the second group was ill-adapted to the environment relative to the first, because it may have possessed more efficient rejection mechanisms, or more sensitive mantle edges, to compensate for the lesser protection of its apertures.

This also explains why so many brachiopods were, and are, able to flourish without possessing zigzags at all. Moreover, since the efficacy of the sensory and rejection mechanisms are unlikely to have been uniform in all taxonomic groups, it also explains the remarkable diversity in the absolute sizes of the 'mature' shells of species with good zigzags (text-figs. 5-12: almost all these drawings are at a uniform scale $\times 1.5$).

Phylogeny of zigzag deflexions. The rigid specification of the paradigm points to the intrinsic probability that zigzag deflexions were evolved many times during the history of the Brachiopoda. This conclusion is supported by the existence of closely convergent zigzags in a different phylum (viz. oysters), and by the observation that the ontogenetic origin and development of zigzags are remarkably varied. As in classical instances of evolutionary convergence, different 'materials' were thus used to form 'organs' with the same function and a close analogical similarity of structure. Obviously two brachiopods are more likely to have acquired this adaptation independently if their zigzags belong to different types than if their zigzags developed by the same ontogenetic sequence. But there are indications that the repetitive evolution of the adaptation was even more widespread than this would suggest. For almost every species with a good zigzag deflexion, it would be possible to cite a related species or genus in which the serial deflexion fails to approach the paradigm so closely, even in the 'mature' shell, either because the crestal number is high or because the relative amplitude is low or because the angulation or grading is poor. Indeed species with good zigzags are probably much outnumbered by those with other less zigzagged serial deflexions, just as the good zigzags characterize only a part of the life-history of the individual. This strongly suggests that serial deflexions primarily fulfilled some other function or functions, and that their modification (in both ontogeny and phylogeny) into the zigzag form represents the greater development of an additional function, namely that of protection. Thus it is easy to conceive how paradigmatic zigzags could have been evolved again and again by the modification of already existing serial deflexions; and the distribution of zigzag deflexions strongly suggests that this indeed occurred (text-fig. 14 and Appendix). There were no true zigzags in the rather sparse Articulata faunas of the Cambrian, but they appeared in several superfamilies in the Ordovician. Thereafter, until the middle of the Cretaceous,



TEXT-FIG. 14. Diagram to show stratigraphical and systematic distribution of zigzag deflexions in fossil brachiopods. Time-scale (m.y) after Holmes 1959; superfamilies after Muir-Wood 1955; higher 'groups' after Williams 1956. Only species cited in the appendix to this paper are marked on this diagram. The size of the symbols indicates, somewhat subjectively, the relative 'quality' of the protection (i.e. degree of approximation to the paradigm).

they were abundant. They were most abundant and varied in the Rhynchonellacea, but some are known from almost every superfamily (excluding the large 'Strophomena group', most of which had concavo-convex shells and may have been significantly different in their mode of life). In whatever way the phylogeny of the Articulata is reconstructed, a multiple origin for the adaptation seems inescapable. Zigzags became rare in the Upper Cretaceous, and apart from one poor Eocene example they are unknown in the Tertiary. This may mean that, in the groups that survived, a gradual increase in the sensitivity of the mantle-edges or the efficiency of the rejection mechanisms made the possession of zigzags less necessary in the environments to which they were adapted.

CONCLUSION

Zigzag deflexions approximating to the paradigm for protective warning devices were thus common among the brachiopods for perhaps 300 or 400 million years, from the

Middle Ordovician until the Lower Cretaceous. Examples are known in almost every superfamily in which the biconvex shell-form was normal. Repeated evolution of this adaptation was predicted as inherently probable on the basis of the inherently rigid specification of the paradigm. This prediction was substantiated by the number of different ontogenetic 'pathways' by which the zigzags developed, and by the remarkable convergent similarity shown in the zigzags of oysters. But it is confirmed even more clearly by the widespread distribution of the adaptation, in time and in taxonomy. This is not dependent on the validity of the superfamilies at present recognized or on any particular reconstruction of their evolutionary connexions. Even if some zigzags were derived directly from similar ones in some other superfamily, many independent origins of the adaptation are still unavoidable. The number of such separate developments that must be postulated in order to 'save the appearances' can only be reduced by increasing, beyond the bounds of plausibility, the number of times that other characters (e.g. punctate shell-structure, spondylia, brachidia, &c.) must be assumed to have been evolved; or by making, again beyond the bounds of plausibility, extreme assumptions about the imperfection of the fossil record for brachiopods. But there is no valid reason for attempting by these means to evade the most coherent explanation of the evidence available: namely, that zigzag valve-edges, as efficient protective warning devices, were evolved again and again in the history of the Brachiopoda.

APPENDIX

List of Selected Brachiopod Species with Zigzag Deflexions

	<i>Deflexion subgroup</i>	<i>Text-fig.</i>	<i>Plate</i>
LOWER TERTIARY			
Rhynchonellacea			
<i>Plicirhynchia plicigera</i> (von Ihering)	B. 1 (?)		
UPPER CRETACEOUS			
Terebratulacea			
<i>Choristothyris plicata</i> (Say)	A. I	7K	24, fig. 5
Rhynchonellacea			
<i>Cyclothyris ala</i> (Bronn)	A. I		
LOWER CRETACEOUS			
Terebratulacea			
<i>Sellithyris upwarensis</i> (Walker)	B. III	12C	28, fig. 4
Rhynchonellacea			
<i>Cyclothyris antidichotoma</i> (Buvignier)	A. II	8A	25, fig. 5
<i>Plicarostrum hauerivense</i> Burri	A. I		
' <i>Rhynchonella</i> ' <i>walkeri</i> Davidson	A. I	6A	
UPPER JURASSIC			
Terebratulacea			
<i>Antiptychina antiplecta</i> (von Buch)	B. III	12A	
<i>Ismenia pectunculoides</i> (Schlotheim)	A. I	7M	23, fig. 7

	<i>Deflexion</i> <i>subgroup</i>	<i>Text-fig.</i>	<i>Plate</i>
Rhynchonellacea			
<i>Rhynchonella loxiae</i> Fischer	B. I	9L	
' <i>Rhynchonella</i> ' <i>funiculata</i> Deslongchamps	B. I		27, fig. 3
' <i>Rh.</i> ' <i>personata</i> von Buch	B. I	6B	26, figs. 5, 6
' <i>Rh.</i> ' <i>subvariabilis</i> Davidson	A. I	6D	
<i>Russirhynchia fischeri</i> (d'Orbigny)	A. I	6C	21, figs. 8, 9
MIDDLE JURASSIC			
Terebratulacea			
<i>Eudesia cardium</i> (Lamarck)	A. I	7H, J	23, fig. 6; 24, fig. 4
Terebratulacea			
<i>Heimia hollandae</i> (Buckman)	B. III	12B	28, fig. 5
Rhynchonellacea			
<i>Curtirhynchia oolitica</i> (Davidson)	B. I	9B	
<i>Globirhynchia suboboleta</i> (Davidson)	A. I	5A-F	21, figs. 6, 7; 22, figs. 3-5
<i>G. tatei</i> (Davidson)	A. I	5G	
<i>Gnathorhynchia liostraca</i> (Buckman)	B. I	9J	27, figs. 1, 2
<i>Homoeorhynchia cynomorpha</i> (Buckman)	B. I	9M-O	
LOWER JURASSIC			
Punctospiracea			
<i>Spiriferina münsteri</i> (Davidson)	B. II	11A	
Rhynchonellacea			
<i>Furcirhynchia cotteswoldiae</i> (Upton)	A. II	8E	
<i>Gibbirhynchia gibbosa</i> Buckman	A. I		21, fig. 3; 23, figs. 2, 3

EXPLANATION OF PLATE 28

Figs. 1-3. Zigzags of Subgroup B. II: Spiriferoidea.

Fig. 1. Spiriferacea: *Howellella elegans* (Muir-Wood). Right antero-lateral view, to show graded zigzag and non-angulate median deflexion. Same specimen as text-fig. 11G, $\times 4.5$.

Fig. 2. *Howellella elegans* (Muir-Wood). Right postero-latero-ventral view, to show early origin and gradual lateral spread of serial deflexion, and predominantly absolute angulation. Same locality as text-fig. 11G, S.M. A. 26800, $\times 4.5$.

Fig. 3. Punctospiracea: *Spiriferellina octoplicata* (Sowerby). Left antero-lateral view, to show graded zigzag with moderate angulation; note punctuation. Same locality as text-fig. 11E, S.M. E. 7238, $\times 4.5$.

Figs. 4, 5. Zigzags of Subgroup B. III: Terebratulacea.

Fig. 4. *Sellithyris upwarensis* (Walker). Left antero-latero-dorsal view, to show development of zigzag by absolute angulation of complex 'fold'. Same specimen as text-fig. 12C, $\times 2$.

Fig. 5. *Heimia hollandae* (Buckman). As Fig. 4. Same specimen as text-fig. 12B, $\times 2$.

Figs. 6-11. Models to show accessory crestral protection of zigzag slits.

Figs. 6, 7. Model of Rhynchonellacean *Tetarhynchia tetrahedra* (Sowerby): Subgroup A. I; cf. Plate 22, figs. 1, 2. Left antero-lateral and lateral views, with valves gaping narrowly, to show inferred crestral protection by setae raised on internal marginal 'platforms'. *c.* $\times 2$.

Figs. 8, 9. As figs. 6, 7; but valves gaping widely in inferred 'normal' (i.e. feeding) position.

Fig. 10. Model of anterior arc of zigzag slit of a rhynchonellid, with inferred crestral protection by setae raised on internal marginal 'platforms'; largest permitted 'particle' represented by steel ball (cf. text-fig. 13E).

Fig. 11. Model of anterior arc of zigzag slit of *Sphaerirhynchia wilsoni* (Sowerby), with crestral protection by internal marginal spines (cf. text-fig. 13C, F); note 'particle' as in fig. 10.



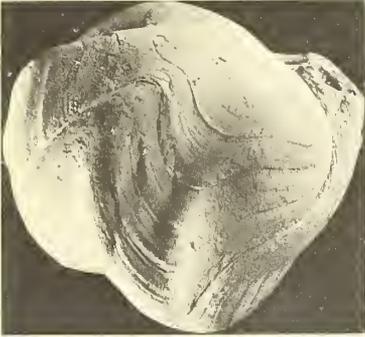
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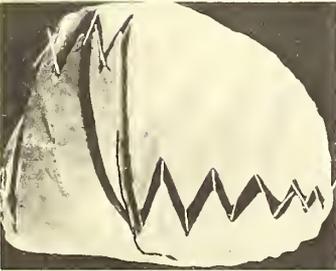
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9



11

	<i>Deflexion</i> <i>subgroup</i>	<i>Text-fig.</i>	<i>Plate</i>
<i>Homoeorhynchia acuta</i> (Sowerby)	B. I	9K	26, figs. 3, 4
<i>H. cynocephala</i> (Richard)	B. I		26, fig. 7
<i>Piarorhynchia juvenis</i> (Quenstedt)	B. I	9C	
<i>Prionorhynchia serrata</i> (Sowerby)	A. I		22, fig. 6
<i>Quadratirhynchia crassimedia</i> Buckman	A. I		21, fig. 2; 23, fig. 1
<i>Rimirhynchia anglica</i> (Rollier)	A. II	8B-D	25, figs. 1-4
<i>Tetrahynchia tetrahedra</i> (Sowerby)	A. I		22, figs. 1, 2; 28, figs. 6-9
UPPER TRIASSIC			
Punctospiracea			
<i>Cyrtina uncinata</i> (Schafhaeutl)	B. II	11B	
<i>Retzia fastosa</i> Bittner	A. I		
Athyracea			
<i>Misolia noetlingii</i> (Bittner)	A. I		
Rhynchonellacea			
<i>Halovella amphitoma</i> (Bronn)	A. I	6N	
' <i>Rhynchonella</i> ' <i>concordiae</i> Bittner	A. I		
' <i>Rh.</i> ' <i>fissicostata</i> Suess	A. I		
' <i>Rh.</i> ' <i>signifrons</i> Kittl	B. I		
MIDDLE TRIASSIC			
Terebratulacea			
' <i>Terebratula</i> ' <i>suborbicularis</i> Münster	B. I		
Rhynchonellacea			
' <i>Rhynchonella</i> ' <i>attiliua</i> Bittner	B. I	9H	
' <i>Rh.</i> ' <i>corneliana</i> Bittner	B. I	9D	
' <i>Rh.</i> ' <i>decurtata</i> Girard	A. I	6E	
' <i>Rh.</i> ' <i>illyrica</i> Bittner	B. I		
UPPER PERMIAN			
Terebratulacea			
<i>Hemiptychina himalayensis</i> (Davidson)	B. I		
<i>Notothyris minuta</i> Waagen	B. I	10H	
Punctospiracea			
<i>Spiriferellina cristata</i> (Schlotheim)	B. II	11D	
Rhynchonellacea			
<i>Terebratuloidea davidsoni</i> Waagen	A. I		
<i>Ucinunellina jabiensis</i> (Waagen)	A. I		21, fig. 10
Orthotetacea			
<i>Kiangsiella pectiniformis</i> (Davidson)	B. I		
Dalmanellacea			
<i>Enteletes waageni</i> Gemmellaro	B. I		27, figs. 6, 7
LOWER PERMIAN			
Punctospiracea			
<i>Crenispirifer angulatus</i> (King)	B. II	11C	
<i>Hustedia hessensis</i> King	A. I	7B	
Rhynchonellacea			
<i>Wellerella truncata</i> Dunbar & Condra	B. I		
Orthotetacea			
<i>Meekella striatocostata</i> (Cox)	B. I	10G	27, figs. 4, 5

	Deflexion subgroup	Text-fig.	Plate
Dalmanellacea			
<i>Euteletes dumblei</i> (Girty)	B. I	10E	
UPPER CARBONIFEROUS			
Punctospiracea			
<i>Punctospirifer kentuckyensis</i> (Shumard)	B. II		
Rhynchoporacea			
<i>Rhynchopora nikitini</i> Tschernyschew	A. I	7A	24, figs. 6-8
Rhynchonellacea			
<i>Wellerella osagensis</i> (Swallow)	B. I		
Dalmanellacea			
<i>Euteletes lamarcki</i> (Fischer)	B. I	10D	
<i>Parenteletes cooperi</i> King	B. I	10F	
LOWER CARBONIFEROUS			
Punctospiracea			
<i>Spiriferellina octoplicata</i> (Sowerby)	B. II	11E	28, fig. 3
<i>Hustedia mormoni</i> (Marcou)	A. I	7L	23, fig. 8
Rhynchonellacea			
<i>Axiodeania platypleura</i> Clark	B. I		
<i>Camarotoechia pleurodon</i> Phillips	A. I	6G	
<i>Paraphorhynchus elongatum</i> Weller	B. I		
<i>Pugnax pugnus</i> (Martin)	B. I	9A	26, fig. 1
<i>Rhynchotetra angulata</i> (L.)	B. I	9E	26, fig. 2
<i>Tetracamara subcuneata</i>	A. I		
UPPER DEVONIAN			
Punctospiracea			
<i>Cyrtiopsis davidsoni</i> Grabau	B. III	12D	
Rhynchonellacea			
<i>Basilorhynchus basilicum</i> Crickmay	B. I		
<i>Calvinaria bransonii</i> Stainbrook	B. I		
<i>Porostictia perchaensis</i> (Stainbrook)	B. I		
<i>Pugnoides calvini</i> Fenton & Fenton	B. I		
MIDDLE DEVONIAN			
Athyracea			
<i>Plectospira ferita</i> (von Buch)	A. I	7N	

EXPLANATION OF PLATE 29

Zigzags in Oysters.

Fig. 1. *Ostrea diluviana* Linnaeus. Antero-dorsal view, to show graded zigzag and dorsal crestal suppression. Chalk Marl (U. Cretaceous); Folkestone, Kent, England. S.M. B. 6455, $\times 2$.

Figs. 2, 3. *Ostrea diluviana* Linnaeus. Ventral and posterior views, to show graded zigzag. Locality as fig. 1. S.M. B. 6452, $\times 1$.

Fig. 4. *Ostrea diluviana* Linnaeus. Ventral arc of zigzag commissure; P = 4. Chalk Marl (U. Cretaceous); near Cambridge, England. S.M. B. 6594, $\times 1$.

Fig. 5. *Ostrea diluviana* Linnaeus. Ventral arc of zigzag commissure, to show predominantly relative angulation; P = 4. Chalk Marl (U. Cretaceous); Cherry Hinton, Cambridge, England. S.M. B. 358 (figured Woods 1913, fig. 135), $\times 2$.

Figs. 6, 7. *Ostrea crista-galli* Linnaeus. Views of four shells, gaping narrowly. Recent; Indo-Pacific. C.M.Z.



1



2



3



4



5



6



7

RUDWICK, Zig-zags in oysters

	<i>Deflexion subgroup</i>	<i>Text-fig.</i>	<i>Plate</i>
Rhynchonellacea			
<i>Isopoma brachyptycha</i> (Schnur)	B. I		
<i>Nayuniella schmuri</i> (de Verneuil)	A. II	8F	25, fig. 6
<i>Yunnanellina hanburyi</i> (Davidson)	B. I		
Stenocismatacea			
<i>Stenocisma gregeri</i> (Branson)	B. I	10J	
LOWER DEVONIAN			
Punctospiracea			
<i>Cyrtina heteroclita</i> (DeFrance)	B. II	11F	
Spiriferacea			
<i>Megakozłowskiella perlamellosa</i> (Hall)	B. II		
Rhynchonellacea			
<i>Monadotoechia monadina</i> Havlíček	B. I	9F	
<i>Phoenicotoechia phoenix</i> (Barrande)	B. I		
<i>Stegerhynchus pseudolivonicus</i> (Barrande)	A. I		
Pentameracea			
<i>Gypidula acutilobata</i> (Sandberger)	B. I	10C	
<i>Sieberella sieberi</i> (von Buch)	B. I		
UPPER SILURIAN			
Rhynchonellacea			
<i>Ancillotoechia modica</i> (Barrande)	B. I		
<i>Linguopugnoides carens</i> (Barrande)	B. I		
<i>Stegerhynchus daphne</i> (Barrande)	A. I	6H	
MIDDLE SILURIAN			
Athyracea			
<i>Rhynchospirina baylei</i> (Davidson)	A. I	7F	
<i>Trematospira salteri</i> (Davidson)	A. I	7G	24, fig. 1
Spiriferacea			
<i>Howellella elegans</i> (Muir-Wood)	B. II	11G	28, figs. 1, 2
Rhynchonellacea			
<i>Camarotoechia borealis</i> (Schlotheim)	A. I	6K	21, fig. 1
<i>Rhynchotreta cuneata</i> (Dalman)	A. I	6J	21, fig. 4
<i>Sphaerirhynchia davidsoni</i> (McCoy)	B. I	9G, 13C	
<i>S. wilsoni</i> (Sowerby)	B. I		28, fig. 11
<i>Stegerhynchus whitii</i> (Hall)	A. I		21, fig. 5
<i>Trigonirhynchia tennesseensis</i> (Hall & Clarke)	A. I		
UPPER ORDOVICIAN			
Rhynchonellacea			
<i>Lepidocyclus capax</i> (Conrad)	A. I	6L	23, fig. 4
<i>Rostricellula ambigena</i> (Barrande)	A. I		
Syntrophiacea			
<i>Parastrophinella reversa</i> (Billings)	B. I	10A	27, figs. 8, 9
Orthacea			
<i>Platystrophia crassa</i> (James)	A. I	7E	23, fig. 2
<i>P. cypha</i> (James)	A. I	7D	24, fig. 2
<i>P. ponderosa</i> Foerste	A. I		24, fig. 3

	Deflexion subgroup	Text-fig.	Plate
MIDDLE ORDOVICIAN			
Rhynchonellacea			
<i>Oligorhynchia angulata</i> Cooper	A. I	6 O	
<i>Rostricellula minuta</i> Cooper	A. I	6M	
Pentameracea			
<i>Parallelelasma pentagonum</i> Cooper	B. I	13A, B	
Syntrophiacea			
<i>Camerella pulchra</i> Cooper	B. I	10B	
<i>Plectocamara costata</i> Cooper	A. I	7C	
Tripleciacea			
<i>Oxyplecia gibbosa</i> Ulrich & Cooper	B. I		

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VOLUME 7 · PART 2

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THE UPPER MISSISSIPPIAN AMMONOID *DELEPINOCERAS* IN NORTH AMERICA

by W. M. FURNISH, J. H. QUINN, and JAMES A. MCCALED

ABSTRACT. The occurrence of a late Mississippian cephalopod, the genus *Delepinoceras*, is reported from Arkansas and Oklahoma. This fossil, not previously described from the Western Hemisphere, indicates precise correlation of the upper Chester Series and the late lower Namurian of Eurasia and Africa.

UNTIL 1958, knowledge of the ammonoid *Delepinoceras* rested on three specimens from two localities; one of the records was of an uncertain nature. In the past few years representatives of the same genus have been discovered at seven additional localities scattered around the world. This distinctive ammonoid also appears to have evolved so rapidly and to have become extinct in such a short span that it is restricted to a narrow time zone. The stratigraphic range of the genus will probably prove to be somewhat greater than is now apparent, but the fossil will also serve as a useful index in Mississippian–Pennsylvanian boundary strata.

The importance of *Delepinoceras* was realized by Ruzhencev who assigned the taxon to a separate family in 1957 and who described an occurrence from the southern Urals in 1958. A specimen from the questionable Springer Formation in Oklahoma (Branson 1962, p. 433) was ‘rediscovered’ in our collections after the appearance of Ruzhencev’s analysis. While this occurrence in Oklahoma was being checked, another example appeared in material from Arkansas. In addition, accounts by Kullmann (1962), Wagner-Gentis (1963), and by Pareyn (1962) have added to our knowledge of the geographic range of this genus.

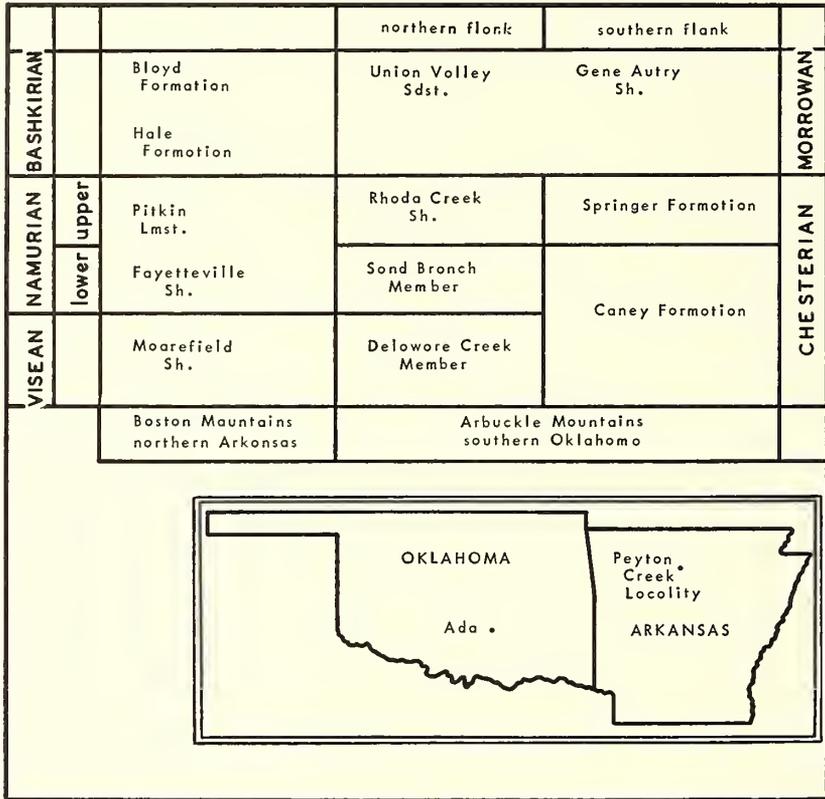
STRATIGRAPHY

In north-western Arkansas and adjacent Oklahoma, the uppermost Mississippian formation is the Pitkin Limestone, the type locality for which is in Washington County. This unit is typically a limestone of some 50 feet thickness bounded by unconformities. In north-central Arkansas, 150 miles to the east, thicker strata with a similar stratigraphic position in the Leslie area of southern Searcy County and northern Van Buren County cannot be correlated lithologically with any particular part of the Pitkin, but are regarded as an approximate equivalent (Easton 1942). The upper 100 feet of predominantly shaly strata in the 200-foot shale and limestone section of this vicinity are known as the ‘Peyton Creek beds’ of the upper Pitkin Formation. A typical development is found at an exposure in Frank Stewart’s Peyton Creek Phosphate Mining Company strip mine about 5 miles south of Leslie (Sec. 12, T. 13 N., R. 15 W.) but across the county line in northern Van Buren County. Another exposure is found nearby in a road cut on U.S. Highway 65 about $\frac{1}{4}$ mile south of the bridge over Peyton Creek.

An abundant molluscan fauna occurs in the Peyton Creek beds at the type locality. Loose fossils are secured from the shales and phosphate-rich layers. Well-preserved

goniatites include *Delepinoceras*, *Anthracoceras*, *Cravenoceras*, *Eumorphoceras*, and *Dimorphoceras* (Quinn 1962b). The nautiloid genera *Brachycycloceras*, *Tylonautilus*, and *Stroboceras* are also represented. Gastropods and pelecypods are abundant; brachiopods and crinoids are relatively rare.

In the Leslie, Arkansas, vicinity there are lithologic variations within the Peyton



TEXT-FIG. 1. Correlation chart of mid-continent goniatile-bearing strata in Upper Mississippian and Lower Pennsylvanian.

Creek beds, especially across the depositional strike. The upper fossiliferous beds at Peyton Creek south of Leslie are not associated with a completely exposed Pitkin section, although about 170 feet of strata crop out. East of Leslie on State Highway 66 (SE $\frac{1}{4}$ Sec. 23, T. 14 N., R. 15 W.) the Fayetteville Shale and 200 feet of younger Mississippian are exposed along the road. Above the Fayetteville, the basal 40 feet of section is a massive limestone; this unit is succeeded by a similar thickness of dark calcareous shale. Above the shale is a bed of conglomeratic limestone 6 feet thick which contains an abundance of large *Eumorphoceras bisulcatum*; specimens as large as 200 mm. diameter have been obtained.

About 120 feet of exposed strata overlie the *Eumorphoceras bisulcatum* horizon in the road section east of Leslie. These upper layers include limestone, shale, and sandstone, most of which are correlated with the 'Peyton Creek shale' locality 5 miles to the south. At the top of the Leslie section there is a limestone grading into calcareous conglomerate above. This upper bed is overlain by about 4 feet of fine-grained sandstone and then some 5 feet of coarse conglomerate containing pebbles and granules of phosphatic material. The phosphatic conglomerate may be of Pennsylvanian age and is believed to represent a hiatus.

CORRELATIONS

In Arkansas, the strata underlying the Peyton Creek *Delepinoceras* beds are of Fayetteville and lower Pitkin age. These strata contain normal *Eumorphoceras* Zone fossils, the *Eumorphoceras-Paracravenoceras-Cravenoceras* assemblage, which occur in the Sand Branch Member of the Caney Shale in southern Oklahoma. Equivalent strata in Europe are of lower Namurian (Pendleian-Arnsbergian) age. According to Collinson, Scott, and Rexroad (1962, chart 5) a correlation of conodont faunas with European goniatite zones indicates that these strata represent middle and upper Chester of the type area. Over fifty years ago, Willis (1912, p. 411-12) presented the same general correlation. Also, in terms of various interpretations of subsequent years (e.g. Moore 1937, p. 31; 1948, p. 398, and Weller *et al.* 1948), this correlation represents a majority opinion. However, other authorities (e.g. Miller, *in* Weller *et al.* 1948, p. 117) have expressed widely different conclusions.

The next younger goniatite fauna includes *Delepinoceras*, *Anthracoceras*, *Cravenoceras*, and *Eumorphoceras* in the Arkansas sequence (Quinn 1962*b*). The fauna appears to fall within the uppermost *Eumorphoceras* Zone, lower Namurian, of Europe (Ruzhencev 1962, Kullmann 1962, Pareyn 1962). On the basis of conodont faunas primarily, Collinson, Scott and Rexroad (1962, p. 27) correlated the uppermost type Chester (Kinkaid) with the European middle Namurian *Homoceras* Zone. Relatively few 'middle' Carboniferous conodont faunas are known in Europe, but Clarke (1960) has described some from Scotland, and Higgins (1961, 1962) records a few species from Staffordshire and northern Spain. Circuitously, it appears that the *Delepinoceras* beds in Arkansas and Oklahoma are probably of latest Chesterian age. If this interpretation is correct, the Springeran (Elias 1956, 1960) lies within the Mississippian and is not a separate stage.

Above the Arkansas Chesterian is the type Morrowan. The basal unit, the Hale Formation, contains abundant *Verneuilites* *sp.* as well as *Baschkirites* *cf. discoidalis* Librovitch and is correlated with the lower part of the Bashkirian (Westphalian) Stage in Europe. The Bloyd Formation, upper Morrowan, contains *Gastrioceras*, *Branneroceras*, *Diaboloceras*, and *Axinolobus*, and is a faunal correlative of the *Gastrioceras* Zone, also within the Bashkirian Stage.

In southern Oklahoma, the Morrowan section contains Bloyd ammonoid faunas in the Union Valley Sandstone (Quinn 1962*a*, p. 116) and the Gene Autry Shale. On the north flank of the Arbuckle Mountains, the Union Valley assemblage contains *Gastrioceras* and *Branneroceras*. South of the main Arbuckle uplift, a slightly younger goniatite fauna in the Gene Autry Formation includes *Axinolobus* and *Diaboloceras*. The Hale ammonoid fauna has not been identified with certainty in this general area.

SYSTEMATIC DESCRIPTION

Genus *DELEPINOCERAS* Miller and Furnish 1954

Type species. Dimorphoceras thalassoide Delépine, in Delépine and Menchikoff 1937, p. 83.

- 1937 *Dimorphoceras* (part) Delépine in Delépine and Menchikoff, pp. 83–85.
 1941 *Dimorphoceras* (part) Delépine, p. 75.
 1951 *Eothalassoceras* (part) Miller in Barker, p. 179.
 1954 *Delepinoceras* Miller and Furnish, p. 690.
 1957, Miller and Furnish, p. 69. 1957, Ruzhencev, p. 58.
 1958a, Ruzhencev, pp. 28, 29. 1958b, Ruzhencev, pp. 489–92.
 1960, Ruzhencev, p. 211. 1960, Kullmann, pp. 336–7.
 1962, Pareyn, p. 134. 1962, Ruzhencev, p. 375.
 1963, Wagner-Gentis, p. 15.

The most distinctive feature of the genus *Delepinoceras* is the nearly symmetrical threefold subdivision of the lateral lobes and prongs of the ventral lobe in the suture. This feature appears during ontogeny at about 15 mm. diameter. The conch is subdiscoidal at maturity with an evenly rounded venter and nearly closed umbilicus. Growth lines are almost straight but biconvex; reticulate sculpture is present as well as constrictions on immature whorls.

Delepinoceras was initially recorded from the Algero–Moroccan border and the Pyrenees; additional specimens have been described since from these areas. Several specimens were secured in the southern Urals, and we are recording the genus in the southern mid-continent of the United States. Mackenzie Gordon, Jr. (personal communication, 1962), has stated that he has also found the genus in the Great Basin. In most of these cases, only a relatively small number of specimens or isolated shells have been reported, but it appears that the stratigraphic level is uppermost Mississippian (late Chesterian) or equivalent (upper *Eumorphoceras* Zone). Another species, *D. eothallassoides* Wagner-Gentis (1963, p. 15), is now known from the lower *Eumorphoceras* Zone (middle Chesterian). Earlier ancestors were probably Late Mississippian goniatitids, such as *Platygoniatites*, which are closely similar except for the secondary elements (Ruzhencev 1960, p. 210); no obvious descendants have been recognized.

The Dimorphoceratidae and the Thalassoceratidae evolved at about the same time as the Delepinoceratidae and all demonstrate at least superficial resemblance to one another. Neither of those two families, however, contain representatives in which trifid lobes are stabilized. *Dimorphoceras* possesses bifid or irregularly subdivided lobes, and in *Thalassoceras* the lobes are serrate or irregularly digitate.

Delepinoceras bressoni Ruzhencev 1958

Plate 30, figs. 1–5

- 1951 *Eothalassoceras* sp. Miller in Barker, p. 179.
 1956 *Eothalassoceras* sp. Miller; Elias, p. 94.
 1958 *Delepinoceras bressoni* Ruzhencev, pp. 490–2, text-figs. 1, 2.
 1960 *Delepinoceras bressoni* Ruzhencev, p. 211.
 1962 *Delepinoceras bressoni* Ruzhencev, p. 375.
 1962 *Delepinoceras bressoni* Ruzhencev; Kullmann, p. 337.
 1962 *Delepinoceras bressoni cantabricus* Kullmann, pp. 337–41, pl. 6, figs. 5–7.

D. bressoni was well illustrated and described by Ruzhencev (1958*b*). The taxon is represented in our collections by two specimens from north-central Arkansas and two from southern Oklahoma. Both of our larger shells (Pl. 30, figs. 4, 5) are estimated to have had a diameter of about 120 mm. The illustrated fragment represents part of a septate whorl some 75 mm. in diameter, with a conch height of 40 mm., a width of about 32 mm. (estimated), and an approximate umbilical diameter of 10 mm. A third specimen (Pl. 30, figs. 1, 2) is 41 mm. in diameter with a height of 24 mm., width of 23 mm., and umbilical diameter of 4.5 mm. The width/diameter proportions of 43 per cent. and 55 per cent. are similar to those in the type.

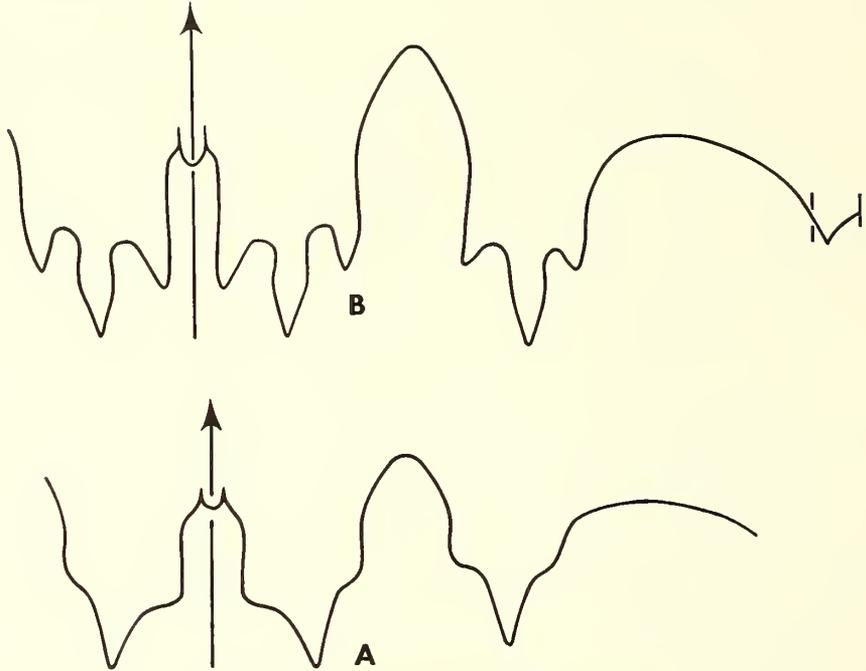
Our material consists of internal moulds and the sutures are clearly visible. The Oklahoma specimens also retain enough of the shell to verify observations by Ruzhencev; the growth lines are relatively straight but with perceptible lateral and ventral sinuses. At about 10 mm. diameter the surface of the test shows reticulate sculpture with the transverse lirae more pronounced than the longitudinal. Moderately prominent, nearly straight constrictions traverse the adolescent conch, three per whorl. The prominently ornamented interior shell surface illustrated by Ruzhencev (1958*b*, text-fig. 1*d*) has been observed on one Arkansas specimen.

Remarks. There is some uncertainty regarding the specific relationships of the type species of the genus *Delepinoceras*. One of the two specimens of *D. thalassoides* from Haci Diab described by Delépine (*in* Delépine and Menchikoff, 1937, pp. 83–85) may not be congeneric, judging by shell sculpture. The smaller individual with visible suture (*ibid.*, pl. 5, fig. 7) is hereby designated the holotype. This type specimen at about 18 mm. diameter possesses an incipiently trifid prong of the ventral lobe and a less prominently subdivided lateral lobe (text-fig. 2*A*). There appears to be little difference between the suture of this form and the paratypes of *D. bressoni* illustrated by Ruzhencev (1958*b*, text-fig. 2) at comparable growth stages. However, according to the original figure of the suture, *D. thalassoides* is distinctly more advanced than *D. bressoni*. A reappraisal based on the plate photograph indicates that differences are very slight, and perhaps the prior name should serve for all. The differentiation of the subspecies *cantabricus* by Kullmann is based primarily upon minor differences in form of the conch, a lateral dimension, which is likely to be influenced by changes during preservation. In any case, the two specimens available from Oklahoma are undistorted and appear to be identical with those illustrated by Ruzhencev. The specimen from Arkansas is obviously crushed and larger, but conforms otherwise.

D. eothalassoides Wagner-Gentis has been interpreted as distinctly more primitive than *D. thalassoides* Delépine or *D. bressoni* Ruzhencev; in addition, it has been found in older strata. The stage of sutural development in *D. eothalassoides* at 35 mm. diameter is comparable to that in *D. bressoni* at 15–20 mm. Also, the prominently striate test indicates closer affinity with a goniatitid ancestry.

Occurrence. The species *D. bressoni* was described from lower Namurian strata in the Aktyubinsk region of the southern Urals; large collections of associated ammonoids are now being monographed by Ruzhencev. Kullman's ten specimens were secured from the Cantabrian Cordillera, the Asturian coast and inland in Leon Province. In northern Spain, the containing beds are correlated with the upper *Eumorphoceras* Zone and contain *Eoasianites*, *Proshumardites*, and 'Praedaraelites' in association. In Arkansas, the

specimens were found together with an abundant goniatite fauna including *Anthraco-ceras*, *Eumorphoceras*, and *Cravenoceras* (Quinn 1962). These beds are at the top of the Chester section in Van Buren County, Arkansas, and should be referred to as the Peyton Creek beds. The fossils have been found in the Frank Stewart Phosphate Mine stripping operation on the south side of Peyton Creek and in a nearby highway cut, about 5 miles south of Leslie (Sec. 12, T. 13 N., R. 15 W.).



TEXT-FIG. 2. External sutures of *Delepinoceras*.

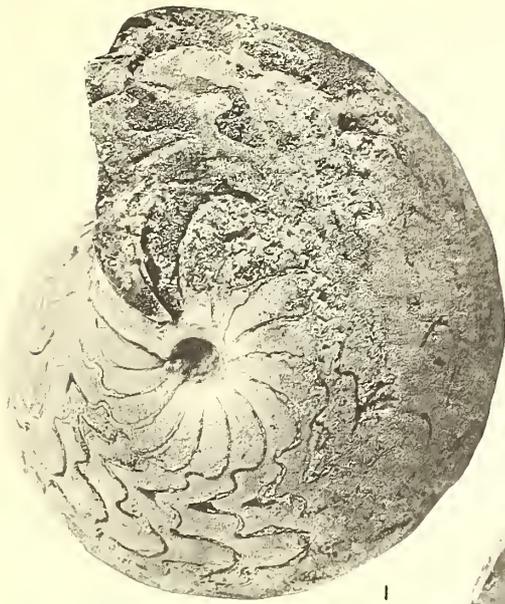
A. *D. thallassoides* Delépine, based on the holotype from Hacı Diab, Algero-Moroccan borderland, at a diameter of about 18 mm. This specimen is from the lower Tagnana Stage or Zone S^{4c}, according to Pareyn (1962). The drawing is based primarily upon the photograph published by Delépine (*in* Delépine and Menchikoff 1937, pl. 5, fig. 7). $\times 6$.

B. *D. bressoni* Ruzhencev, based on a hypotype (University of Arkansas) from the upper Chesterian at Peyton Creek, Van Buren County, Arkansas, at a diameter of about 75 mm. $\times 2$.

Two specimens were secured from concretions in shale on the flank of the Arbuckles, Pontotoc County, Oklahoma. The horizon is in the vicinity of the type section of the Rhoda Creek Member of the Springer Formation. Barker (1951, p. 178) collected one

EXPLANATION OF PLATE 30

Figs. 1-5. *Delepinoceras bressoni* Ruzhencev. 1, 2, Two views of a specimen (SUI 10986) from Rhoda Creek Shale, in the upper portion of the Springer Formation, near the type locality of the member, south-east of Ada, Pontotoc County, Oklahoma. $\times 2$. 3, Another specimen (SUI 11258) from the same general locality to show immature inner whorls. $\times 4$. 4, 5, Two views of a specimen (University of Arkansas) from Peyton Creek beds in Peyton Creek, Van Buren County, south of Leslie, Arkansas. $\times 2$.



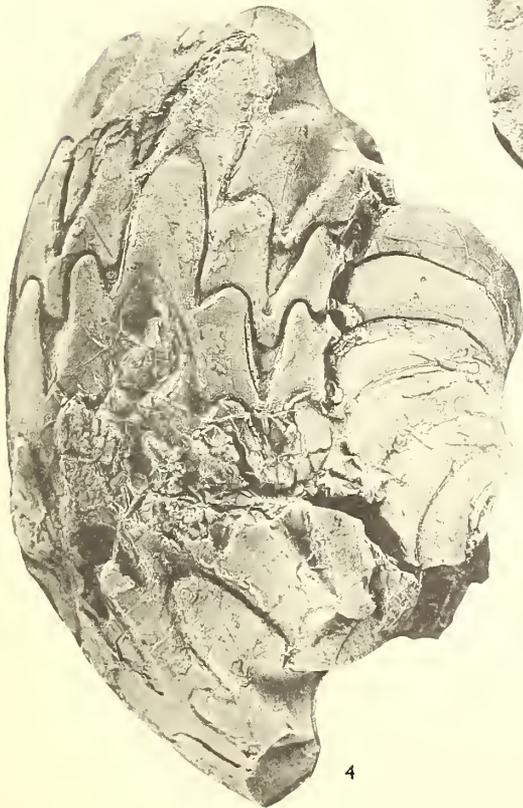
1



2



3



4



5

of the specimens, and Elias (1956, p. 91) referred the fauna to the basal Pennsylvanian. The associated ammonoids represent *Cravenoceras? friscoense* (Miller and Owen), *Eoasianites sp.*, and *Reticuloceras sp.* The exact locality is south-central Sec. 5, T. 2 N., R. 7 E., on Clear Boggy Creek (larger specimen), and a similar locality less than five miles north-west on the same creek in Sec. 23, T. 3 N., R. 6 E.

On the basis of *D. bressoni*, primarily, it seems logical to correlate shales of the Springer (Rhoda Creek) Formation and Peyton Creek Shale. Both are to be regarded as uppermost Chesterian in age.

Types. Primary types are in the Palaeontological Institute, Academy of Science, Moscow. Hypotypes described and illustrated from the southern mid-continent are deposited at the University of Iowa, University of Oklahoma, and the University of Arkansas.

Acknowledgements. We are indebted to Mr. Frank Stewart of Leslie, Arkansas, for having discovered a specimen of *Delepinoceras* and making it available for study; he has taken a great interest in aiding the search for fossils in the Peyton Creek area. James C. Barker submitted another specimen obtained during his thesis study of the Lawrence Uplift north of the Arbuckle Mountains; Carl C. Branson, Robert H. Dott, and George G. Huffman made the material available for study.

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A NEW DASYCLADACEAN ALGA, *NANOPORA*, FROM THE LOWER CARBONIFEROUS OF ENGLAND AND KAZAKHSTAN

by ALAN WOOD

ABSTRACT. *Nanopora*, a new genus of dasycladacean algae, is found abundantly in the Yoredale limestones at Hardrow Scar, Yorkshire, and in the uppermost D₁ of the Avon Gorge. Specimens from Kazakhstan have previously been described by Maslov (as *Anthracoporella*).

THOUGH dasycladacean algae were previously considered to be inexplicably absent in Lower Carboniferous rocks (Garwood 1931), ten genera have now been found in rocks of this age. One, *Koninckopora*, has been recorded from Europe, North Africa, North America, and Japan, apparently being restricted to rocks of Viséan age. Other genera occur more sporadically, presumably because they lived within a narrow range of conditions in shallow clear waters. The present genus occurs in considerable abundance in the Hardrow Scar Limestone (D₂) at Hardrow Scar, in the uppermost D₁ of the Avon Gorge and, very probably, in the Lower Carboniferous of Kazakhstan.

The Dasycladaceae are green algae, fixed to the substratum and therefore indicative of shallow water. Their thallus consists of a large elongated central cell around which radiate branch-like prolongations which vary in form from genus to genus. A calcareous precipitate may envelop the branches, wholly or in part, and, more rarely, the outer wall of the central cell. The calcareous structure preserved in the fossil state is therefore an external mould of part of the plant. It generally has the form of a hollow tube pierced by numerous pores. Diagrams illustrating the general structure of Dasycladacean algae may be found in Pia (1927), Wood (1941), and Rezak (1959).

NANOPORA gen. nov.

Diagnosis. An elongate dasycladacean alga, subcylindrical in form, rarely bent or twisted, probably expanding in diameter gradually with growth. The central cell apparently unbranched and usually unstricted. Branchlets departing from the central cell at an angle of 90°, arranged in equally spaced verticils, the number of branchlets varying with the age of the specimen, generally about twenty to forty. Branchlets in successive verticils alternating with those above and below. The shape of the branchlets as seen in longitudinal sections varies with the amount of calcification, in general they widen outwards and are somewhat widely separated at the level of calcification, tending to be elliptical in transverse section with the long axis of the ellipse parallel to the growth axis of the plant.

Remarks. The branchlets do not divide within the thickness of the calcareous envelope in any of the present specimens. The thickness of the calcareous precipitate varies, perhaps with the age of the fragment observed, and in specimens with a thin calcareous layer the branchlets may appear parallel sided. The walls are neither fibrous nor granular but consist of clear calcite crystals of varying size and irregular outline which are often

continuous from the outer to the inner wall and may extend laterally to enclose several pores. They resemble the crystals making up the wall of *Coelosporella*, which have been interpreted as being formed by recrystallization of a precipitate of aragonite (Wood 1940). The Yorkshire specimens are contained in a very fine-grained limestone, while those from the Avon Gorge are surrounded by a coarse matrix, probably recrystallized. The specimens from the Avon Gorge also show a fine-grained outer coating, interpreted as a post-mortem precipitate.

The structure of this genus contrasts strongly with that of *Koninckopora*, the other common Lower Carboniferous dasycladacean alga. In the latter the wall is formed of minute grains of calcite, probably still nearly as originally precipitated, except for grain growth, and the branchlets are irregularly placed, closely adpressed, and become polygonal in shape by mutual pressure. In the regular arrangement and spacing of the branchlets *Nanopora* carries further a tendency seen in *Primicorallina* of the Silurian and in this feature resembles the Mesozoic rather than the Palaeozoic members of the Family. *Koninckopora* on the other hand retains the irregularity of arrangement seen in such a form as *Mastopora*.

The strictly symmetrical arrangement of branchlets in verticils transverse to the axis of growth is unusual in the Palaeozoic,¹ though the cylindrical form is seen in *Rhabdopora* of Silurian age. In the symmetry of its branching *Nanopora* resembles Triassic members of the Diploporae, but can be separated from them by its small size and the shape and spacing of the branchlets. Certain Permian forms figured by Endo (1961) as *Gyroporella* resemble the present genus in the regular arrangement of their branchlets, but the shape of the branches is different, and the specimens are nearly ten times as large. The only previous record of the present genus is due to Maslov (1939) who illustrated three specimens (as *Anthracoporella fragilissima*) from the Lower Carboniferous. They differ from *Anthracoporella* in the regular arrangement of the branchlets and their less close packing. The maximum known diameter of specimens of this genus is also thirty times less than the maximum in *A. spectabilis* Pia, the genotype. The genera described by Korde (1950) Maslov and Kulik (1956) and Chvorova (1949) from the Lower Carboniferous of the U.S.S.R. are all clearly different from the present form.

The generic name refers to the small size of the thallus, the specimens being among the smallest Dasycladaceae known.

Nanopora anglica sp. nov.

Plates 31, 32

Diagnosis. Diameter of calcareous tube ranging generally from 0.1 to 0.17 mm., occasionally up to 0.20 mm. Pores in well-grown and lightly calcified specimens slightly elliptical, external transverse diameter 0.01 to 0.013 mm., occasionally reaching 0.015 mm.; diameter parallel to axis of growth 0.012 to 0.018 mm. Verticils equally spaced, from five to seven in 0.1 mm. in well-grown specimens. Calcareous tube circular in cross-section, typically straight, increasing in diameter very gradually. The central lumen of the calcareous tube generally parallel sided in the short longitudinal sections available,

¹ The forms described as *Verticillopora* and *Phragmoporella* by Rezak (1959) from the Silurian, supposed to show this feature, are probably not algae, as I hope to show in a later communication.

rarely a sudden increase in diameter followed by a constriction occurs. Branching not observed.

Remarks. The specimens occur in abundance in a dark fine-grained limestone, and are obviously portions of broken elongated tubes. The longest fragment observed measures 1.3 mm. Sections of fragments cut parallel to the outer wall (Pl. 31, fig. 3) show that the pores are truly elliptical, a fact which could not be conclusively demonstrated in oblique sections like those on Plate 31, fig. 1. Some specimens, however, have circular pores, and even elliptical and circular ones may occur in the same fragment. A similar variation is seen in the shape of the pores in longitudinal section, some are parallel-sided as they traverse the wall of the tube, others widen towards the exterior (the commonest case) and some widen and contract again so that they appear club-shaped.

The ratio of the diameter of the interior lumen to the external diameter of the calcareous tube, often considered to be of importance in the fossil *Dasycladaceae*, varies considerably in this species, ranging from 40 to 60 per cent. according to the degree of calcification. There is some evidence that the degree of calcification, that is the thickness of the wall of the tube, was greater in the older parts of the plant, and in thick-walled portions the pores may appear smaller and be more indistinct, possibly because the branchlets were here more flaccid. Tubes of large diameter may be thickly calcified, however, and as shown in Plate 32, fig. 1, may show what can be interpreted as the growing point of the plant, so that there was probably variation in degree of calcification from plant to plant.

Oblique cross-sections such as those shown in Plate 31, fig. 1, yield the most information. In such sections the external and internal diameter of the tube can be accurately obtained, and at the ends any variation in diameter of the branchlets as they passed from the interior of the tube to the outside is clearly visible. The number of rows of verticils in 0.1 mm. can be measured on the side of the section and checked by direct measurement on the obliquely cut ends of the tube. It is quite common to find that the pores are slightly larger in diameter at one end of the elongate obliquely cut section than at the other (Pl. 31, fig. 1). On cross-sections the number of branchlets in one verticil can be estimated, but never very accurately because it is difficult to be certain that the pores counted belong to one verticil only. The number of branchlets in a verticil appears to have varied from 20 to 30; some specimens with 40 or more pores are considered to belong to another species.

One section shows an expansion of the central cell, followed by a constriction (Pl. 32, fig. 2), and this condition is more indistinctly seen in four other specimens. The arrangement of the pores radiating upwards around the constricted portion indicates that the growth of the branchlets was affected by this variation in diameter of the central cell and proves that this is an original feature connected with the growth of the alga. Its significance is unknown. Other sections (Pl. 31, fig. 2) show that the alga was, rather rarely, flexed. The difference in the two ends of the specimen shown in Plate 32, fig. 1, either indicates that the calcified tube was quite sharply bent with one end turning down out of the plane of the section, or shows the actual growing point of the plant.

In some portions of the rock sections traces of small calcified tubes without pores are seen (Pl. 32, fig. 3). These are composed of crystals of calcite similar to those making up the calcified tubes of *Nanopora*, and are quite different in structure from the

concentrically laminated spines of *Productus*, which also occur in this rock. None of these tubes has been seen attached to *Nanopora*, but it is considered that they may well be portions of the calcified holdfasts of this plant.

There is considerable variation in the pore diameter and spacing of the verticils among the specimens studied. There appears to be a complete range of variation from the well-grown specimens described above, to specimens with a pore diameter ranging from 0.04 mm. (interior) to 0.07 or 0.08 mm. (exterior) and the number of verticils in 0.1 mm. may rise to as high as nine in these specimens. Part of this variation may certainly be due to age of the specimens, but the pore size is not strictly dependent on the diameter of the tube, and a real variation in these features is certainly present, which renders it difficult to define the boundaries of the species. The work of Egerod (1952) shows how variable the degree of calcification and the form of the thallus can be in modern Dasycladaceae.

Type specimen. That shown in Plate 31, fig. 1. Deposited in the British Museum (N.H.), registered number V.45813.

Locality and horizons. Hardrow Scar Limestone, top bed, Hardrow Scar, near Simonstone, Yorkshire (D₂), also at New Close Sike, Raydale (south of Semerwater), and Coal Sike, Siley Gill, Swaledale. National Grid References SD869918, SD893848, SD900978. Also with *Girvanella wetheredii* in a bed of dark limestone with argillaceous material, 9 inches thick, immediately below an oolitic bed 10 feet thick, a short distance below the junction of the road from Clifton with that along the banks of the River Avon, Bristol (Upper D₁). National Grid Reference 31/563734.

Nanopora fragilissima (Maslov)

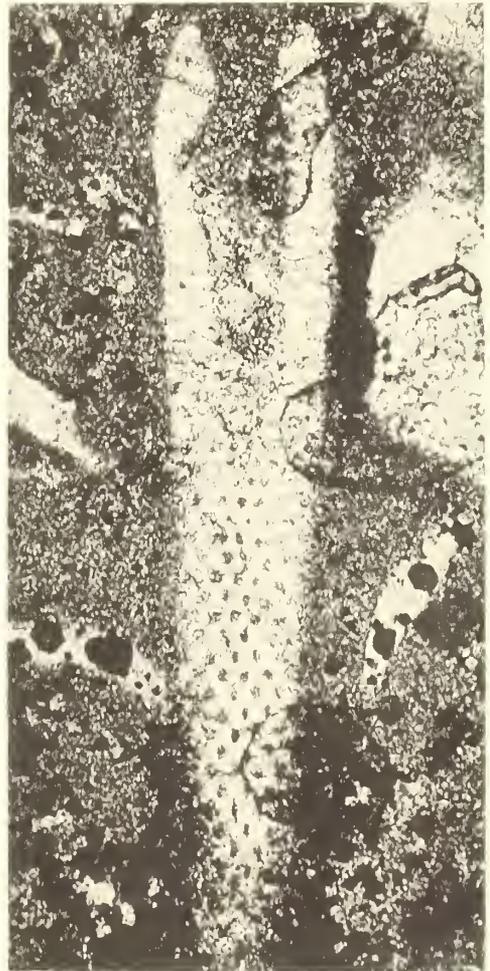
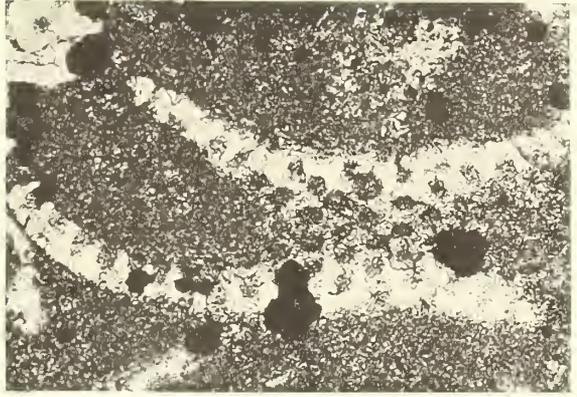
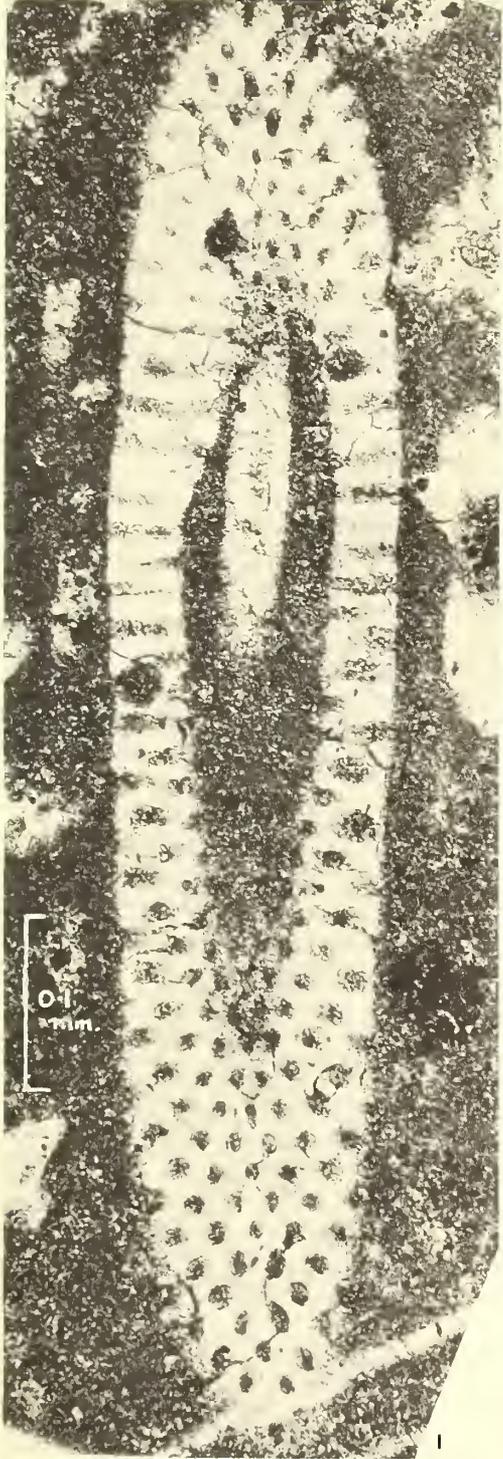
Original diagnosis. Cylinders straight with the outer diameter ranging from 0.075 to 0.15 mm. Cylindrical walls are perforated by closely spaced and very fine pore-canals but no bifurcation of the latter is observed. Differs from the foregoing species [*Anthra-*

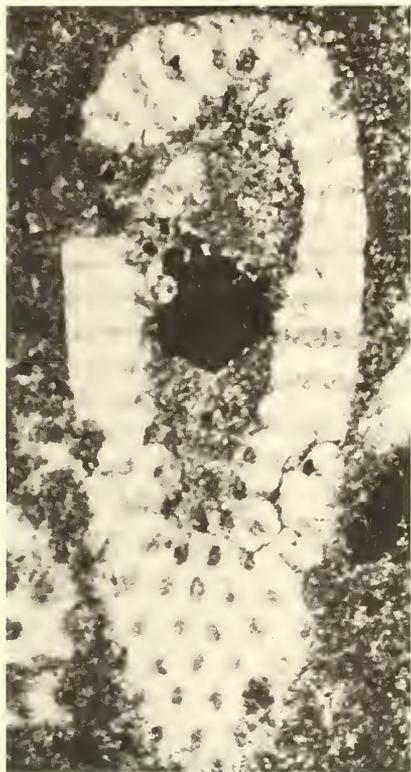
EXPLANATION OF PLATE 31

Figs. 1-3. *Nanopora anglica* gen. et sp. nov., ×230. 1. Holotype. Oblique section, showing at the top the pores widening from the interior to the exterior, and near the base variation in shape of the cross-sections of the pores. The circular cavity filled with matrix seen about half-way up the left-hand side, and the two similar cavities near the top of the specimen are considered to be traces of boring creatures, not reproductive bodies. Top bed, Hardrow Scar Limestone, Hardrow Scar, Yorkshire. B.M. (N.H.). Registered number V.45813. 2. Fragment to show curvature of the calcareous envelope. Same horizon and locality. Wood collection, slide W560. 3. To show variation in size and spacing of pores, also their elliptical nature and verticillate arrangement. Note constriction near upper end, also seen in the specimen figured in Plate 32, fig. 2. Same horizon and locality. Wood collection, slide W561.

EXPLANATION OF PLATE 32

Figs. 1-4. *Nanopora anglica* gen. et sp. nov., ×230. 1. Oblique section, to show (rarely found) difference at two ends. Either the calcareous tube is sharply bent out of the plane of the section at the top end, or this represents the growing point of the plant. Top bed, Hardrow Scar Limestone, Hardrow Scar, Yorkshire. B.M. (N.H.). Registered number V.45813. 2. Section showing expansion of interior cavity, followed by constriction (see p. 183). Same horizon and locality. Wood collection, slide W562. 3. Sections of calcareous tubes associated with *N. anglica*, possibly representing fragments of holdfast. Same horizon and locality. B.M. (N.H.). Registered number V.45813. 4. Cross-sections of calcareous tube, to show general appearance and variation. The bifid appearance seen in the calcareous wall of the upper section is due to alternating pores from a verticil at a different level being cut by the section. Same horizon and locality. B.M. (N.H.). Registered number V.45813.





3



2



4

coporella kasachensis] in the thinner walls of the cylinder, from 0.015 to 0.020 mm. thick. The inner diameter ranges from 0.054 to 0.1 mm.

Remarks. Attempts to borrow the original slides of this species have failed but Dr. Maslov has kindly sent me a photograph of two of the original specimens. He informs me that his material is not very well preserved. There can be little doubt that the original of Maslov's figure 3c, at least, is a species of *Nanopora*, and it is here chosen as the type of this species. It shows the characteristic features of *Nanopora*, the straight calcareous tube, the unbranched pores arranged in verticils, and the alternation of the pores from one verticil to the next. The diameter of the calcareous tube and the thickness of the wall fall within the range of variation of *N. anglica*, but the pores seem to be more minute and more widely spaced. In typical specimens of the British species the pores are nearly as wide as the calcareous layer which separates them, and it is unlikely that the pores are as wide as this in *N. fragilissima* or Maslov would not have represented them by a single line in his drawings of transverse sections.

Type specimen (here chosen). The specimen figured by Maslov (1939) in figure 3c.

Horizon and locality. Lower Carboniferous, left bank of Uhlenta River, south of Semiz-Bugu Mt., Kazakhstan.

Acknowledgements. I am much indebted to Dr. Derek Moore who originally submitted these specimens for study and very kindly collected more material from Hardrow Scar, and to Professor Lily Newton for helpful discussions.

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AMYELON IN AMERICAN COAL-BALLS

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ABSTRACT. *Premnoxylon iowense* Pierce and Hall is recombined as *Amyelon iowense*. These cordaitean roots resemble the stilt roots of modern mangroves. They are usually siphonostelic and possess aerenchyma composed of phloem and phelloderm. Increase in circumference of a deep-seated periderm distended the outer part of the phloem. Aerenchymatous phelloderm was laid down and cortex was sloughed, leaving periderm the outermost tissue. Lenticels flank clusters of lateral rootlets.

DURING the Pennsylvanian Period, cordaitean plants dominated some American coal swamps and their roots are often overwhelmingly abundant in coal-balls. Knowledge of these specimens provides new details of anatomy and morphology and leads to speculation on the biology and environment of deposition of American cordaitean plants. The American roots show similarities to *Amyelon radicans* (Williamson) Williamson, and I refer them to the genus *Amyelon*. Nevertheless, they show distinctive characters necessitating recognition of a different species. I propose to call this species *A. iowense* (Pierce and Hall) comb. nov., since the material studied shows agreement with *Premnoxylon iowense* Pierce and Hall (1953), but indicates that the differences between *A. radicans* and *P. iowense* are not as fundamental as previously supposed.

THE GENUS *AMYELON*

A. radicans is the type species of the genus *Amyelon* (Barnard 1962). Since there is substantial agreement between this root and a root attached to an American cordaitean stem (Andrews 1942) there is no doubt of the natural affinities of *Amyelon*. It can unhesitatingly be referred to the family Cordaitaceae of the Cordaitales. That is to say, *Amyelon* should be considered an organ-genus (Lanjouw *et al.* 1961, art. 3). Therefore, to refer additional specimens to *Amyelon*, an investigator should present evidence of their correct assignment to the Cordaitaceae. A recent revision of *Amyelon* (Barnard 1962) includes roots not proven as members of the Cordaitaceae. One, named *A. bovius*, is perhaps suggestive of a root of *Eristophyton* (Barnard 1962); the other, *A. equivius*, is possibly the root of *Bilignea resinosa* (Barnard 1962). I believe they should be excluded from *Amyelon*.

Genus *Amyelon* Williamson 1874

Type species. *A. radicans* (Williamson) Williamson 1874.

Emended diagnosis. Cordaitean roots bearing clusters of rootlets on conspicuous protuberances. Roots protostelic or siphonostelic. Primary xylem exarch; frequently tetrarch or triarch, sometimes diarch; tracheids spiral, annular, scalariform, reticulate, and multiseriate. Secondary xylem composed of radially arranged tracheids and uniseriate rays. Tracheids usually with three to five rows of bordered pits on their radial walls, pits crowded and hexagonal or oval and separate. Tangential pitting occasional.

[Palaeontology, Vol. 7, Part 2, 1964, pp. 186-209, pls. 33-37.]

Cross field pitting uniseriate and oblique. Only cambium, phloem, and periderm outside the xylem of mature roots. Periderm deep in origin, cortex sloughed early in development. Periderm divisible into phelloderm and phellem. Rootlets usually diarch, primary xylem tracheids with spiral and annular thickening, sometimes with hexagonal pitting in the metaxylem. Some phloem cells with dark contents; endodermis thick-walled. Cells of inner cortex thin-walled, with dark contents or colourless. Outer cortex of thin-walled colourless cells. Root hairs absent.

Amyelon radicans (Williamson) Williamson 1874

Holotype and synonymy. See Barnard (1962).

Remarks. The following should be added to Barnard's (1962) emended diagnosis: Protoxylem touching the secondary xylem. Excentric growth-rings present in the secondary xylem of all but young specimens. Phloem compact. Phelloderm extensive and compact, no cells with brown contents. Rootlets usually diarch or triarch with spiral or annular thickening or hexagonal pitting.

Amyelon iowense (Pierce and Hall) comb. nov.

1942 Root attached to *Mesoxylon nauertianum*, Pyramid Mine, Perry County, Illinois. Coal No. 6, Kewanee Group. Andrews, pl. 4, figs. 13-16 only (text-fig. 1; pl. 3, figs. 8, 9, show coenopterid rootlets).

1953 *Premnoxylon iowense* Pierce and Hall, Ellis Mine, SW $\frac{1}{4}$ sect. 7, T. 74 N., R. 15 W., Mahaska County, Iowa. Desmoinesian Stage.

Emended diagnosis. Large roots protostelic or siphonostelic, pith entire, or with a lacuna at the centre, some pith cells filled with brown contents. Primary xylem exarch, usually tetrarch, sometimes triarch or diarch. Protoxylem touching the secondary xylem or separated from it by several parenchymatous cells. Protoxylem tracheids with spiral, annular, or scalariform thickening. Metaxylem tracheids with uniseriate or biseriate simple pits, or with crowded, hexagonal, bordered pits. Secondary xylem composed of radially arranged tracheids and uniseriate rays. Tracheids with one to five rows of bordered pits on their radial walls. Uniseriate bordered pits occurring on the tangential walls rarely. Rays, one to eight cells high, some cells with brown contents. Cross field pitting uniseriate and oblique. Phloem consisting of sieve elements, phloem parenchyma, phloem rays and phloem fibres. Outermost part of the phloem usually aerenchymatous, with phloem rays greatly stretched radially. Phelloderm extensive, usually aerenchymatous, some cells very long, with brown contents. Phellem cells rectangular, tangentially elongated. Lenticels present. Lateral rootlets borne in clusters on conspicuous protuberances of the main root, protuberances always occurring between two lenticels. Rootlets 500 μ in diameter. Primary xylem usually diarch, rarely triarch or tetrarch. Cells with brown contents present in phloem and inner cortex. Endodermis thick-walled. Outer cortex composed of colourless, thin-walled cells. Cortex of young main roots sloughed by development of periderm arising from a deep-seated phellogen. Phellogen arising before extensive development of secondary xylem and phloem.

Syntype specimens. Coal-ball UM 110 and a series of unnumbered slides, Paleobotanical Collection, University of Minnesota, Minneapolis.

Other material studied

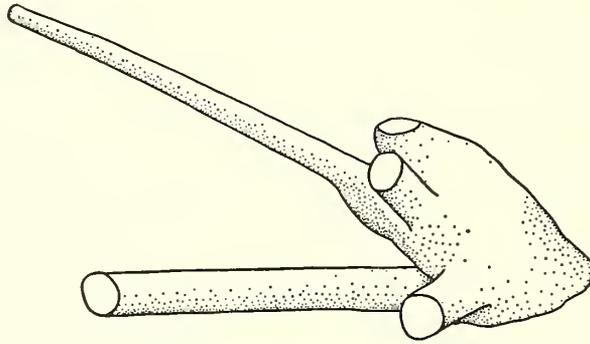
Locality 1. Pittsburg and Midway Coal Company's open strip mine, 2 miles north of Halowell, Kansas. Sect. 4, T. 33 S., R. 22 E., Cherokee County. Mineral and/or Fleming Coal, Cabaniss Formation of the Cherokee Group, Desmoinesian Stage. Coal-ball KU 1021, Botany Department, Kansas University, Lawrence. Coal-ball KU 1016, Botany Department, Kansas University, Lawrence. Coal-ball KU 1044, Botany Department, Kansas University, Lawrence.

Locality 2. Kruger Coal Company's abandoned shaft mine, $\frac{1}{4}$ mile north of Cherokee, Kansas. S $\frac{1}{2}$ SW $\frac{1}{4}$ Sect. 7, T. 31 S., R. 24 E., Crawford County. Weir-Pittsburg Coal, Cabaniss Formation of the Cherokee Group, Desmoinesian Stage. Coal-ball KU 1115, Botany Department, Kansas University, Lawrence.

Locality 3. Atlas Coal Mine, 2.9 miles north and west of Eddyville, Iowa. W $\frac{1}{2}$ SW $\frac{1}{4}$ Sect. 18, T. 74 N., R. 15 W., Mahaska County. From a part of the Desmoinesian Stage including the Seahorne Limestone and the Bevier Coal. Coal-ball IU 1755, Botany Department, Illinois University, Urbana.

Locality 4. Mine on a 40-acre plot belonging to Tom Elsloo *et al.*, on east side of State Highway No. 137, north-east of Givin and 3.9 miles south of Oskaloosa, Iowa. NW $\frac{1}{4}$ NE $\frac{1}{4}$ Sect. 12, T. 74 N., R. 16 W., Mahaska County. From a part of the Desmoinesian Stage including the Seahorne Limestone and the Bevier Coal. Coal-ball IU 1823, Botany Department, Illinois University, Urbana.

Peels were prepared using the cellulose acetate film technique (Joy *et al.* 1956). These were supplemented by occasional poured peels (Darrah 1936) and a few ground sections.



TEXT-FIG. 1. Reconstruction of a large specimen with five branches. Extra-xylary tissues omitted. KU 1021, $\times 0.5$.

LARGE ROOTS

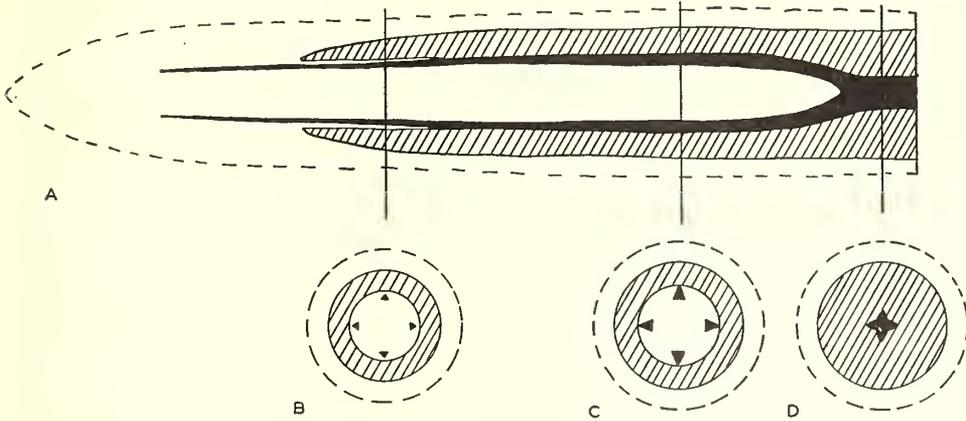
The mode of branching of large roots is shown in text-fig. 1 and their general organization is shown in Plate 33, fig. 1. A central pith with four exarch primary xylem poles at its periphery is surrounded by a cylinder of secondary xylem. Cambium occurs at the edge of the secondary xylem and there is a zone of compact secondary phloem. Aerenchymatous tissue, partly secondary phloem and partly phelloderm, accounts for the largest volume of root. Phellogen and fairly thick, compact phellem occur outside the aerenchymatous phelloderm.

Pith. In transverse section, pith cells are rounded and thin-walled (Pl. 33, fig. 1), measuring 70–160 μ , while in longitudinal section they are rectangular, 95–260 μ long, and are arranged in axial rows. Some of them have light brown contents. Frequently the pith is

entire, but in larger specimens there is a central lacuna. There is absolutely no indication of the chambered pith so characteristic of cordaitean stems.

Some specimens have no pith, but serial sections through several roots show a transition from a protostelic condition near the point of attachment to a supraordinate root (Pl. 33, fig. 2, text-fig. 2A, D), to a siphonostelic condition further away (Pl. 33, fig. 1; text-fig. 2A, B, C).

Primary xylem. There are from two to four exarch primary xylem poles, with the protoxylem either touching the secondary wood or separated from it by several rows of parenchymatous cells (Pl. 34, fig. 1). Where diarch primary xylem plates occur they



TEXT-FIG. 2. A, Theoretical radial section through an entire root. Attachment to a supraordinate root to the right, root apex to the left. B-D, Transverse sections at levels indicated by the lines passing through A. B, Tetrarch siphonostele; primary xylem separated from the secondary xylem by parenchyma cells. C, Tetrarch siphonostele; primary xylem in contact with the secondary xylem. D, Tetrarch protostele; primary xylem in contact with the secondary xylem. Conventions: primary xylem, solid black; secondary xylem, diagonal lines; outer limit of root, broken line; parenchymatous tissues left blank. Not to scale.

measure about $600\ \mu$ from protoxylem to protoxylem. Where the primary xylem is triarch or tetrarch, isolated primary xylem poles are triangular in transverse section and measure about $250\ \mu$ along the base and $275\ \mu$ radially. Protoxylem cells are about $23\ \mu$ in transverse section, while metaxylem cells are about $57\ \mu$. Wall sculpturing of protoxylem tracheids is spiral, annular (Pl. 34, fig. 2) and scalariform, while the region transitional from protoxylem to metaxylem has tracheids with simple, uniseriately arranged pits on their radial walls (Pl. 34, fig. 3). These simple pits are transversely elongated and look intermediate between scalariform thickening and true pitting. Many metaxylem tracheids have uniseriate, or alternately arranged biseriate, simple pits about $8\ \mu$ in diameter on their radial walls (Pl. 34, fig. 4). Those furthest from the protoxylem poles have alternately arranged, crowded and hexagonal bordered pits with slightly oblique slit apertures on their radial walls, as in secondary xylem tracheids.

Secondary xylem. The secondary xylem is composed entirely of tracheids and xylem rays (Pl. 34, fig. 8). In transverse section the tracheids are square and measure $35\text{--}70\ \mu$ across,

while the ray cells are elongated radially and measure about $60 \times 16 \mu$. The tracheids are pitted almost exclusively on their radial walls with one to five rows of pits, although three rows are typical. The pits are of the crowded, hexagonal type (Pl. 34, fig. 5), or else they are less crowded, but still flattened above and below by contact with each other (Pl. 34, fig. 6). Where the pits are crowded and hexagonal they measure 23μ radially $\times 12 \mu$ axially and the almost transverse or slightly oblique pit apertures measure $16 \times 2 \mu$. There is no torus in any pit pair.

Uniseriate pits occur on the radial walls of tracheids adjacent to the cambium of one specimen (Pl. 34, fig. 6). These pits measure 23μ radially $\times 12 \mu$ axially and are flattened by contact above and below. Their apertures are diagonal slits (measuring $16 \times 2 \mu$), in contrast to the nearly horizontal slits in other pits, but none are crossed. A tracheid of the same root shows uniseriate bordered pits on a tangential wall (Pl. 37, fig. 5). This tracheid is 26μ across, the pits are $18 \times 14 \mu$, are flattened where they contact above and below, and have obliquely orientated slit-like apertures which are $12 \times 1 \mu$. Hence it is both narrower and bears smaller pits than the tracheids with pitting on their radial walls.

Xylem rays are uniseriate and are from one to eight cells high (Pl. 34, fig. 8) with individual cells measuring 60μ radially $\times 50$ – 80μ axially. Some have brown contents. The cross field pitting (Pl. 37, fig. 4) is uniseriate and in each ray cell there are at least three simple oblique cross pits, measuring $16 \times 2 \mu$.

Cambium. The cambium and its immediate derivatives form a well-defined zone about six cells deep, surrounding the secondary xylem (Pl. 35, figs. 1, 3, 4). These cells are tangentially elongated and measure about $28 \times 12 \mu$ in transverse section. Plate 35, fig. 3

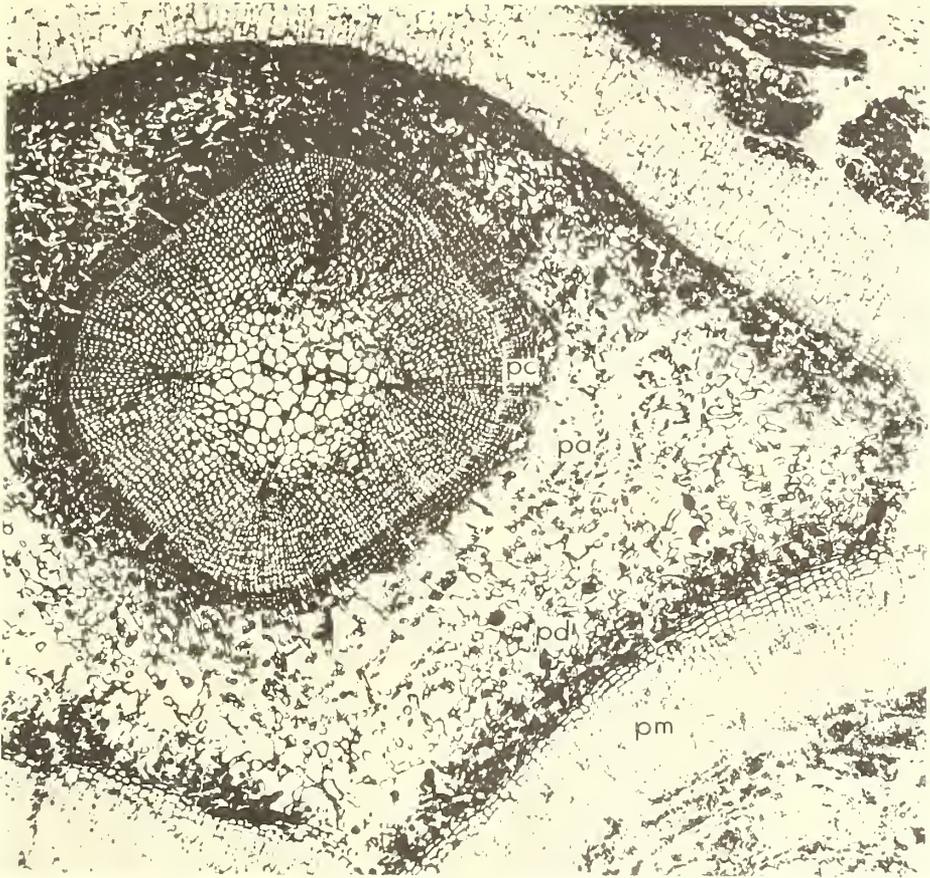
EXPLANATION OF PLATE 33

The following abbreviations are used in Plates 33–37: *c*, cambium. *pa*, aerenchymatous phloem. *pc*, compact phloem. *pd*, aerenchymatous phelloderm. *pe*, periderm. *pf*, phloem fibre. *ph*, phloem. *pm*, phellem. *pp*, phloem parenchyma. *pr*, phloem ray. *r.s.*, radial section. *s*, sieve cell. *T.L.S.*, tangential section. *t.s.*, transverse section. *x*, xylem.

Figs. 1–4. *Amyelon iowense* (Pierce and Hall) comb. nov. 1, General features of a root. KU 1021 F, $\times 15$: T.S. 2, Root near its attachment to a supraordinate root. At the centre there is a poorly preserved tetrarch protostele. Note the growth ring in the secondary xylem. KU 1021 j, 513; slide 727, $\times 10$: T.S. 3, Part of the root in Plate 37, fig. 2 showing a xylem pole, phloem, periderm, and part of the inner cortex; $\times 60$. 4, Rootlet showing thick-walled endodermis. Vascular tissue to the right and cortical tissue to the left. KU 1021 F, 76; slide 361, $\times 250$: R.S.

EXPLANATION OF PLATE 34

Figs. 1–9. *Amyelon iowense* (Pierce and Hall) comb. nov. 1, Primary xylem pole separated from secondary xylem by several parenchymatous cells. IU 1755 F, 2, $\times 100$: T.S. 2, Protoxylem tracheid with annular thickening. KU 1021 G, 7; slide 421; $\times 300$: T.L.S. 3, Uniseriate simple pits. Primary tracheids in a region transitional between protoxylem and metaxylem. IU 1755 C, $\times 600$: R.S. 4, Metaxylem tracheids, one with uniseriate simple pits, another with biseriate, alternate simple pits. IU 1755 C, 4, $\times 600$: R.S. 5, Radial wall of a secondary tracheid. KU 1021 G, 11; slide 425, $\times 300$. 6, Secondary tracheids with uniseriate pits. KU 1021 G, 14; slide 428, $\times 200$: R.S. 7, A root near its attachment to a supraordinate root. Its growth has been restricted by adjacent roots and no aerenchyma has developed. The convolutions at the lower right-hand side are lenticels. KU 1021 j, 357; slide 703, $\times 8$: T.S. 8, Tracheids and uniseriate rays of secondary xylem. KU 1021 G, 3; slide 417, $\times 100$: T.L.S. 9, Phloem fibre with uniseriate simple pits. KU 1021 G, 7; slide 421, $\times 250$: R.S.



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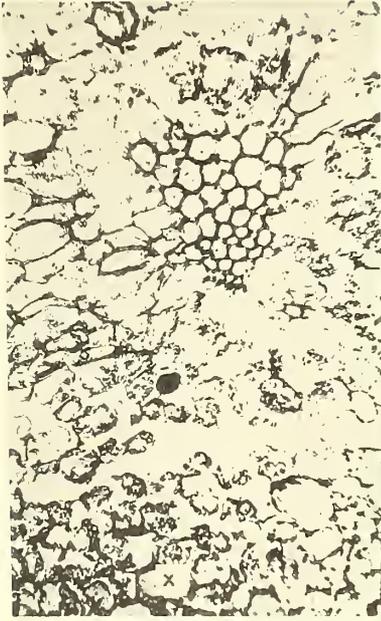
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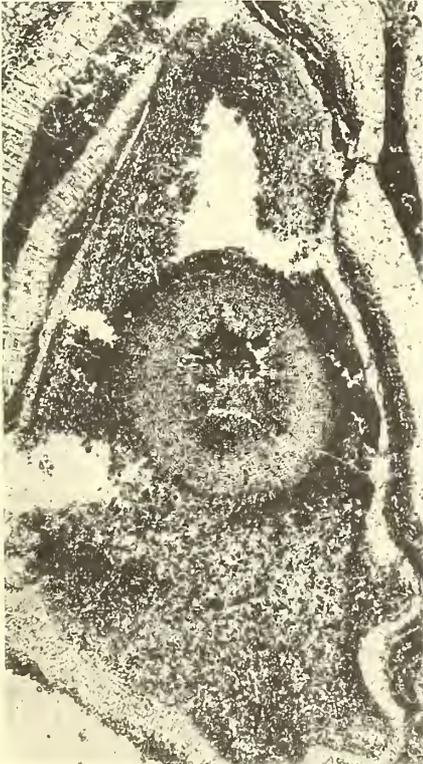
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probably shows an actual cambium cell, while in Plate 35, fig. 4 the gradual transition between phloem and cambium is clear.

Phloem. There are two regions of phloem (Pl. 33, fig. 1; Pl. 35, fig. 1; Pl. 37, fig. 7); an inner compact region, about $200\ \mu$ thick with radially arranged rows of cells and an outer aerenchymatous region, about 1.5 mm. thick, with cells less regularly arranged. Externally, the aerenchymatous phloem abuts against an aerenchymatous phelloderm.

Several types of cells can be recognized in the compact phloem. Those with thick dark walls are most conspicuous and I interpret them as phloem fibres. In transverse section they are rectangular, tangentially elongated, measure approximately $35 \times 16\ \mu$ and occur in tangential rows (Pl. 35, figs. 1, 4, 6). Cases of poor preservation demonstrate them as the phloem cells most resistant to decay. These dark, thick-walled, phloem fibres are conspicuous in longitudinal sections (Pl. 35, fig. 2). Some have a single row of simple pits about $9\ \mu$ in diameter on their radial or tangential walls (Pl. 34, fig. 9). Fibres of similar structure occur in the secondary phloem of *Taxodium distichum* where they have a comparable arrangement in tangential rows, characteristic of the living Taxodiaceae and some Cupressaceae (Chang 1954).

Transverse sections also show rounded or square thin-walled cells of two sizes in the phloem (Pl. 35, fig. 4). Those of larger diameter measure $30\text{--}40\ \mu$ across, while those of smaller diameter measure about $20\ \mu$ across. Radial sections show that the thin-walled cells of larger diameter are rectangular, have horizontal end walls and are only $105\ \mu$ long (Pl. 35, fig. 2) and occasionally have brown contents. I interpret them as phloem parenchyma cells. Radial sections also show that the thin-walled cells of smaller diameter have transverse end walls, but are longer. I suggest that they are sieve elements, but no unequivocal details support this view. Phloem rays are present and in transverse section their radially elongated cells measure approximately $35 \times 58\ \mu$, except near the edge of the compact phloem where they are frequently conspicuously enlarged (Pl. 35, figs. 1, 4) and measure $70\ \mu$ radially $\times 46\ \mu$ tangentially.

At the edge of the compact phloem there is a transition to aerenchymatous phloem (Pl. 35, figs. 1, 7; Pl. 37, fig. 7). Phloem fibres persist for some distance beyond the edge of the compact phloem and the enlarged ray cells extend through the aerenchyma as tortuous chains. The distribution of phloem fibres is well illustrated in Plate 35, fig. 6, where the general preservation is poor and only the resistant xylem tracheids and phloem fibres are preserved. Here the phloem fibres occur for a considerable distance beyond the zone of compact phloem, occupying a zone corresponding to the inner part of the aerenchyma in better-preserved specimens. Interpretation of the inner part of the aerenchyma as phloem is supported by radial sections. In Plate 36, fig. 1 there are two prominent rays. That in the upper left-hand part of the photograph extends as an organized unit for some distance into the aerenchyma, an anatomical feature not found in aerenchymatous cortex. The ray cells furthest from the xylem are longer radially than the ray cells in the xylem, and two of them, at the bottom of the ray, have distinct projections of varying lengths. At the lower right-hand side of Plate 36, fig. 1 there is a ray with conspicuously radially elongated cells. A similar ray in the aerenchymatous phloem is shown in Plate 36, fig. 2. In this case, although the ray is still organized as a distinct unit, the cells are considerably radially elongated and measure $250 \times 40\ \mu$. I interpret this radial elongation as a result of stretching during secondary growth.

Phelloderm. Externally the aerenchymatous phloem abuts directly against aerenchyma of different structure, about 1.3 mm. across (Pl. 33, fig. 1; Pl. 37, fig. 7). Since this outer aerenchyma is apparently derived from the same meristematic region giving rise to the phellem (Pl. 35, fig. 8), I regard it as phelloderm. Its cells look similar in transverse and longitudinal sections. They are frequently rounded, measuring about $90\ \mu$ across, with short projecting arms, but are sometimes larger and more or less rectangular, measuring about $200 \times 90\ \mu$. These larger cells are often constricted at the middle and thus shaped like a peanut fruit. The phelloderm cells tend to be arranged in axial rows. In addition, the phelloderm has some large cells, up to $150\ \mu$ across, with brown contents (Pl. 33, fig. 1). Plate 35, fig. 5 shows these cells in longitudinal section, one measuring over 8 mm. with no traces of cross walls. In radial sections the aerenchymatous phelloderm can be readily differentiated from the aerenchymatous phloem by the presence of these cells and by the absence of phloem fibres and phloem rays (Pl. 37, fig. 7).

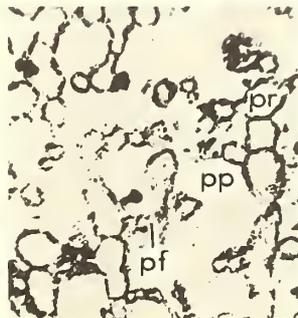
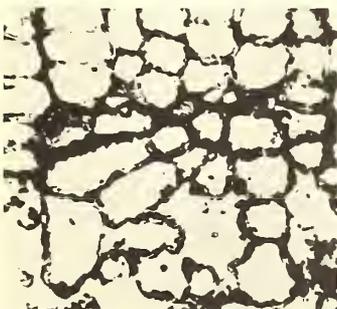
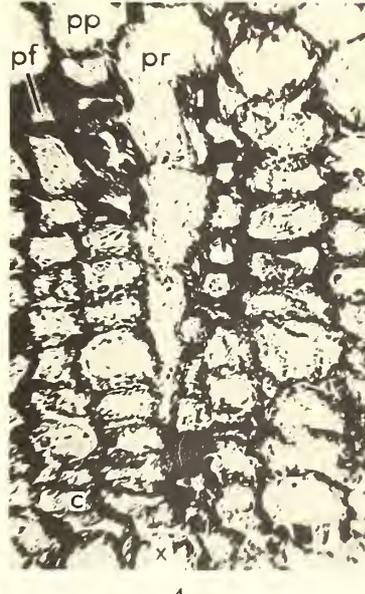
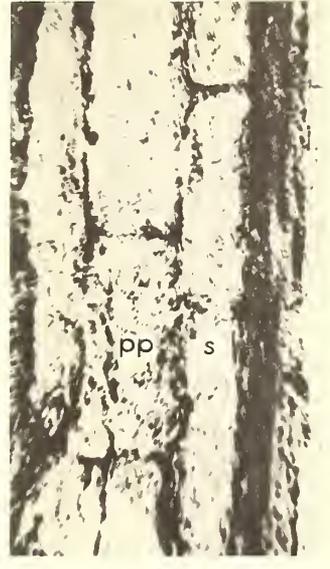
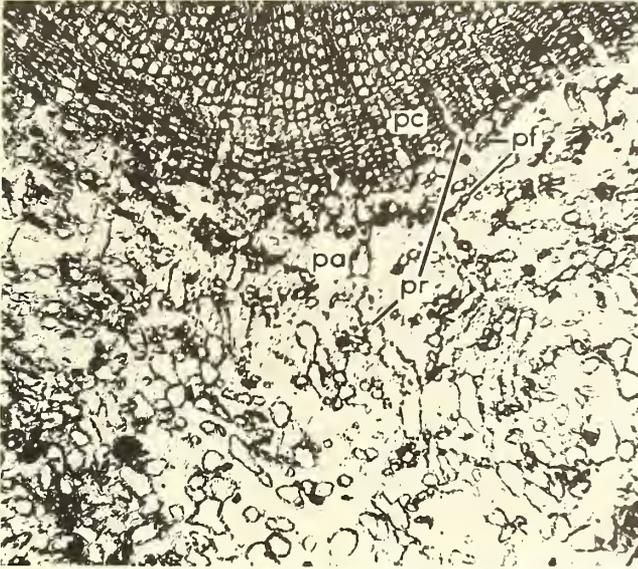
The aerenchymatous phloem and phelloderm described above are typical of mature roots, but there are some variations in structure. Plate 34, fig. 7 shows the same root illustrated in Plate 33, fig. 1, but is a transverse section close to the point of attachment to a larger root. In this region the root lies between two other roots, its more or less triangular shape suggesting that growth was restricted. No aerenchyma is present. Instead, the phloem is compact and up to $500\ \mu$ thick, over twice as thick as the compact phloem in the region of the same specimen shown in Plate 33, fig. 1, and the phelloderm is a fairly compact tissue with only small intercellular spaces. Both these facts suggest that restriction of growth by the adjacent roots inhibited normal distension of phloem and phelloderm to form aerenchyma. Further variation in the structure of tissues between

EXPLANATION OF PLATE 35

Figs. 1-8. *Amyelon iowense* (Pierce and Hall) comb. nov. 1, Root showing secondary xylem, cambium, and phloem with a transition from compact phloem to aerenchymatous phloem. KU 1021 F, 2; slide 338: T.S. 2, Compact phloem. Short rectangular cells are interpreted as phloem parenchyma and narrower, longer cells with transverse end walls may be sieve cells. At the right, a dark phloem fibre is visible. KU 1021 G, 17; slide 431, $\times 400$: R.S. 3, Cambium and its immediate derivatives: phloem above, xylem below. KU 1021 E, 2; slide 318, $\times 350$: T.S. 4, The outer edge of the secondary xylem, the cambium, and its immediate derivatives. KU 1021 E, 2; slide 318, $\times 350$: T.S. 5, Aerenchymatous phelloderm containing long wide cells with dark contents, and aerenchymatous phloem with much thinner phloem fibres. KU 1021 H, 4; slide 503, $\times 10$: T.L.S. 6, Poorly preserved specimen with only secondary xylem and phloem fibres preserved. KU 1021 j, 83; slide 640, $\times 20$: T.S. 7, Aerenchymatous phloem showing the stretched and meandering phloem rays, phloem fibres, and phloem parenchyma. KU 1021 E, 2; slide 318, $\times 50$: T.S. 8, Aerenchymatous phelloderm, phellogen, and phellem. KU 1021 f, 3; slide 409, $\times 100$: T.S.

EXPLANATION OF PLATE 36

Figs. 1-5. *Amyelon iowense* (Pierce and Hall) comb. nov. 1, Outer part of the secondary xylem, cambium, compact phloem, and the inner part of the aerenchymatous phloem. KU 1021 G, 16; slide 430, $\times 100$: R.S. 2, Aerenchymatous phloem with radially stretched phloem rays, phloem fibres, and a vertical chain of parenchyma. KU 1021 G, 15; slide 429, $\times 50$: R.S. 3, Rootlet showing diarch primary xylem surrounded by brown debris. The outer cortex has large colourless cells. KU 1021 F, 45; slide 351, $\times 100$: T.S. 4, Root in which the only aerenchyma developed is phelloderm. Phloem is a compact tissue which has been torn away from the internal tissues. Note the growth-ring in the secondary xylem. IU 1755 B, 2, $\times 10$: T.S. 5, Root showing ten clusters of lateral rootlets. KU 1115 C, 12; slide 744, $\times 2$: oblique longitudinal section.



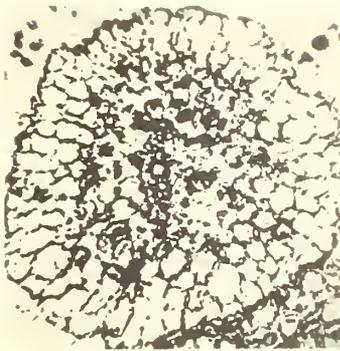
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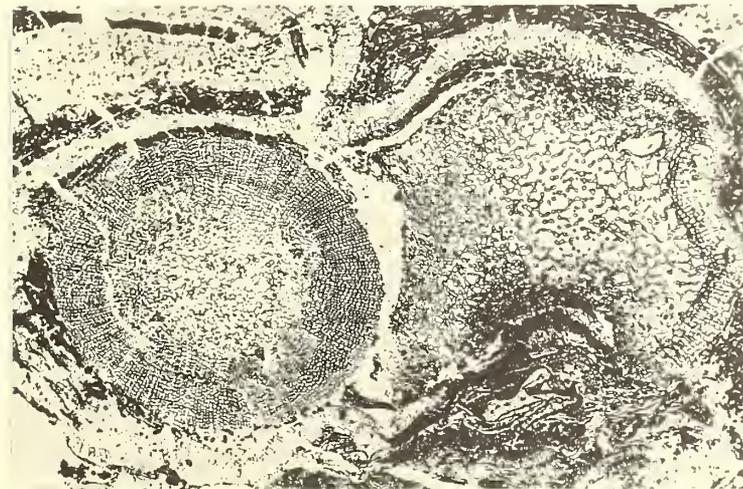
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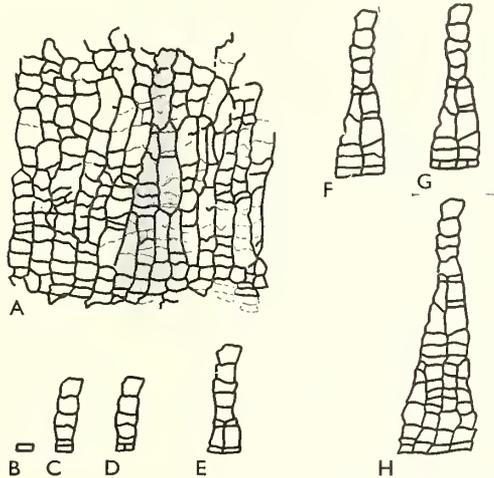
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xylem and phellem is shown by the specimen in Plate 36, fig. 4. In this case, the aerenchyma is exclusively phellogen and the phloem is a compact zone of tissue about $250\ \mu$ across.

Phellem. Smaller mature roots are surrounded by phellem composed of thin-walled cells, rectangular in transverse section, measuring $150\ \mu$ tangentially $\times 80\ \mu$ radially. These cells are arranged in simple radial rows, reflecting their derivation from the phellogen. In larger roots the phellem is more extensive, attaining a thickness of up to 3 mm., with parts exhibiting cell arrangements reflecting a growth pattern where phellogen cells divided radially and increased the diameter of the root (text-fig. 3A, stippled area).

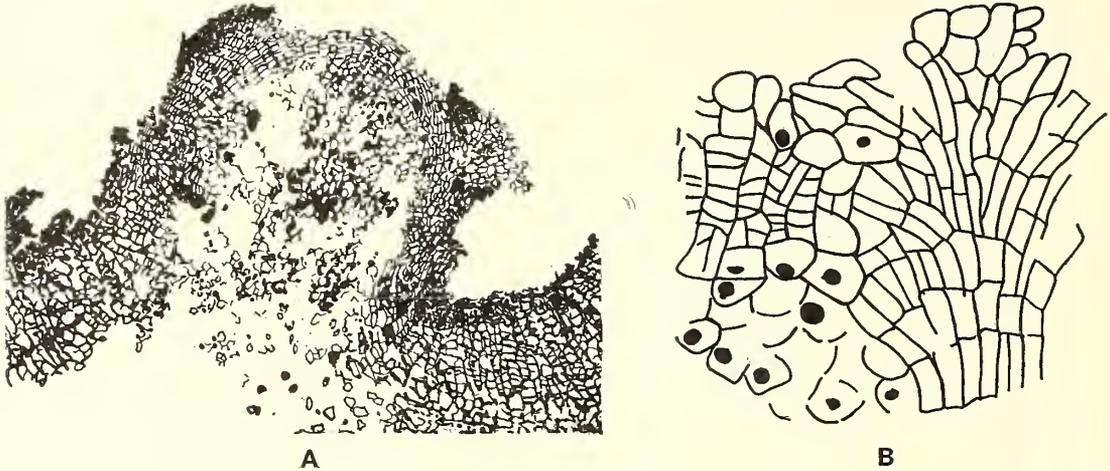


TEXT-FIG. 3. Phellem of a mature root and hypothetical stages in its development. A, Phellem of a mature root. Poorly preserved thin cell walls indicated by broken lines, all other cell walls indicated by bold lines. B-H. Hypothetical stages in the development of the stippled area. H is comparable to the stippled area in A. A is based on KU 1021 E, 2; slide 318, $\times 30$.

Theoretical stages in this growth process are shown in text-fig. 3B-H. At first (text-fig. 3B) a single phellogen cell cut off a single row of phellem cells (text-fig. 3C). Then there was a radial division in the phellogen cell (text-fig. 3D), tangential enlargement of each daughter phellogen cell to the normal size and subsequently two rows of phellem cells were cut off (text-fig. 3E, F). This process continued (text-fig. 3G, H) until the root had a greater circumference. There was evidently little or no compensating growth of soft tissues inside the phellogen, and the expansion of the phellogen led to the development of radially acting tension, causing the formation of aerenchymatous phloem and phellogen. Radial subdivision did not occur in every phellogen cell. If it had done so the phellem would have rapidly developed large cracks and would have been of little protective value. Even so, in older specimens quite large cracks sometimes developed in the phellem, but by this time it was about to be sloughed and a new phellem was usually being differentiated.

Lenticels. Many transverse sections show that the phellem has an irregular outline, with distinct convolutions (Pl. 34, fig. 7; Pl. 37, fig. 1; text-fig. 4A) which bear resemblances

to the lenticels of some modern plants. These lenticel-like convolutions occur in pairs, and clusters of lateral rootlets arise between them (text-fig. 5B). In transverse section the convolutions measure as much as 3 mm. across the base, project approximately 3.5 mm. They are 2–3 mm. long. In the distal part of the convolution the phellem is noticeably thinner than elsewhere. Transition between numbers of rows of cells is abrupt and the additional rows are reflexed as prominent lips, often with several such lips on each



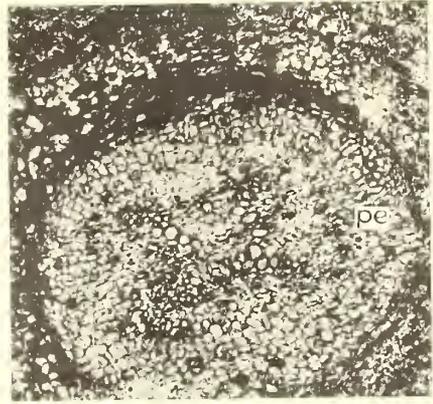
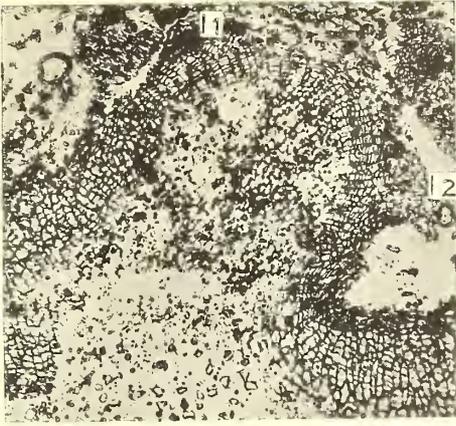
TEXT-FIG. 4. Lenticel. A, See Plate 37, fig. 1, $\times 20$. B, Transverse section through part of a lenticel. There is a burst closing layer to the right. Above and to the right of the intact closing layer there are some large cells, some containing gum (indicated in solid black). KU 1021 E, 60; slide 327, $\times 100$.

convolution. Analogy can be made between the thin region of phellem in these convolutions and the closing layer in modern lenticels, and the lips can be compared to burst closing layers.

Phelloderm inside the lenticels is composed of cells rounded in transverse section and measuring about 75μ across, some with brown contents. These cells have occasional, very small intercellular spaces between them, and there is a gradual transition from this kind of phelloderm to the aerenchymatous phelloderm described previously. Occasionally there are phellem convolutions where the distal part is no thinner than the rest of

EXPLANATION OF PLATE 37

Figs. 1–7. *Amyelon iowense* (Pierce and Hall) comb. nov. 1, Lenticel showing a thin area at the top of the convolution of phellem. Several lip-like flaps comparable to broken closing layers are visible. l_1 was probably once joined to l_2 . KU 1044 B; slide 736, $\times 20$: T.S. 2, Small tetrarch root. KU 1021 j, 165; slide 646, $\times 25$: T.S. 3, Phellem and an aerenchymatous part of the phelloderm. Slide 1109, Henry Shaw School of Botany, St. Louis, $\times 50$: T.S. 4, Xylem rays showing the cross field pitting. KU 1021 G, 14; slide 428, $\times 500$: R.S. 5, Uniseriate pits on the tangential wall of a tracheid. There are xylem rays to the right and left of this tracheid. KU 1021 G, 3; slide 417, $\times 400$. 6, Root with several immature lenticels. IU 1877 B, 2, $\times 6$: T.S. 7, Xylem, compact phloem, aerenchymatous phloem with radially elongated phloem rays and phloem fibres, aerenchymatous phelloderm with vertical chains of peanut-shaped cells and large cells with dark contents, and phellem. KU 1021 G, 6; slide 420, $\times 15$: R.S.



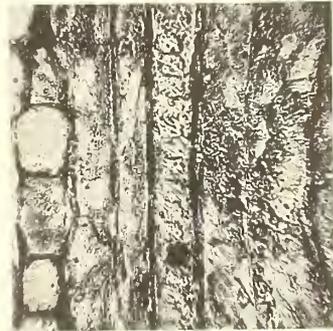
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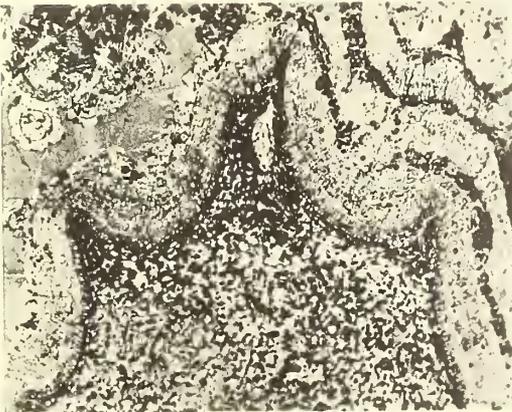
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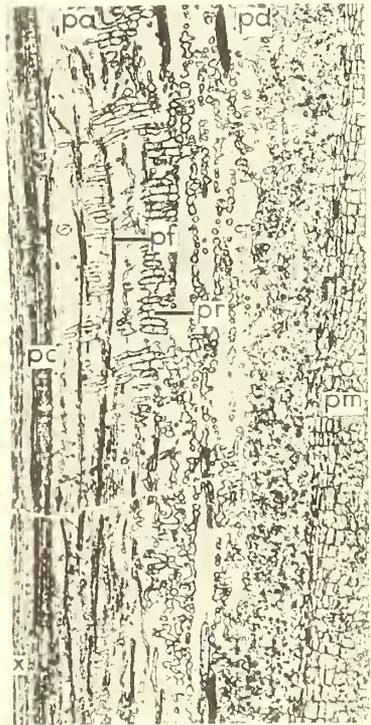
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the phellem and there are no prominent lip-like flaps (Pl. 37, fig. 6). These may be immature lenticels.

ROOTLETS

Clusters of up to twenty rootlets are borne on conspicuous phellem-covered protuberances of the large roots, and each cluster of rootlets is associated with two flanking lenticels (text-figs. 5B, L, O; 6A, F, G). Each protuberance protrudes about 3 mm. from the main part of the root, measures 3 mm. tangentially, and just over 3 mm. axially. The bulk of the protuberance is compact phelloderm, composed of rounded cells measuring $85\ \mu$, some with dark contents. Externally the protuberance is covered by phellem.

In most specimens the clusters of lateral rootlets show no regular taxy, but one specimen (Pl. 36, fig. 5) is a notable exception. Here the clusters of rootlets are much more abundant than usual (there are ten of them on a piece of root 10 cm. long) and they are all borne along one side of the root. Perhaps this root ran over the surface of the soil, with the clusters of rootlets borne on its lower surface.

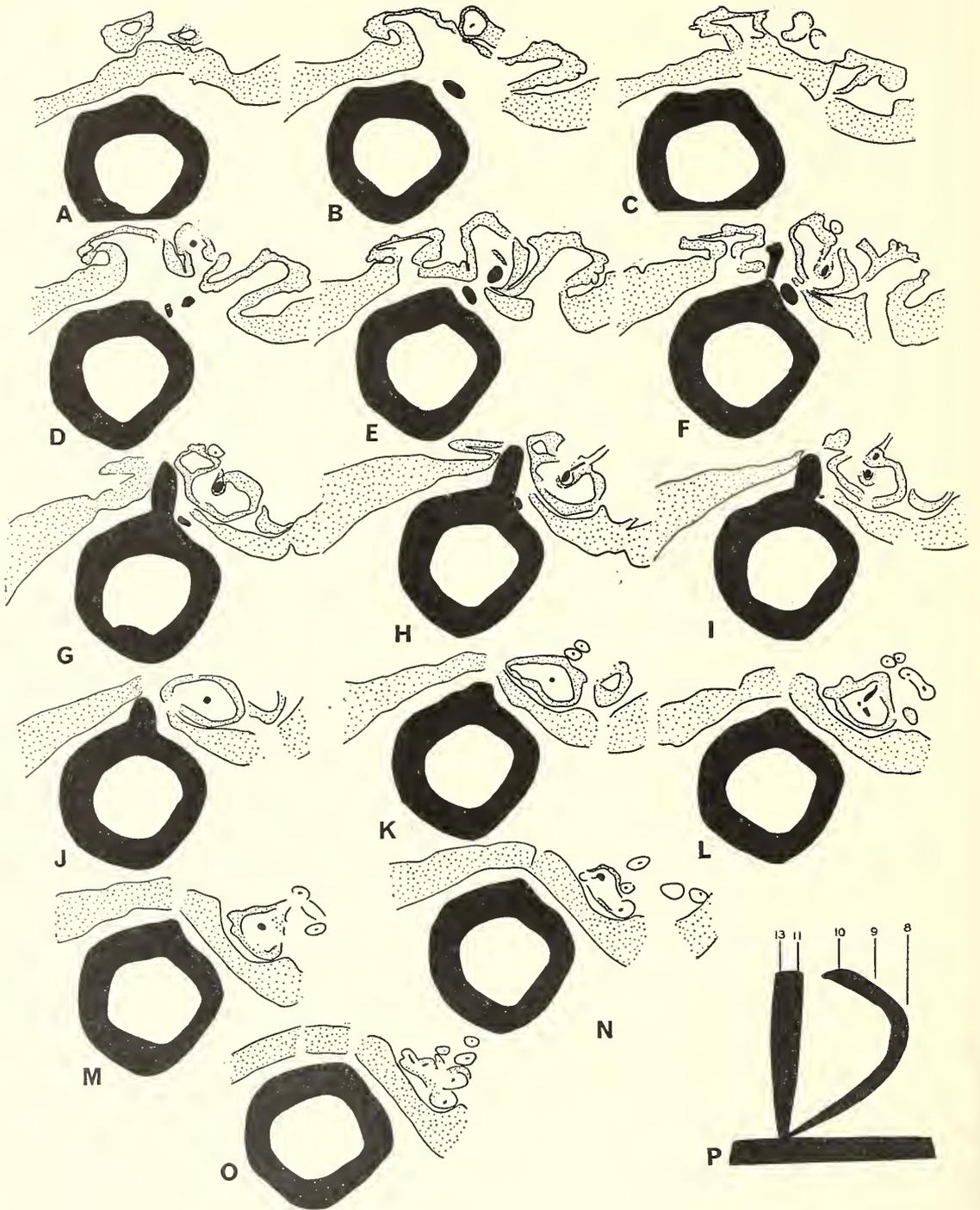
Xylem. Plate 36, fig. 3 is a transverse section of a rootlet approximately $500\ \mu$ in diameter. There is a diarch primary xylem plate composed of only a few tracheids. The central tracheid, which I interpret as a metaxylem tracheid, is largest and measures $22\ \mu$ across. Two adjacent tracheids, which may be metaxylem or protoxylem, are only $14\ \mu$ across, while at the ends of the xylem plate some smaller, but very poorly preserved tracheids must certainly be interpreted as protoxylem.

In longitudinal sections of rootlets the only xylem elements recognized were protoxylem tracheids with spiral and annular thickenings, but none is preserved well enough to be illustrated. The narrowness of the primary xylem plate in the rootlets, combined with the frequent imperfect preservation of the cells, makes it difficult to study the tracheids adequately.

Phloem and inner cortex. Two regions can be recognized in the tissues surrounding the diarch plate. An inner region, $140\ \mu$ thick, representing the phloem and the inner part of the cortex, is poorly preserved and contains much brown debris. In some rootlets preservation is favourable enough to determine that cells of the inner cortex are about $32\ \mu$ across, but no details of phloem cells can be distinguished.

Outer cortex. Surrounding the inner cortex there is a region of thin-walled cortical cells, up to $150\ \mu$ thick, composing the rest of the root. These cortical cells are rounded to hexagonal in transverse section and have no dark contents. They measure about $45\ \mu$ across and are at least $100\ \mu$ long. There is some suggestion that the peripheral walls of the outermost layer of cells are slightly thickened, as in an epidermis, but no cell is piliferous.

Endodermis. No attached rootlet shows the endodermis clearly, but in a radial section of a detached rootlet a row of cells with greatly thickened walls can be seen close to the xylem (Pl. 33, fig. 4). These cells, which measure $46\ \mu$ radially and $100\text{--}160\ \mu$ axially, probably represent a thick-walled endodermis. Although detached rootlets lack distinctive characters and are easy to misassign, I am confident that this rootlet is correctly



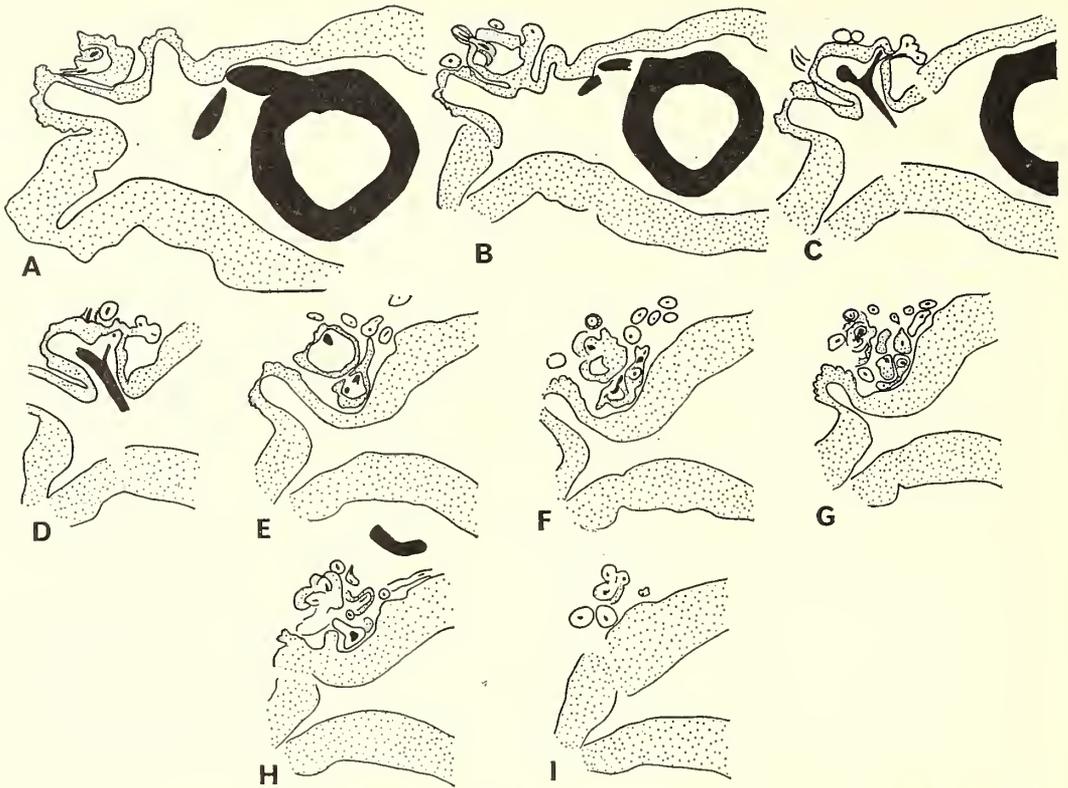
referred to *A. iowense*, since similar cells were seen in some attached rootlets, but were too poorly preserved to photograph.

Periderm. The rootlet in Plate 37, fig. 2, and Plate 33, fig. 3 calls for special comment since although a deep-seated periderm has arisen, the cortex has not been sloughed. Part of the outer cortex is still present, but not the epidermal layer. Part of the inner cortex is moderately well preserved and many of its cells have brown contents (Pl. 33, fig. 3). It is impossible to verify the presence of an endodermis, because the cells immediately outside the periderm have decayed. Periderm, about $200\ \mu$ thick, is composed mainly of radial rows of cells measuring $35\text{--}40\ \mu$ tangentially by $12\text{--}23\ \mu$ radially, but some cells are nearly square and measure just over $40\ \mu$ across. Periderm cells are slightly thicker-walled than cortical cells and thinner-walled than xylem tracheids. The periderm of this rootlet was not seen in longitudinal sections, but in some peels it was cut obliquely. These oblique sections help verify the identification of the tissue, because they show no evidence of pitting on any of its cell walls. On the other hand, tracheids in the same oblique sections have clear indications of pitting on their walls. Within the periderm there is a tetrarch protostele with exarch primary xylem poles. Although the position of the phloem is indicated in Plate 33, fig. 3, no structural details can be determined.

Possession of a deep-seated periderm suggests that this specimen will eventually develop into a large root bounded by periderm, comparable to those already described. Another indication that this rootlet will develop into a large root comes from the number of protoxylem poles. It is uncommon to find rootlets with more than two protoxylem poles, while most large roots are triarch or tetrarch. A similar situation exists in *A. radicans*, where Osborn (1909) suggested that small triarch and tetrarch specimens are immature primary roots.

TEXT-FIG. 5. Representative transverse serial sections through two lenticels and a basal protuberance bearing a cluster of lateral rootlets. All $\times 3$. Xylem, black; phellem, stippled.

A, Stele, phellem, part of a lenticel and part of the protuberance. KU 1021 I, 73; slide 546. B, As in A, but with part of a second lenticel. KU 1021 I, 104; slide 570. C, As in B, but the protuberance has vascular tissue and part of the trace supplying it is seen in oblique longitudinal section. KU 1021 I, 115; slide 571. D, Two parts of a curved trace supplying the protuberance are present (cf. text-fig. 5P). KU 1021 I, 132; slide 573. E, Parts of the curved trace supplying the protuberance are present (cf. text-fig. 5P). KU 1021 I, 162; slide 579. F, Vascular supply within protuberance partly enclosed by a few layers of phellem cells continuous with those covering the protuberance. The trace supplying the protuberance is near the xylem of the main root and another well developed trace is present. KU 1021 I, 172; slide 580. G, Vascular supply of protuberance is near the base of the large trace. The protuberance is subdivided and rootlets lie close to it. KU 1021 I, 186; slide 580. H, As in G, but showing the departure of a rootlet devoid of phellem. KU 1021 I, 189; slide 583. I, As in H, but the section is from a region past the subdivision of the protuberance and nearly past the lenticels. Only part of one lenticel is seen to the right of the protuberance. KU 1021 I, 199; slide 585. J, Only the large trace is visible. The vascular supply in the protuberance is devoid of phellem. Part of a lenticel is shown to the right. KU 1021 I, 211; slide 587. K, As in J, but with two rootlets present. KU 1021 I, 222; slide 588. L, Note the rootlets derived from the protuberance and the branching vascular tissue within the protuberance. KU 1021 I, 244; slide 590. M-O, Further branching of the protuberance into rootlets. M, KU 1021 I, 252; slide 591. N, KU 1021 I, 267; slide 594. O, KU 1021 I, 275; slide 595. P, Theoretical longitudinal section of the traces shown in text-fig. 5C-J.



TEXT-FIG. 6. Representative transverse serial sections through a cluster of lateral rootlets, their basal protuberance and its two associated lenticels. Xylem, black; phellem, stippled. All $\times 3$.

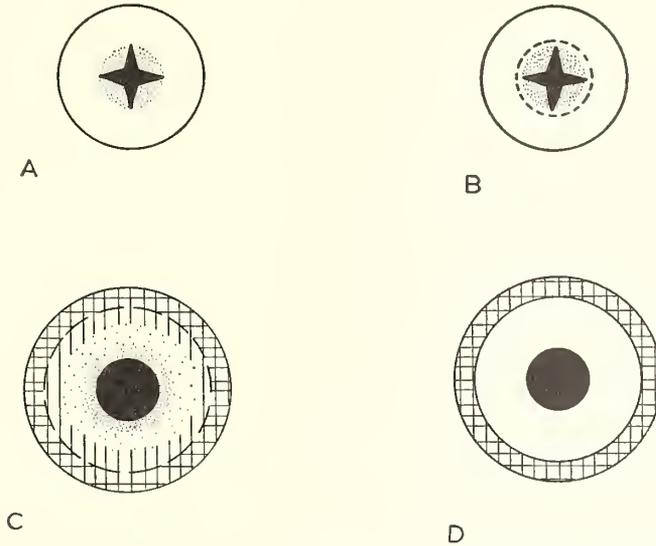
A, Note the protuberance, with its vascular supply, between two lenticels. Two parts of a large trace supplying the protuberance are also visible. KU 1021 I, 3; slide 534. B, As in A, but with the protuberance giving rise to several rootlets. KU 1021 I, 44; slide 539. C, Vascular supply entering the protuberance, which has given rise to several rootlets. KU 1021 I, 73; slide 546. D, As in C. KU 1021 I, 85; slide 557. E-I, Sections showing rootlets departing from the protuberance, ultimately passing into a region showing few rootlets. E, KU 1021 I, 132; slide 573. F, KU 1021 I, 148; slide 576. G, KU 1021 I, 161; slide 578. H, KU 1021 I, 174; slide 583. I, KU 1021 I, 198; slide 584.

SPECIMENS OF *AMYELON IOWENSE* SHOWING ANOMALOUS STRUCTURE

Two specimens showing anomalous features were studied critically. The features judged to be anomalous are: growth-rings in the xylem, outer part of xylem C-shaped in transverse section and associated with a knob-like protrusion showing tracheids cut obliquely, intraxylary phellem and callus, and, prominent nodular projections from the surface of the root. Most probably these represent wound reactions, but I am unable to interpret them unequivocally. In these circumstances presentation of a detailed record of these features is a tedious and elaborate affair, fit rather for archives (Cridland 1961) than for publication.

DISCUSSION

Pith is a feature unknown in other cordaitan roots. Evidently when roots of *A. iowense* were small they were protostelic, but as they grew the apical meristem increased its size, and its functioning was modified so that a siphonostele was laid down (text-fig. 2). This common type of change in function of apical meristems is called epidogenesis



TEXT-FIG. 7. Stages in the development of secondary tissues in *Amyelon iowense*. A, Young rootlet before the inception of secondary thickening. Xylem indicated by solid black, phloem by stippling, cortex shown in white with no attempt to differentiate inner and outer cortex. B, Later stage, after the inception of a deep-seated phellogen (shown by a broken circle). C, Still later stage, after much activity by the phellogen and the vascular cambium. The xylem (solid black) is surrounded by a cambium and a zone of compact phloem (closely spaced stippling) recently derived from the cambium. Outside the compact phloem there is a zone of aerenchymatous phloem (sparse stippling), aerenchymatous phelloderm (vertical lines), phellogen (broken circle), and phellem (cross hatching). D, Specimen comparable to that shown in diagram C, in which the aerenchymatous phloem and phelloderm have decayed before preservation, leaving a space between phellem and xylem.

(Eggert 1961). Further variation in the structure of *A. iowense* was presumably controlled by changes in function of the apical meristem. In some roots the primary xylem contacts the surrounding secondary xylem cylinder, but in others there are several intervening rows of parenchymatous cells. Different specimens have different numbers of parenchymatous cells, suggesting a gradual transition between these two conditions (text-fig. 2).

The extensive aerenchyma of mature roots and its absence in rootlets is best considered in relation to depth of origin of the phellogen and subsequent development of phellem and phelloderm. Changes in structure, and the manner in which I believe they occurred, are shown in text-fig. 7. Text-fig. 7A shows a rootlet with four primary xylem poles. In text-fig. 7B, a deep-seated phellogen has arisen outside the phloem. I have not

seen a specimen with a single row of deep-seated phellogen cells, but in Plate 37, fig. 2, radial rows of deep-seated periderm can be seen adjacent to the stele. This deep origin agrees with *A. radicans* (Osborn 1909; Scott 1909, p. 531; Halket 1930) and *Radiculites reticulatus* (Lignier 1911). In text-fig. 7c there has been considerable secondary growth. Conspicuous phellem has developed, which delimits the outer surface of the root, all tissues outside being sloughed. Patterns made by the phellem cells when seen in transverse section suggest that as a result of radial divisions of the phellogen, and perhaps of radial subdivisions of phellem cells, the phellem increased the circumference of the root markedly (text-fig. 3). Evidently there was no comparable compensating growth in diameter of soft tissues within the phellem and the tangential expansion of the phellem must have placed a considerable radially acting tension upon them. The outer part of the phloem was distended to form aerenchyma (Pl. 36, figs. 1, 2), while aerenchymatous phellogen was laid down (Pl. 37, fig. 7). This view that tangential expansion of phellogen and consequent increase in diameter of the root has caused the development of aerenchyma is supported by the lack of aerenchyma where part of the root has been prevented from expanding by its proximity to other roots (Pl. 34, fig. 7). In some roots, there is no aerenchymatous phloem, only an aerenchymatous phellogen (Pl. 36, fig. 4). Again this may be a result of submaximal tangential expansion of the phellogen and its derivatives.

If radial sections of specimens at the stage of development shown in text-fig. 7c were not studied critically, it would be easy to misinterpret the aerenchyma as cortex. Text-fig. 7d shows a root at a comparable stage of development, where the aerenchyma has decayed. Many specimens of *A. iowense* are preserved thus, and if there were no knowledge of the aerenchyma from other specimens it would be logical to assume that the space represents a decayed cortex. This hypothesis of a deep-seated phellogen, but with the phellem derived from it eventually delimiting the surface of the root, has implications in the interpretation of other cordaitan roots. It resolves the different views regarding depth of origin of periderm in cordaitan roots. Some were believed to develop periderm superficially (Williamson 1874; Renault 1879, 1896), while in others, a deep-seated phellogen has been demonstrated (Osborn 1909; Scott 1909, p. 531; Lignier 1911; Halket 1930). In my opinion the phellogen of all known cordaitan roots was deep-seated and any apparently different position results from distension of phellogen and/or phloem.

Aerenchymatous phloem is unusual in vascular plants, but is preceded in the pneumatophores of *Laguncularia racemosa* (Schenck 1889b). As in *A. iowense* the phellogen is deep-seated; it expands tangentially by radial cell divisions and the outer part of the phloem is eventually stretched to form aerenchyma. Where elm trees grow in excessively moist conditions, abnormal radial cell elongation in the phloem may also lead to the formation of aerenchymatous phloem (Sorauer 1909, p. 327). Large pieces of bark are shed and whole branches may be decorticated (Graebner 1924, p. 356). As far as I am aware, aerenchymatous phellogen is not recorded in modern plants, but it has a parallel in aerenchymatous phellem (Schenck 1889a; Eames and MacDaniels 1947, pp. 390-1).

In *Psaronius*, near the stem, roots are narrow and occur in a compact zone, joined to each other by parenchymatous tissue. Farther away they are much larger, have conspicuous aerenchyma, and are free. Reed (1949) postulated that the aerenchyma is

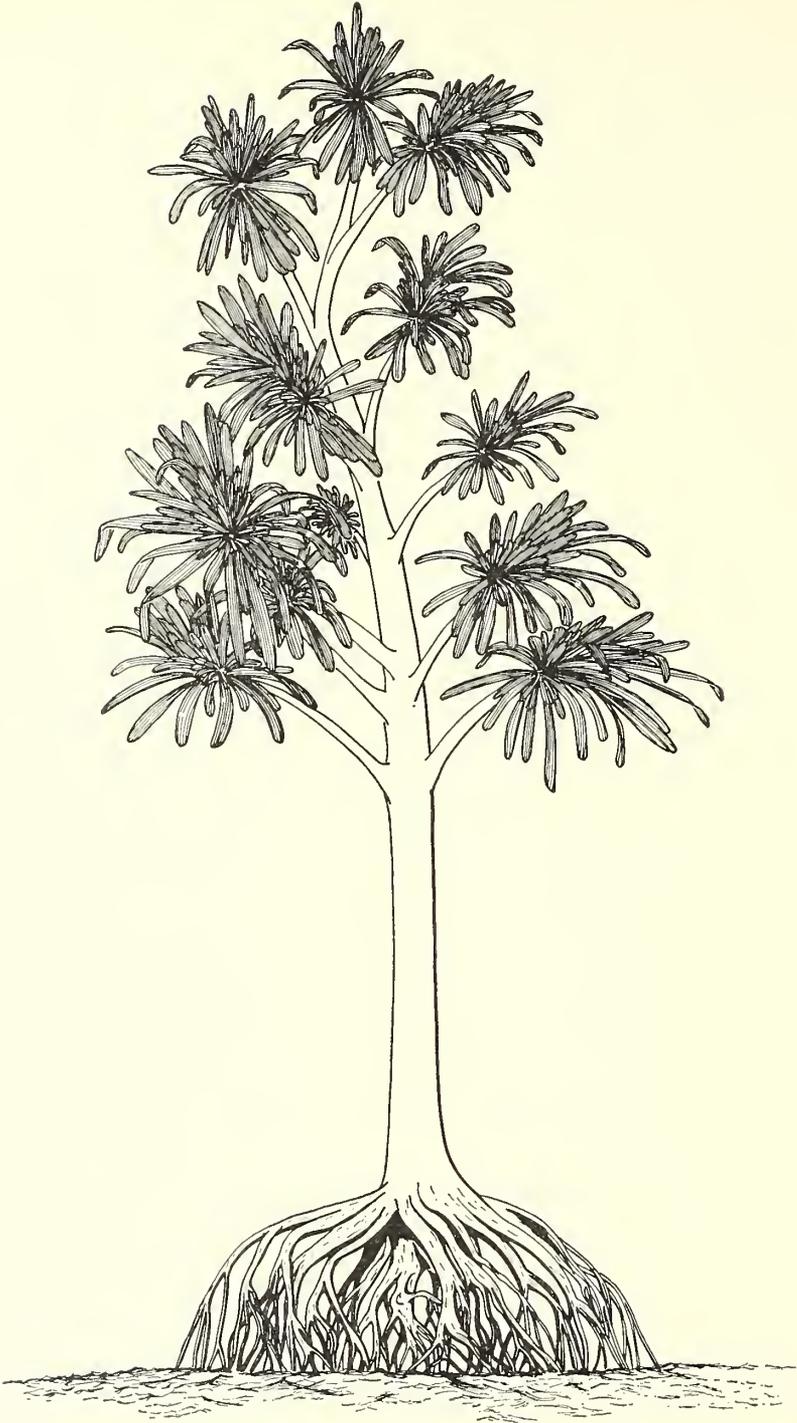
phellogen, which also gave rise to four or five rows of phellem cells (called periderm by Reed, 1949) to the outside. Such interpretation shows substantial agreement with the development of *A. iowense*, but the critical reader should be aware that Morgan (1959) has denied the validity of Reed's interpretations.

Roots of *Medullosa noei* Steidtmann are reported to have aerenchymatous cortex and superficial periderm (Baxter 1949, Stewart 1951). They should be worth re-examining in the light of the developmental stages of *A. iowense*.

Beck's (1958) observations on *Levicaulis* and other fossil lycopods may also be discussed with reference to *A. iowense*. In *Levicaulis* several zones of periderm (called secondary cortex by Beck) develop. Increase in circumference of the stem is apparently effected by intrusive growth of new radial rows of cells. There is no comparable increase in the size of the cortex, which is pulled outwards from the stellar tissues. Wedge-shaped tears occur at its inner margin and a lacuna is formed between cortex and stele. Other fossil lycopods show comparable periderm development and have a lacuna between stele and outer cortex resulting from decay of a fragile parenchyma. In several specimens this delicate tissue (often described as hyphal or trabecular tissue) is composed of radially orientated, stretched cells, with numerous intercellular spaces. According to Beck the trabecular tissue represents an intermediate stage in the formation of the lacuna. Based on the sequence of events in *A. iowense*, the trabecular tissue might easily be the normal condition in these lycopods.

Although there is not absolute agreement between the supposed lenticels of *A. iowense* and the lenticels of a given modern plant, there is a general approximation in structure. Further, the arrangement of the lenticels upon the roots of *A. iowense* has a parallel in modern plants. They occur in pairs and a cluster of lateral rootlets arises between them (text-fig. 5E, L, o). In dicotyledons, lenticels on roots are invariably paired, one on either side of the base of each rootlet (Devaux 1900; Wetmore 1926). Although in *A. iowense* it is a case of clusters of rootlets borne on a protuberance between the lenticels, and in dicotyledons it is a case of a single rootlet, the general arrangement is quite similar.

Possession of lenticels communicating with aerenchyma is particularly significant in connexion with two other features of these roots; the possession of pith and clusters of lateral rootlets. Because they have a pith it is possible that the roots were aerial organs. Pith occurs in some subterranean roots, but is not a common feature. On the other hand, many aerial roots possess pith, particularly those growing in mangrove swamps (Schenck 1889b; Liebau 1914; Bowman 1921; Buscialoni 1921; Ernould 1922; Mullan 1932-3; Ogura 1940). I know of no plants other than mangroves whose roots have lenticels, aerenchyma, pith, and clusters of lateral rootlets occurring together. The mode of branching of the mature roots (text-fig. 1) is more like that seen in stilt roots than in negatively geotropic pneumatophores. I believe the habit of the cordaitean plants in American coal-balls was something like that of the genus *Rhizophora*, a view expressed in the reconstruction (text-fig. 8), where the cordaite shown is a small tree, like specimens of *Rhizophora* growing closest to the sea. The suggested mangrove habit of *A. iowense* has implications in considering the environment in which these fossils grew. Modern mangroves with stilt roots are restricted to tropical or subtropical saline swamps of sheltered marine shores and estuaries, and *A. iowense* may have grown in a similar habitat. If this were so, a clue is provided to the environment of deposition of the



TEXT-FIG. 8. Reconstruction of a cordaitan plant bearing stilt roots. No attempt has been made to include lenticels and clusters of lateral rootlets. 1/28th natural size.

Mineral, the Fleming and the Weir-Pittsburg coals of Kansas, some of the Desmoinesian coals of Iowa and the No. 6 coal of Illinois, which all have coal-balls containing *A. iowense*. It may well be that the debris forming many other coals of the mid-continent U.S.A. and other parts of the world, accumulated under similar conditions.

COMPARISON WITH PREVIOUSLY DESCRIBED CORDAITEAN ROOTS

Premnoxylon iowense

When Pierce and Hall (1953) described *Premnoxylon*, similarities to *Amyelon* were pointed out, but the following differences were noted: (1) *Premnoxylon* possesses a pith. (2) The pith contains scattered tracheids, i.e. it is a mixed pith comparable to that of *Lepidodendron vasculare*. (3) Primary xylem is separated from secondary xylem by several rows of parenchymatous cells. (4) There is a complex method of trace formation.

The significance of the differences between *Premnoxylon* and *Amyelon* is weakened by reference to text-fig. 2. The transverse section illustrated in text-fig. 2D is referable to *Amyelon*, while that shown in text-fig. 2B, with its pith and its primary xylem poles separated from the secondary xylem by several rows of parenchymatous cells, has some of the attributes of *Premnoxylon*. Text-fig. 2C shows an intermediate condition in which the root has a pith, but the primary xylem poles are in contact with the secondary xylem. In the cordaitean roots I studied there is no mixed pith, but some longitudinal sections pass through a few metaxylem cells and their presence gives an illusion of a mixed pith. Lateral traces in the syntypes of *P. iowense* show no essential differences from the lateral traces of other cordaitean roots. I conclude that *P. iowense* and the specimens of *Amyelon* described in this paper should be identified together. *Premnoxylon* is a synonym of *Amyelon*, but since *P. iowense* is not specifically identical with *A. radicans*, I propose the new combination *A. iowense* (Pierce and Hall) Cridland.

Roots of Mesoxylon nauertianum

Andrews (1942) described a protostelic *Amyelon* root attached to a specimen of *Mesoxylon nauertianum*. It is bounded by phellem within which there is phelloderm containing many large cells with dark contents (a tissue Andrews (1942) interpreted as cortex). There is a slightly thinner zone of compact phloem outside the secondary xylem. In a region of this root there is slight development of aerenchymatous tissue, but a root associated with *M. nauertianum* in another coal-ball shows much better aerenchyma (Pl. 37, fig. 3).

Although the root attached to *M. nauertianum* is probably identical with *A. iowense*, Andrews's paper should not be used to modify the nomenclature. The attached root never received a separate name, and it is useful to have a specific name for the detached organs. While it would no doubt avoid the use of an excess and somewhat superfluous name to refer to both attached and detached roots simply as the roots of *M. nauertianum*, this simple and straightforward course is not open. *M. nauertianum* is not clearly differentiated from other species of *Mesoxylon* (Andrews 1942) and unless further study indicates otherwise, this name cannot be applied to any but the type specimen.

Andrews (1942) also described some detached rootlets with abundant root hairs, which he suggested may belong to the genus *Amyelon*. I have re-examined these beautiful

rootlets, and it is my conclusion that they cannot be correctly attributed to *Amyelon*, but instead, a closer comparison can be made between them and the roots of coenopterid ferns. I cite the rootlets of *Psalixochlaena cylindrica* (Holden 1960) as comparable organs, but I do not imply generic identity. The following points should be considered: (1) Andrews's (1942, figs. 8, 9) rootlets and other comparable rootlets (especially Slides 1114–18) have a piliferous layer with extremely long and abundant root hairs, looking like those of *P. cylindrica* (Holden 1960, Pl. 10, fig. 4). In contrast no undoubted cordaitean rootlet has root hairs. (2) Andrews's (1942, figs. 8, 9) specimens have a layer of cells with dark contents beneath the piliferous layer and a similar layer of cells surrounding the stele, corresponding to the exodermis and endodermis of *P. cylindrica*. Although there is an endodermis in other cordaitean rootlets (Lignier 1906; Osborn 1909; Carpentier 1924; Halket 1930; Zimmermann 1933) there is no exodermis. (3) Cortical cells in Andrews's rootlets are larger ($60\ \mu$) in transverse section than those in cordaitean rootlets ($45\ \mu$). (4) Secondary xylem was beginning to form in a rootlet Andrews (1942) illustrated in text-fig. 1*b*, and its tracheids are polygonal in transverse section, as in coenopterid rootlets (Holden 1955). Comparable tracheids in *Amyelon* are more or less square.

Amyelon radicans (Williamson) Williamson

A. radicans occurs exclusively in European coal-balls of Lower Westphalian or equivalent age. This root is well known (Williamson 1872*a*, 1872*b*, 1874; Felix 1886; Osborn 1909; Scott 1909; Thomson 1914; Coulter and Chamberlain 1917; Seward 1917; Leclercq 1928; Koopmans 1928; Halket 1930; Cridland 1962). Rootlets are similar to those of *A. iowense*, and they are borne in similar clusters on conspicuous protuberances ('large globular masses' of Williamson, 1874; 'parenchymatous roots' of Halket, 1930) from the parent root. There are no lenticels beside the protuberances. In addition to the clusters of lateral rootlets, occasional rootlets are attached directly to the main axis (Halket 1930), a feature not observed in *A. iowense*. As in *A. iowense*, in most rootlets of *A. radicans* the walls of the endodermal cells are uniformly dark brown and are thicker than the walls of adjacent cells. Halket (1930) recognized two younger developmental stages, but neither is illustrated, and I have been unable to relocate them on those of her slides I have examined (Cridland 1962).

There are two regions of tissue outside the xylem in large roots of *A. radicans*. Because of the deep-seated phellogen in *A. radicans* (Osborn 1909; Halket 1930) and the developmental stages of *A. iowense*, I believe that the inner region of parenchyma (Williamson's (1874) 'inner bark') is phelloderm, and that the outer region (Williamson's (1874) 'outer bark') is phellem. The compact phelloderm in *A. radicans* presents a striking contrast to the aerenchymatous phelloderm of *A. iowense*. Similarly, in contrast to *A. iowense*, *A. radicans* evidently developed no aerenchymatous phloem. One result of this lack of aerenchyma is that in *A. radicans* the phloem and the phelloderm account for only about one-tenth of the root diameter, much less than in *A. iowense*, where these tissues account for about six-tenths of the root diameter. Unlike *A. iowense*, mature roots of *A. radicans* are always protostelic (Williamson 1874, figs. 46, 56, 57; Scott 1909, fig. 191; Seward 1917, fig. 477; Coulter and Chamberlain 1917, fig. 203; Leclercq 1928, fig. 7; Koopmans 1928, fig. 61). While the protosteley of the roots in Leclercq's (1928, fig. 7) may perhaps be attributed to the proximity of the roots to the point of

branching, this explanation surely cannot be applied to all the specimens cited above. I have searched carefully through several collections of European coal-balls and have not succeeded in finding a siphonostelic specimen of *A. radicans*. It is remotely possible that siphonostele occurs in specimens described by Felix (1886). Several have an empty space at the middle, or at least a break occurs between the central tracheids, but it is not clear whether this space resulted from decay of parenchyma cells or tracheids. These specimens are not illustrated, and it is difficult to be sure how significant the space is, but it is probably inconspicuous.

Excentric growth-rings occur with high frequency in the xylem of *A. radicans*. In contrast, while growth-rings do occur in some specimens of *A. iowense*, they are rare and are usually associated with other anomalous features.

Roots of Cordaites described by Renault (1879, 1896)

In both publications Renault described petrified plants from the Permian at Autun and the Stephanian Assise de St. Etienne near Grand Croix. He did not specify the locality of the unnamed cordaitan roots, but since he stressed the abundance of cordaitan remains in the Assise de St. Etienne, I presume they came from that stratum. Based on a textbook account of similar roots (Renault 1881), Osborn (1909, p. 603) claimed that the roots are from Autun, but I can find nothing to support this assumption in Renault's text.

Detached rootlets were described scantily, but large roots were described in detail. They have an exarch protostele and secondary xylem with hexagonal pitting. Phloem is preserved, and surrounding it there is a layer Renault interpreted as cortex and then a somewhat sinuose and convoluted layer he interpreted as periderm.

In most specimens, the inner part of the tissue Renault called cortex has decayed, but in some it is preserved and proves to be aerenchyma composed of ramose cells (Renault 1896). Unfortunately the aerenchyma is not illustrated.

Renault's roots can be reinterpreted in the light of *A. iowense*. I suggest that no cortical tissue is preserved. Instead, a deep-seated phellogen arose and produced radial rows of phellem towards the outside and less regularly organized phelloderm towards the inside. As a result of the development of periderm and the subsequent increase in root diameter, the cortex was sloughed, and I presume that aerenchyma was formed by distension of phloem and/or phelloderm. Contorted areas of phellem (Renault 1879, Pl. 15, fig. 14), which Renault considered were formed when part of the tissue he called cortex decayed, show a surprising agreement with immature lenticels of *A. iowense*. A fair analogy can be made between the specimen in Renault's (1879) Plate 15, fig. 13 and *A. iowense*, particularly the regions of *A. iowense* close to their attachment to a supraordinate root (Pl. 34, fig. 7), where there is no aerenchyma and the primary xylem is protostelic, but I do not imply that Renault's specimen is close to its attachment to a supraordinate root.

Radiculites reticulatus Lignier

Cordaitan rootlets from the Assise de St. Etienne were described by Lignier (1906, 1911) as *R. reticulatus*. An identical rootlet from the same horizon was described by Zimmermann (1933) and Permian specimens which I identify with *R. reticulatus* were

described by Carpentier (1924). *Radiculites* Zalesky (1937), a later homonym for compressed roots of uncertain affinity, has no relationship to *Radiculites* Lignier (1906).

The relationship of *R. reticulatus* was established by a case of attachment to a larger, definitely cordaitean rootlet (Lignier 1911), which unfortunately is not mature enough for close comparison with Renault's (1879, 1896) roots. A reticulum of thickening material in the cortex of *R. reticulatus* is a striking and unusual feature not known in *Amyelon*. Nor is it known in *Kaloxylon*, lyginopterid roots which Barnard (1962) suggests are difficult to differentiate from *Radiculites*. The network in *R. reticulatus* compares favourably with the lignified cortical network in the roots of many living gymnosperms and dicotyledons (Van Tieghem 1870-1, 1888; Scott and Whitworth 1928; Guttenberg 1940, pp. 121-2, 1941, pp. 20-31; Van Fleet 1948). Halket (1930) suggested that the cortical thickenings are artifacts of preservation, but she did not examine specimens. Had she done so, I am confident she would not have made this suggestion. The network is strikingly clear, and Zimmermann (1933), apparently unaware of the works of Lignier (1906, 1911) and Halket (1930), described and illustrated this feature independently.

In *R. reticulatus* periderm arose within the pericycle and the cortex was ultimately sloughed (Lignier 1911). This deep origin of periderm is consistent with Halket's (1930) observation of phellogen in the pericycle of *A. radicans* and with the deep origin of phellogen in *A. iowense*.

Other Cordaitean roots

Amyelon in a coal-ball from the Desmoinesian of Iowa, was figured by Wilson and Johnston (1940, fig. 6), but no details of its anatomy were described. This figure, which shows only xylem in transverse section, is insufficient for comparison with *A. iowense*.

There is a record of *Amyelon* from the Calhoun Coal of Illinois (Underwood 1934). This report is in an unpublished thesis which I should not consider had not Fischer and Noé (1938) already drawn attention to it. I have re-examined the specimens which Underwood studied and conclude that none can be confidently assigned to *Amyelon*. Those she illustrated in figs. 72-75 are medullosan roots; while the rootlets she illustrated in figs. 76 and 77 are poorly preserved and have no special characters.

There is no basis for comparison of *A. iowense* with other presumed cordaitean roots. Williamson's catalogue name, *A. reticulatum*, refers to *Sphenophyllum* (Barnard 1962). The little known about the specimens of *A. radiatus* (Spencer 1881, 1882) carries no conviction that they are cordaitean roots. Gordon's (1914) Lower Carboniferous record of *Amyelon* is excluded since there are no described or illustrated specimens, while Barnard's (1962) Lower Carboniferous species are excluded because there is no evidence that they are members of the Cordaitaceae. No comparison can be made with the roots attached to *Rhizocordaites* and similar stumps (Grand'Eury 1877, 1890) since their anatomical structure has not been studied. Likewise, no anatomical details are known concerning the South African root-bearing stumps assigned to *Cordaitea hislopi* by Seward (1917, p. 263).

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NEW SPECIMENS OF *TRAQUAIRASPIS* FROM CANADA

by D. L. DINELEY

ABSTRACT. Lower Devonian rocks in British Columbia have yielded fragmentary remains of a number of ostracoderms, amongst which is a new species of *Traquairaspis*. The Knoydart Formation of Nova Scotia has provided new material of *Traquairaspis symondsii* (Lank.), a species hitherto recorded in Britain only. The stratigraphical and palaeogeographical implications of these new fossils are discussed.

THE genus *Traquairaspis* was erected by Kiaer in 1932 on the basis of a single dorsal disk of *Cyathaspis campbelli* Traquair from the 'Cowie Fish-band' at Cowie Harbour, Kincardineshire, Scotland. The fossil, showing the typical ornamentation, was figured (Kiaer 1932, pl. xi) but only the briefest of generic descriptions was possible. The identity of the English *Psammosteus anglicus* Lankester and the subsequently described *Phialaspis* Wills (1935) with *Traquairaspis* did not appear until 1948 (White and Toombs 1948; White 1950). In South Wales and the Welsh Borderland *Traquairaspis* has proved to be of stratigraphical value in marking the upper part of the Downtonian stage (White 1946, 1950, 1961; Ball and Dineley 1952, 1961; Dineley and Gossage 1959). White and Toombs (1948, p. 5) recognized two zones at the top of the stage:

2. *Traquairaspis symondsii* (Lank.)
1. *Traquairaspis pococki* White

The upper zone in the Brown Clee Hill area of Shropshire has been described in some detail by Ball and Dineley (1961, p. 201). In other parts of the Anglo-Welsh area the species *T. symondsii* occurs within the same fairly narrow stratigraphical limits (Dineley MS) and, although the dimensions of the individual plates and even their actual proportions within the carapace may vary considerably, the distinctive ornamentation and other features remain constant. The genus was also reported by Føyn and Heintz (1943) from north-west Vestspitsbergen and Ørvig (1961, p. 523) called attention to specimens referred to *T. plana* (Brotzen) in the Lower Devonian Czortkow Group in Podolia. Gross (1961, p. 76), referring to similar new material from glacial erratics near Berlin as *Traquairaspis* sp., has given a detailed account of the histology of *Traquairaspis* plates.

At the turn of the century H. W. Ami sent to A. S. Woodward a collection of ostracoderm fragments gathered from the Knoydart Formation of Nova Scotia. Amongst them was a specimen referred to *Psammosteus* cf. *P. anglicus* Traquair (Ami 1901, pp. 309, 311-12), this being virtually the only record of a possible *Traquairaspis* in North America to date. A. J. Boucot collected 'several specimens which Dr. Wolfgang Schmidt and Dr. Tor Ørvig identified as an orbital plate with a dentine band resembling *Traquairaspis*' (Boucot 1960, p. 291). The writer has not seen this material. Now two new faunules yielding the material described below have been discovered, and are of great local importance in establishing the age of the formations. They also show that

the geographical range of the genus extends from north-west Europe, Spitsbergen, and Nova Scotia to northern British Columbia. Since the discovery of the British Columbia material, Dr. R. H. Denison has reported (1963) an unusual new ?*Traquairaspis* species in a heterostracan fauna in the Yukon.

SYSTEMATIC DESCRIPTIONS

Order HETEROSTRACI

Family TRAQUAIRASPIDIDAE

Genus TRAQUAIRASPIS Kiaer 1932

Traquairaspis denisoni sp. nov.

Plate 38; text-figs. 1-4

Diagnosis. A *Traquairaspis* of large size with dorsal disk reaching a length of about 10 cm., of generally oval outline and lacking a dorsal spine. External ornamentation similar to that of other species but with tubercles drawn into long fine ridges, continuous and running apparently parallel to the edge of the plate.

Name. After Dr. R. H. Denison, Curator of fossil fishes, Chicago Natural History Museum.

Holotype Internal mould of dorsal disk with parts of plate adhering. National Museum of Canada fossil vertebrate catalogue number 10371.

Locality and horizon. Thirty miles north-west of Muncho Lake, British Columbia (mile 450 on the Alaska Highway); 59° 07' 30" N.: 126° 22' W. This material comes from a horizon yielding many other ostracoderms and which is probably equivalent to a horizon high in the British Downtonian or lower Dittonian (Lower Devonian).

Material. The collection consists of nine large fragments or nearly complete plates of *Traquairaspis* (nos. PF 3683B, PF 3731, PF 3732, PF 3733, PF 3734, PF 3735, and PF 3736 in the collections of fossil fish, Chicago Natural History Museum, and nos. 10371 and 10372 in the fossil fish collections, National Museum of Canada). It was made available to the author by Dr. Denison, having been collected by geologists of the California Standard Company. The rock in which the fossils are preserved is a hard, fine limonitic and slightly calcareous silt, locally preserving the surface details of the fossils. It is extremely indurated and may even have suffered a very low degree of metamorphism. Unfortunately the plate tissue itself is extremely and unusually thin and badly carbonized and has largely flaked away so that the fossils are casts and moulds. The pieces are identified as follows:

One dorsal disk, almost complete internal mould (holotype, N.M.C. no. 10371).

One dorsal disk, almost complete external cast (N.M.C. no. 10372).

Two ? dorsal disks, large pieces of external mould (PF 3731, PF 3732).

Two ventral disks, large pieces of external mould (PF 3733, PF 3734).

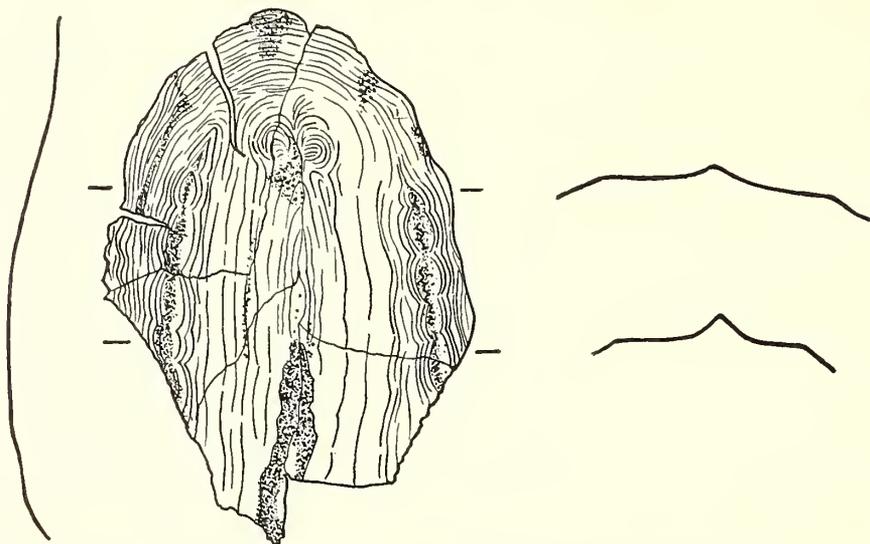
One ventral disk, large part of internal cast (PF 3683B).

One orbital plate, incomplete (PF 3735).

One ? branchial plate, large fragment (PF 3736).

Description. DORSAL DISK (text-figs. 1 and 2; Pl. 38, figs. 1 and 2). The two almost complete specimens (N.M.C. nos. 10371 and 10372) are disks of large dimensions and generally oval outline. Both have been slightly distorted in the rock: the holotype is arched more sharply to one side of the median line than the other. Along the (incomplete) median line the length is almost 9 cm., and the greatest width is 6.5 cm. The other specimen has been slightly torn during flattening by rock pressure (see text-figs. 1 and 2).

Although in each case the hind margin is imperfect, the shape is very reminiscent of *T. pococki*. Only specimen 10371 shows the faintest suggestion of a sinus in the anterior margin. The plates are vaulted, but the crest of the arching is sharply marked by a low ridge which arises some 3 cm. from the front margin of the disk and persists unbroken to the hindmost part of the plate. Although there are signs that the plates have been very slightly distorted in the rock, the maximum height of the disk, which occurs three-quarters of the way back along the median line, is 1.6 cm. in 10371 and 1.0 cm. in 10372. Two lateral carinae are developed in the posterior two-thirds of the disk and extend



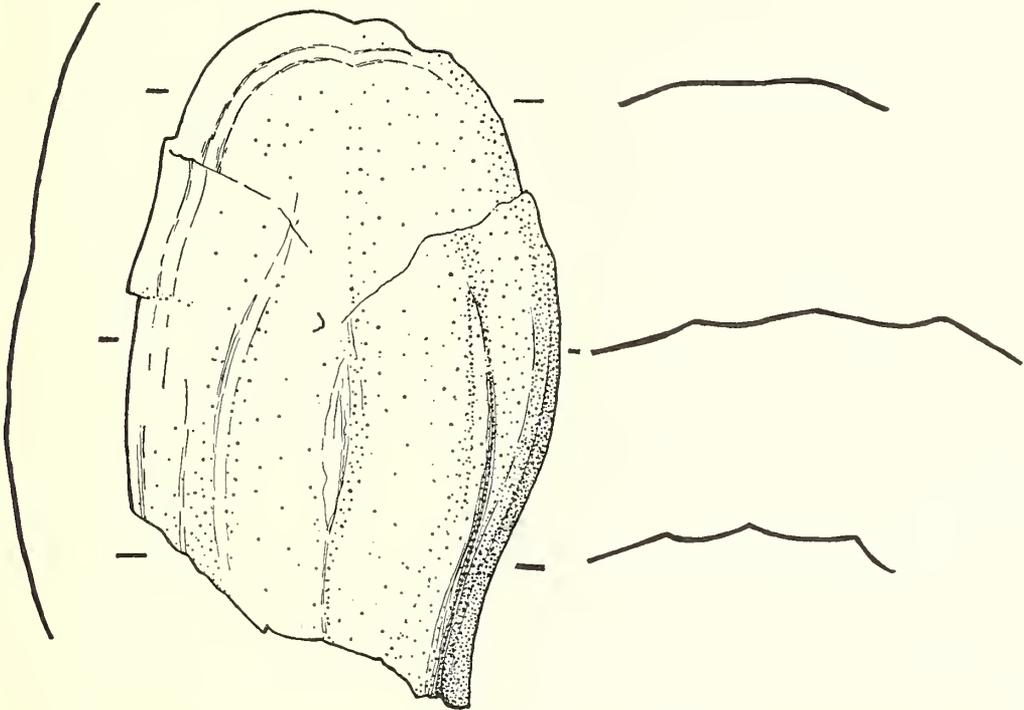
TEXT-FIG. 1. *Traquairaspis denisoni* sp. nov. Dorsal disk (N.M.C. no. 10371) outline and profiles, general pattern of ornamentation shown diagrammatically. $\times 1$.

roughly parallel to the lateral margins. They lie about half-way across each flank of the disk and appear to be produced by a sudden change in the angle of lateral slope from the median line rather than by any local thickening or ridging of the tissue.

There is no sign of a dorsal spine comparable to that known in *T. symondsi*, and here again the features are more like those of the smaller species *T. pococki*. Unfortunately the preservation of this part of both specimens has suffered, but it seems fairly certain that there was little or nothing on the exterior surface to take the place of a dorsal spine, except perhaps a somewhat enlarged single tubercle. The inner surfaces of the disks are smooth, showing none of the imperfect ridges that lie beneath the sensory canals of the disks in the two British species. There is, however, in each specimen a continuous zone of faint 'growth-lines' which extends inwards 1.5 cm. from the margins.

VENTRAL DISK (text-fig. 3; Pl. 38, fig. 3). The ventral disk in *Traquairaspis* possesses a smooth flat central area and a brim ornamented with tubercles. Specimens PF 3683B and PF 3733 show that the most distinctive smooth central portion also occurs in the new species. The largest fragment (PF 3683B) consists of the internal cast of the greater part of the smooth flat central area and most of the front and left portions of the brim.

It is 7 cm. in length and when complete must have been 9 to 10 cm. long. In outline it is indistinguishable from the disk of British species with the central area fairly sharply defined on the inner surface, flat and showing a very slight median indentation of the anterior margin. The brim also is flat and slopes very gently away from the central area. It has a remarkably constant width, reaching about 1.8 cm. near the front left 'corner' and only slightly less over the rest of its extent. Faint growth-lines occupy a zone up to 1 cm. wide along the lateral margin.



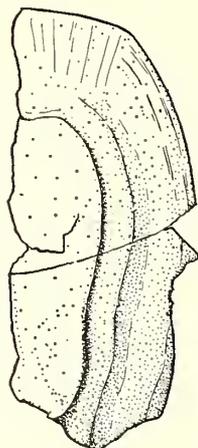
TEXT-FIG. 2. *Traquairaspis denisoni* sp. nov. Dorsal disk (N.M.C. no. 10372) outline and profiles of holotype. $\times 1$.

ORBITAL PLATE (text-fig. 4). The irregular and broken margins of the only specimen of this plate (PF 3735) give little indication of its true shape and size. It is, however, remarkably flat and measures 2 cm. across its greatest dimension. The orbit is round and 0.3 cm. in diameter.

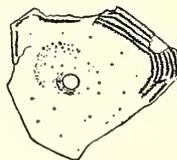
? BRANCHIAL PLATE. A narrow, somewhat bowed fragment, 4.7 cm. long, may represent part of a branchial plate. It is not well preserved and reveals no unusual features.

SENSORY CANAL SYSTEM (text-fig. 1). Only in specimen 10371, the external mould of the dorsal disk, is there any trace of the sensory canal system, and this is restricted to short lengths of canal showing tubuli under the lateral carinae. As in the material described by White (White 1946, p. 218, figs. 3 and 4; p. 229, fig. 39A), the canals seem to be just under the outer surface of the plate rather than in the cellular middle layer.

ORNAMENTATION. The ornamentation of *Traquairaspis denisoni* appears to be very uniform and distinctive. It consists of very fine somewhat crimped ridges or extremely long and thin tubercles running roughly parallel to the margins of the plates. It is rather reminiscent of the ornamentation in *Cyathaspis* and a density of twenty to twenty-two tubercles per centimetre across the disk seems to be fairly constant. The tubercles on the carinae on specimen 10372 are deflected into a series of short curves concentric upon ? single short tubercles spaced about 1 cm. apart along each carina. This is an arrange-



TEXT-FIG. 3



TEXT-FIG. 4

TEXT-FIG. 3. *Traquairaspis denisoni* sp. nov. Ventral disk (C.N.H.M. no. PF 3683B) sketch made from latex pull of original. $\times 1$.

TEXT-FIG. 4. *Traquairaspis denisoni* sp. nov. Orbital plate (C.N.H.M. no. PF 3735). $\times 0.8$.

ment very similar to that of the ornamentation around the enlarged tubercles or bosses seen in *T. pococki* (White 1946, figs. 1 and 2) and *T. symondsii* (White 1946, figs. 52 and 54).

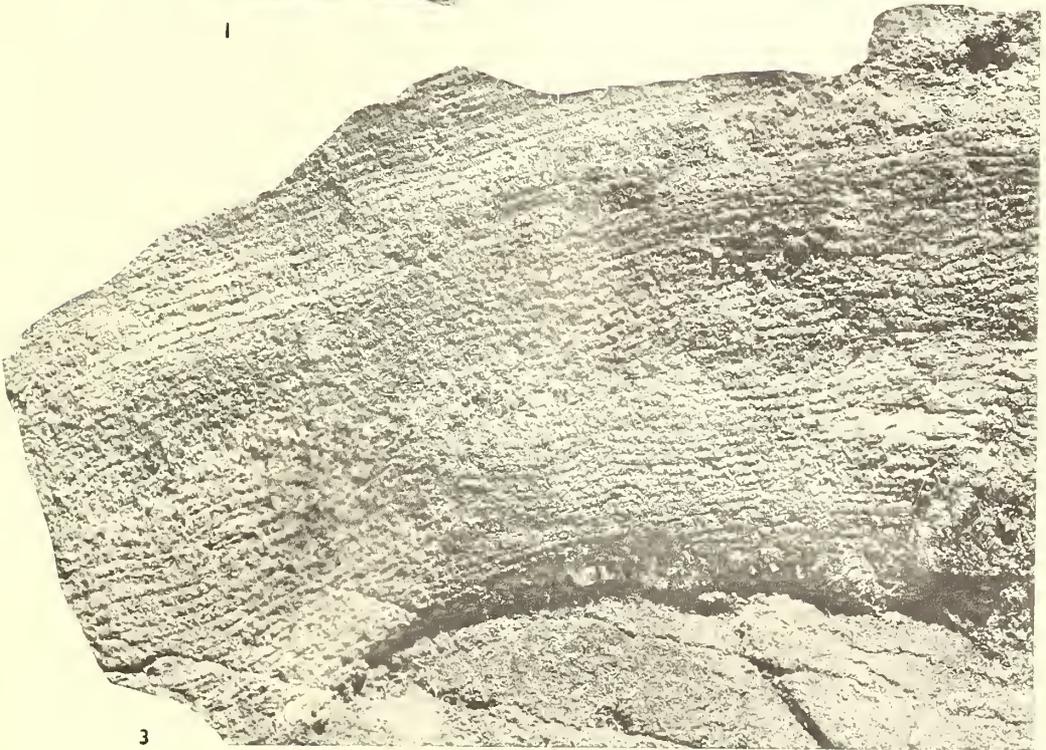
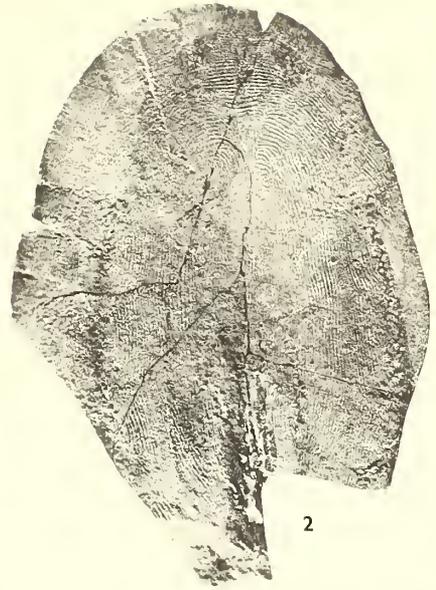
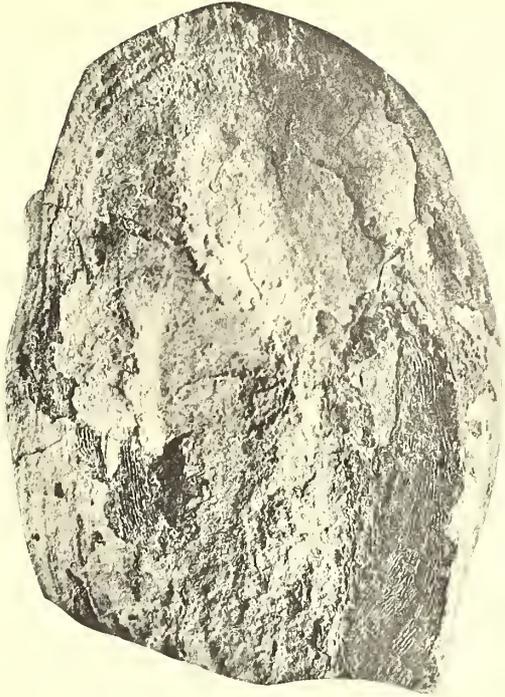
An additional feature of note in specimen 10371 is the double 'whorl' of ridges near the front end of the disk (Pl. 38, fig. 2). Behind this whorl the ornamentation runs directly back parallel to the median line. White (1938, figs. 16 and 17) illustrated a similar occurrence in the dorsal disk of *Pteraspis dixonii* White from South Wales, and Stensiö (1958, p. 278, text-fig. 14C-F) has commented on them (as *Penygaspis dixonii* (White)) and on other similar specimens. It seems probable that the 'whorls' and bosses are remnants of the cyclomorior structure of the disk—the initial units which fused together

EXPLANATION OF PLATE 38

Fig. 1. *Traquairaspis denisoni* sp. nov. Lower Devonian, Muncho Lake area, B.C. Internal mould with attached portions of plate (N.M.C. no. 10372). $\times 1$.

Fig. 2. *Traquairaspis denisoni* sp. nov. Type specimen. Lower Devonian, Muncho Lake area, B.C. Dorsal disk, external mould showing distinctive ornamentation (N.M.C. no. 10371). $\times 1$.

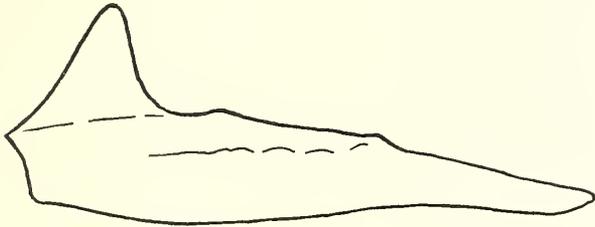
Fig. 3. *Traquairaspis denisoni* sp. nov. Lower Devonian, Muncho Lake area, B.C. External mould of part of ventral disk showing part of the smooth flat central portion and typically ornamented brim (C.N.H.M. no. PF 3733). $\times 1$.



to produce the disk. The ridges or tubercles near the margins indicate the last growth stage when bony material was added peripherally.

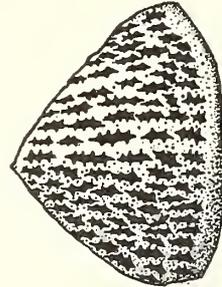
The smooth central area of the ventral disk, like that in *T. symondsii*, is seen in specimen PF 3733 not only to be raised but slightly to overhang the ornamented brim.

Microstructure. The actual plate tissue is not well preserved, being badly carbonized and compressed. Where it has been possible to examine the structure the middle cancellous layer seems to be reduced to about 0.02 cm. in thickness and the complete thickness of the plate excluding tubercles is only 0.06 cm. The tubercles in the holotype are up to about 0.05 cm. high. Post-depositional changes in the rock appear possibly to account



TEXT-FIG. 5

TEXT-FIG. 5. *Traquairaspis symondsii* (Lankester). Dorsal disk (N.M.C. no. 10373) reconstructed profile. $\times 1$.



TEXT-FIG. 6

TEXT-FIG. 6. *Traquairaspis symondsii* (Lankester). ?Flank scale (N.M.C. no. 10374) sketch of external mould. $\times 4$.

for compression of the tissue. In the British specimens of *Traquairaspis*, where the rock matrix has suffered little change, the dorsal disk is 0.05 cm. to 0.1 cm. thick. The proaspids from the western U.S.A., on the other hand, have carapaces which are almost as thin as the British Columbian material.

Remarks. This species of *Traquairaspis* shows a number of similarities to *T. pococki*, notably in the shape of the dorsal disk, the absence of a dorsal spine and the fineness of the ornamentation. It is similar to *T. symondsii* in its overall size. The ornamentation, however, is in detail quite distinctive: the great length and thinness of the individual tubercles and the absence of the stellate tubercles found in *T. pococki* and *T. symondsii* being sufficient to set it apart from these species. The presence of the 'whorled' ornamentation on specimen 10371 may be regarded as a primitive feature on a par with that seen in certain pteraspids. The absence of a dorsal spine perhaps also denotes an early stage of evolutionary development.

Traquairaspis symondsii (Lankester)

Plate 39; text-figs. 5, 6

Diagnosis. White (1946, p. 237) gives the diagnosis for *Phialaspis symondsii*, and, apart from the name, this remains unchanged for *T. symondsii*.

'A *Traquairaspis* of large size. Ventral disc attaining a length of nearly 10 cm.,

generally roughly oval but truncated in front and irregularly scalloped behind. External ornamentation composed of numerous tubercles, each ringed at base by conspicuous groove or shelf where dentine ends. On upper surface of branchio-cornual plate tubercles are short and more or less evenly distributed in longitudinal rows, especially along free margin; those on brim of ventral disc longest in front and along sides of central area, and shortest behind. Radial extensions of central area short.'

'Sensory canal system partly discontinuous; anterior V-shaped canal of ventral disc absent'.

To this may now be added:

Dorsal disk roughly quadrate but with produced median posterior margin at base of dorsal spine. Dorsal spine broadly triangular in side view with large tubercles on flanks aligned at about 45 degrees to front end of spine base.

Locality and horizon. The field immediately south of the main Arisaig-Merigonish road and 250 yards east of McArras Brook, Antigonish Co., N.S., was marked in 1961 by a shallow excavation for road metal. On the western side of this pit an outcrop of hard dark red silty mudstone yielded a large number of small fragments of vertebrate material, including that described here. This bed lies approximately 450 feet above the base of the Knoydart Formation.

Material. The most important piece of the *Traquairaspis* material is the left half of a dorsal disk (National Museum of Canada no. 10373); other fragments are small and of uncertain position in the *Traquairaspis* carapace. Two virtually complete scales (Nat. Mus. of Canada nos. 10374, 10375) are also present. Each of these fossils was exposed in the matrix with the ornamented side downwards and has been developed by etching in hydrochloric acid.

Description. DORSAL DISK (text-fig. 5, Pl. 39). White (1946, p. 229) gave a description of the dorsal disk based on three moderately large fragments (together with a possible fourth) from different localities in the Welsh Borderlands. Subsequent discoveries by White and Toombs in Monmouthshire and by the present author in Shropshire (White 1961, pp. 246-7) have confirmed the description and show the plate to be generally similar in outline to that of *T. pococki*.

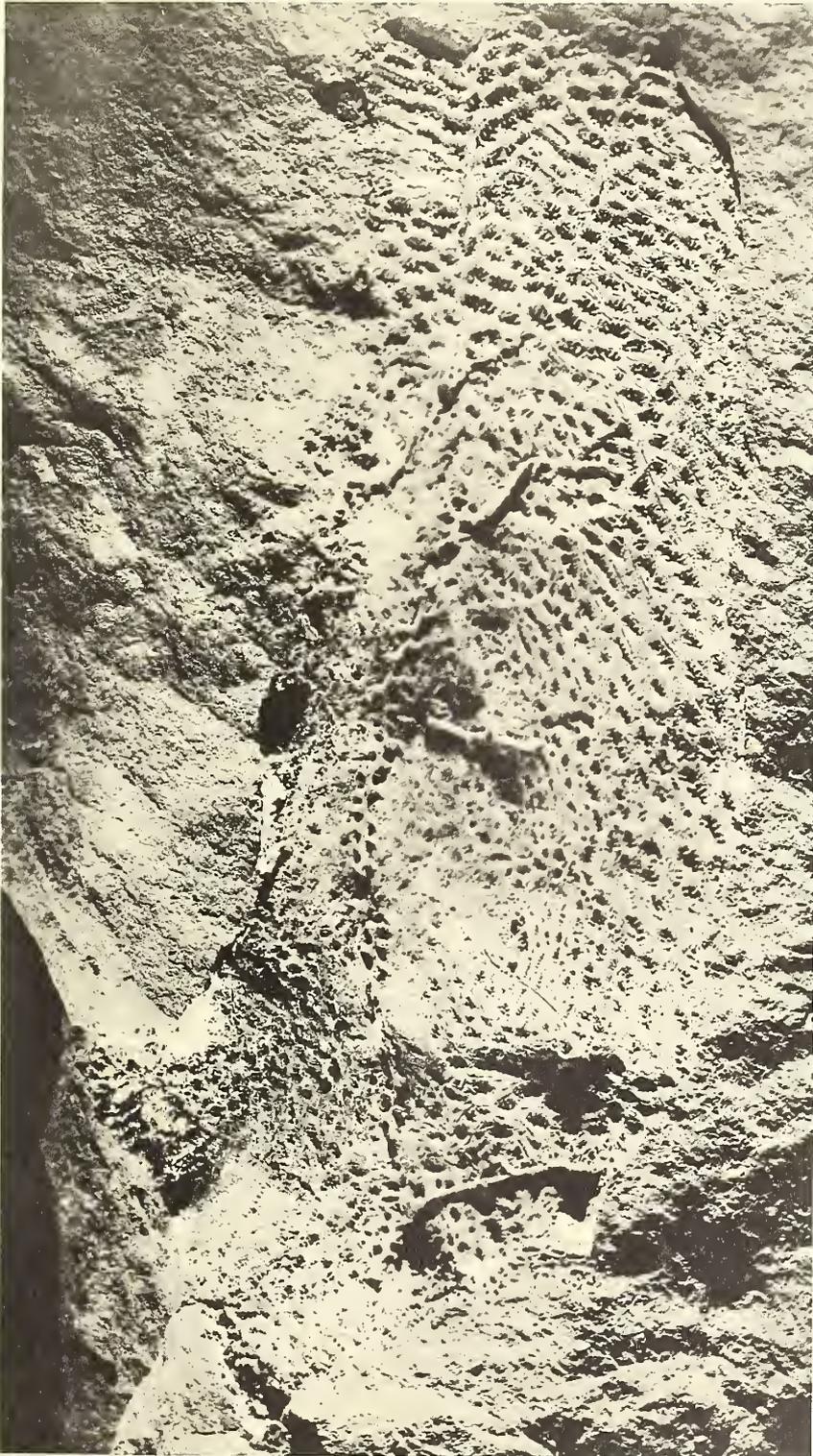
The present specimen measures 7.5 cm. in length and 2.4 cm. across its flank, thus corresponding in general size with the British specimens. In outline the complete plate is sub-rectangular with only gently convex lateral margins, a rather wavy anterior margin and a posterior margin with a blunt median angle. The dorsal spine has a blunt triangular outline with an almost vertical anterior edge. In front of the spine there is evidence of a single small 'boss' of tubercles, but the median row of large tubercles seen in the British specimens is not apparent.

The sensory canals are discontinuous, possibly owing to imperfect preservation, and the characteristic tubuli project alternately to right and left. Parts of the periorbital canal and the inner longitudinal canal remain; the outer one is missing, and fragments of the transverse canals survive.

The ornamentation is typical and the disk bears lines of 'bosses' of tubercles on each side of the median line, in corresponding positions to the lateral carinae in *T. denisoni*.

EXPLANATION OF PLATE 39

Traquairaspis symondsii (Lankester) Knoydart Formation, MacArras Brook, Nova Scotia. Dorsal disk, etched external mould of left half of the plate with adhering haematite-filled portions of the sensory canal system (N.M.C. no. 10373). $\times 2.7$.



DINELEY, *Traquairaspis*

Two similar 'bosses' occur at the lateral extremity of the hind margin. Stensiö (1958, pp. 285-9) has interpreted these 'bosses' as being originally cyclomorials scales fused at an early age in the ontogeny.

SCALES (text-fig. 6). Amongst the many small fragments collected are two reasonably complete and quite different scales. One (Nat. Mus. of Canada no. 10374) is a thick flank scale, roughly triangular in outline and with gently convex margins. The interior surface was badly weathered so that its features could not be described, but since the tissue has been etched away the exterior surface shows an ornament-free margin behind which occur approximately parallel lines of small elongate tubercles.

The other scale (Nat. Mus. of Canada no. 10375) is much less well preserved and etching has further damaged the outline. The front margin is square to the laterals and the hind margin is pointed. The ornamentation is of tubercles arranged parallel to the lateral margins and with a line of very small stellate tubercles near the front edge. In relief the scale is rather pyramidal, rising to a focal tubercle. The position of this scale in the squamation is uncertain, but it probably lay on the flank.

STRATIGRAPHICAL POSITION

In Britain *Traquairaspis* has a narrow stratigraphical range at the top of the Downtonian stage and in the lowest part of the Dittonian (Dineley and Gossage 1959). It is a typical member of the highest Downtonian faunas but is rare in the Dittonian where the pteraspids are the most conspicuous fossils. A similar situation appears to obtain in Spitsbergen and other parts of Europe. Ami (1901) quoted A. S. Woodward on the identification of the ostracoderm fragments found in the Knoydart Formation of Nova Scotia at the end of last century. *Pteraspis* cf. *P. crouchi* and *Psammosteus* cf. *P. anglicus* Traquair are included in the list of identifications, but it is not certain that they came from the same stratum. The synonymy of *Traquairaspis symondsi* (Lank.) includes Traquair's *Psammosteus anglicus* (1898, p. 67, pl. i, figs. 1, 2) and it seems possible that the Knoydart specimen examined by Woodward would today be referred to *Traquairaspis*. The pteraspid material was subsequently allocated to a new species *P. novae-scotiae* by White in 1935 with the remark that it resembled *P. leathensis* White (1935, pp. 444-6). *Pteraspis (Simopteraspis) leathensis* is now regarded as the earliest British pteraspid, its range overlapping that of *Traquairaspis symondsi*. In 1955 Denison described further pteraspid fossils from the Knoydart Formation. He erected the species *P. (S.) whitei* for this material from a horizon estimated by the present writer to be less than 100 feet above the new *T. symondsi* locality. Thus the stratigraphical occurrence of the Knoydart *T. symondsi* and *Pteraspis (Simopteraspis)* seems to duplicate very closely the range of these forms in Britain. With the discovery of a British species of *Traquairaspis* in Nova Scotia the problem of migration and dispersal of the ostracoderm fishes is sharply underlined. White (1958, pp. 219-23) has considered this problem and argues convincingly that localities for *Pteraspis* as widespread as Spitsbergen, Belgium, Britain, and Nova Scotia were accessible to ostracoderms as a result of the animals' ability to live in shallow coastal waters. Each of the mentioned areas of Old Red Sandstone deposition was in direct communication with the sea and was reached by ostracoderms swimming in from the coastal waters. This idea is discussed and supported in a recent article by L. B. Tarlo (1962, pp. 152-3).

Dineley (1962) has made a detailed comparison of the Knoydart Formation with the Downtonian and Dittonian rocks of England and Wales and found a remarkable correlation of lithological, sedimentological and (other) palaeontological characters between them. There is no doubt that the same kind of environment, which produced a peculiar and distinctive combination of lithologies, sedimentary structures, &c., was present in both areas. That these two regions were directly connected by an area of at least not very different sedimentation seems likely. Denison (1963) has described a probable *Traquairaspis*, ? *T. angusta*, from the Yukon. It is a member of a large and interesting fauna suggestive of a very late Silurian age. The stratigraphical position of *T. denisoni* from British Columbia is as yet less certain than that of either the Nova Scotia specimens or the species from the Yukon. The Lower Devonian formations of the Canadian Rocky Mountains frequently appear to rest on a transgressive diachronous base, locally with the development of basal red sandstones or yellowish ferruginous siltstones. The age of these basal members is usually uncertain and although fish remains have been found at a number of points in the Rabbit River area of B.C. not far from Muncho Lake (Gabrielse 1961), they are of little correlative use and the field relations of the strata are obscure. Undoubtedly the fossil vertebrates from the Muncho Lake locality are Lower Devonian and Denison's study of the ostracoderms associated with *Traquairaspis* should help to establish a close correlation with other regions. In the meantime it seems highly probable that *T. denisoni* is of Upper Downtonian or lowermost Dittonian age. This is somewhat older than the Beartooth Butte and Water Canyon formations of Colorado and Wyoming, which are regarded as uppermost Dittonian or Breconian (lower Siegenian).

It is unlikely that a route for the westward dispersal of *Traquairaspis* existed south of the present Canadian Shield area, though it is interesting to find the upper Dittonian *Pteraspis carmani* as far west as Ohio (Denison 1960). Ostracoderms of both Upper Silurian and Lower Devonian age have been found in the Canadian Arctic Islands (Thorsteinsson 1958, pp. 76-78; Thorsteinsson and Tozer 1964), and open-water routes between the north-eastern and the north-western regions of North America could have persisted north of the Canadian Shield (see Thorsteinsson and Tozer 1960). Work in progress on the ostracoderm faunas of the Canadian arctic will be valuable in assessing the extent to which that region was linked with the north-west European ostracoderm province. Ostracoderm migration and movement across this part of the western arctic may have been a frequent if not continuous activity.

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BRACHIAL PLATE STRUCTURE IN THE BRACHIOPOD FAMILY PENTAMERIDAE

by THOMAS W. AMSDEN

ABSTRACT. The pentameracean family Pentameridae is characterized by long, rod-like or blade-like brachial processes, buttressed at their posterior end by high plates extending forward far enough to enclose the brachial muscle field. Variations in the internal structure of the brachial valve, combined with changes in external form of the shell, permit the family to be divided into three subfamilies: Pentamerinae, Gypidulinae, and Clorindinae. The articulating muscles in the pedicle valve were seated in the trough-like spondylium which has remained relatively stable and unchanged throughout the history of the family. The Pentameridae range from the Late Ordovician into the Late Devonian.

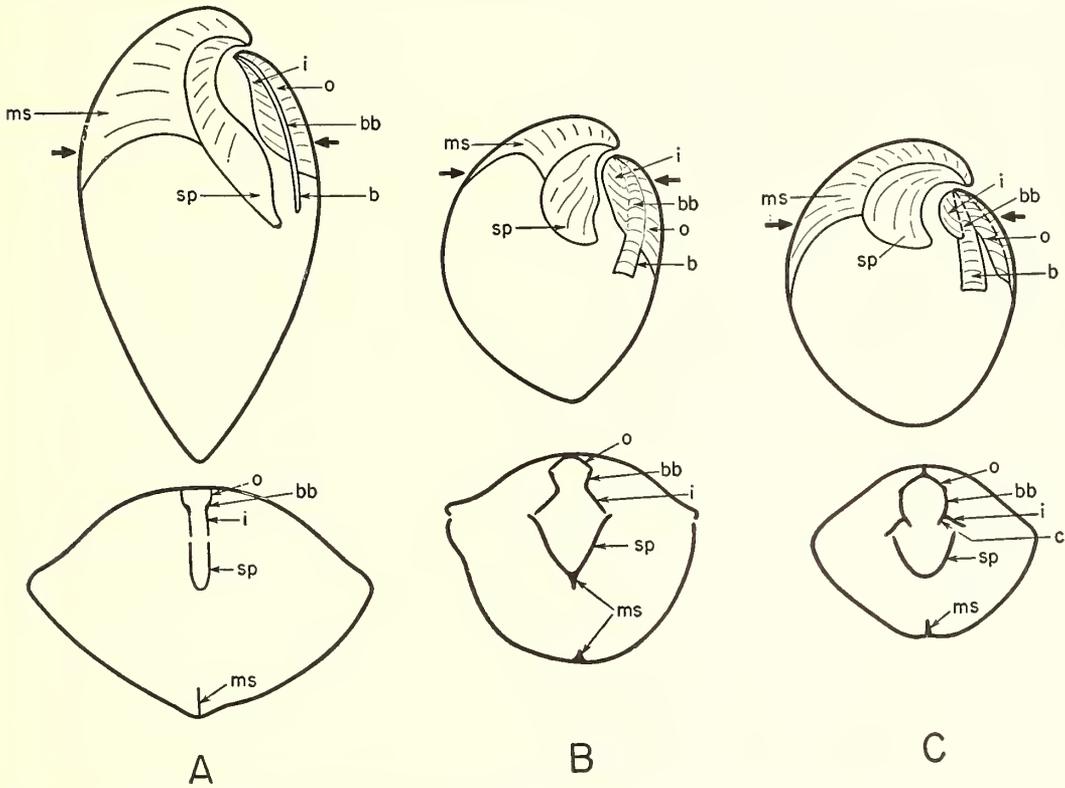
A new genus *Clorindella*, type species *C. areyi*, is proposed for costate Clorindinae with a brachial cruralium. The genus *Pentameroides* Schuchert and Cooper, 1931, is redescribed and the subfamily *Pentameroidinae* Amsden, 1953, is abandoned. *Pentamerella* Hall, 1867, is redescribed on the basis of Hall's type specimens of *P. arata*. Additional information is furnished on the internal structure of *Conchidium munsteri* St. Joseph, 1938, based on topotype material from Zone 5b of Norway.

THE writer has been studying the brachiopod superfamily Pentameracea in preparation for the forthcoming *Treatise on Invertebrate Paleontology*. A number of genera representing the family Pentameridae have been restudied by means of serial sections. Some of the shells sectioned are extremely well preserved and an examination of these thin sections and parlodion peels, as well as some etched material, indicates the need for some revision in previously recognized taxa, and the introduction of a new genus, *Clorindella*.

The terminology herein applied to the plate structure of the brachial valve is essentially the same as that employed by Schuchert and Cooper (1932, pp. 162-5), and by the writer in 1953 (pp. 137-40), and is illustrated by means of labelled photomicrographs (Pls. 40 to 43), and by line drawing (text-fig. 1). The cardinalia of the Pentameracea consists of fairly long, rod-like or blade-like *brachial processes* supported at their posterior end on plates of various lengths. This apparatus attains its strongest development in the Pentameridae where its basic structure may be referred to three sets of plates: *outer plates*, *brachial processes*, and *inner plates*. The outer plates rest directly on the floor of the valve and may be parallel and discrete, or they may unite to produce a cruralium. The inner plates are subparallel at their forward ends, but towards the posterior they curve outward to meet the lateral walls of the valve. The sockets are excavated out of the posterolateral parts of the inner plates (Pl. 40, fig. 6), and the entire apparatus thus served to buttress the articulating mechanism and to strengthen the lophophore supports.

The morphology of the pedicle valve is relatively stable and is treated only briefly in this report. All pentameraceans have a well-developed spondylium, which served as the seat of attachment for the principal muscles. The spondylium is generally supported on a median septum for at least a part of its length (Pl. 40, figs. 1, 2, 4, 7, 8; text-fig. 1). Kozłowski (1929, p. 124, fig. 38) called this a spondylium duplex and thought that the supporting septum was formed by the two walls of the spondylium being brought into contact. According to Kozłowski the septum in transverse section appeared to be com-

posed of two layers separated by a well-defined line of junction. This interpretation has been accepted by many subsequent investigators, but, in a recent study of *Enantiosphen vicaryi*, Williams and Wright (1961, pp. 164-5, text-fig. 8) presented evidence to show that the supporting septum, at least in this species, was composed of a thin median layer,

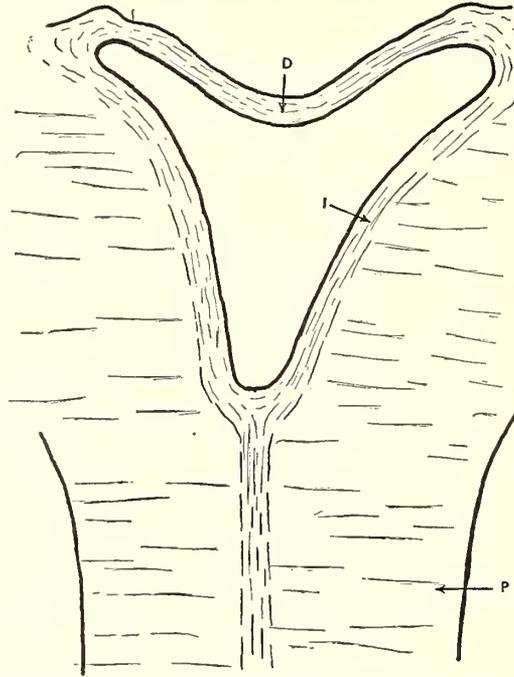


TEXT-FIG. 1. Longitudinal (above) and transverse (below) sections showing the internal structure of the three subfamilies of the Pentameridae. Heavy, unlettered arrows on longitudinal sections show position of transverse sections. A, Subfamily Pentamerinae. *Pentamerus* cf. *P. oblongus* Sowerby, Reynales Limestone, Rochester, N.Y.; photomicrographs of this species on Plate 40, fig. 4, and Plate 42, figs. 1, 2. B, Subfamily Gypidulinae. *Sieberella roemeri* Hall and Clarke, Henryhouse Formation, Pontotoc Co., Okla.; photomicrographs of this species on Plate 43. C, Subfamily Clorindinae. *Cloriudella areyi* (Hall and Clarke), Irondequoit Limestone, Rochester, N.Y.; photomicrographs of this species on Plate 42, figs. 3-5.

b—brachial process; bb—posterior extension of brachial process; c—carinae; i—inner plate; ms—median septum; o—outer plate; sp—spondylium.

in part discontinuous, lined on both sides with a thicker layer of secondary calcite. Thin sections of other species studied by the writer appear to support Williams and Wright's interpretation. The thin section of *Sieberella roemeri* (Pl. 40, figs. 1, 2), shows that the spondylium and supporting septum are composed of a thin median layer which is coated on both sides with a thicker layer of shell material, the latter presumably representing the outer part of the secondary layers (compare with text-fig. 8c of Williams and

Wright). This basic shell structure is especially well shown in thin sections and parolodion peels of *Pentamerus* cf. *P. oblongus* from the Reynales Limestone (Pl. 40, fig. 4; text-fig. 2). At suitably high magnifications the median septum of this species may be seen to be composed of a thin median layer, and a fairly thick, outer prismatic layer of clear calcite. The inner layer can be followed from the central part of the septum into the spondylium and the deltidium (text-fig. 2). This is similar to the relationship observed by Alexander (1948, p. 147, fig. 3) on *Conchidium knighti*, where she recognized three shell layers: an



TEXT-FIG. 2. *Pentamerus* cf. *P. oblongus* Sowerby. Transverse section of a part of the spondylium and the deltidium showing the shell layers. This is an enlarged drawing of the photomicrograph shown in Plate 40, fig. 4.

D—deltidium; P—prismatic layer; S—inner layer.

outer layer, an inner layer, and a thick prismatic layer. In the specimens studied by the writer the distinction between the inner shell layer and the prismatic layer is obscure, and supports the conclusion of Williams (1956, pp. 249–51) that the prismatic layer is simply a modification of the inner secondary layer. This layer is thick at the posterior end of the shell, and thins markedly towards the front. The prismatic layer is well displayed on the specimen of *Pentameroides* sp. (Pl. 41, figs. 6–12); at the posterior end of the brachial valve it almost completely buries the brachial apparatus (Pl. 41, fig. 6), but thins sharply towards the front (Pl. 41, fig. 10).

A deltidium has been observed on species of *Pentamerus* (Pl. 40, fig. 4), *Conchidium*, *Aliconchidium*, and *Enantiosphen*, and, since it is a thin, delicate structure which would be easily destroyed, it may be more commonly developed than present knowledge indicates.

The different pentameracean genera show some variation in the length of the spondylium and in the development of the supporting septum. In some genera, such as *Holorhynchus* and *Cymbidium*, the septum is absent and the spondylium is attached directly to the valve floor; in other genera such as *Harpidium* (Pl. 40, fig. 8) it is relatively short whereas in still others it is much longer, reaching an extreme in such genera as *Brooksina* (Pl. 40, fig. 7) where it almost divides the interior of the shell into two parts. Aside from these modifications the spondylium was a conservative structure, exhibiting little phylogenetic variation throughout the history of the Pentameracea, and consequently the morphology of the pedicle valve has not been used in classification above the generic level.

Sapelnikov (1963, p. 65) proposed a new subfamily, Subrianinae, for those Pentameridae without any supporting median septum in the pedicle valve; this subfamily included three genera: *Holorhynchus* Kiaer, 1902, *Cymbidium* Kirk, 1926, *Subriana* (*Subriana*) Sapelnikov, 1960, and *Subriana* (*Vagranella*) Sapelnikov, 1960. As noted above, the length of the median septum is variable and in the writer's opinion does not constitute a valid distinction for a new subfamily. *Holorhynchus* Kiaer, 1902 is here assigned to the family Virgianidae and *Cymbidium* Kirk, 1926 is assigned to the family Pentameridae, subfamily Pentamerinae; the writer has not seen Sapelnikov's description of *Subriana* (*Subriana*) and *Subriana* (*Vagranella*).

The Pentameracea comprise the following five (four?) families of middle Palaeozoic brachiopods: [?] Parallelelasmataidae Cooper, 1956; Stricklandiidae Hall and Clarke, 1894 (emended Boucot and Ehlers, 1963); Virgianidae Boucot and Amsden, 1963; Enantiosphenidae Torley, 1934; Pentameridae McCoy, 1844. All of these brachiopods have a pedicle spondylium, usually resting on a median septum, and fairly long brachial processes, which supported at least a part of the lophophore. The brachial processes are free at their distal ends, except in the family Enantiosphenidae where they terminate in a loop. The processes are supported at their posterior ends by plates which, in the families Pentameridae, Parallelelasmataidae, and Enantiosphenidae, extend forward far enough to enclose the muscle field, but which, in the Virgianidae and Stricklandiidae, are so abbreviated that they exclude the area of muscle attachment. The Parallelelasmataidae include a small group of Middle Ordovician brachiopods the inclusion of which within the Pentameracea has recently been questioned by Williams (1962, pp. 231-2). With the exception of this family, which the author provisionally retains within the superfamily, the Pentameracea range from the Late Ordovician (Ashgillian) to the Late Devonian, being fairly abundant in the shelly faunas of the Silurian and Early Devonian. Almost all of the Late Ordovician (Ashgillian) and Early Silurian (early and middle Llandoveryan) pentameraceans have abbreviated supports for the brachial processes. This group comprises the Virgianidae, which are believed to be confined to the Late Ordovician (Ashgillian) and Early Silurian (Llandoveryan), and the Stricklandiidae which appear to be confined to the Lower and Middle Silurian. Recently Nikiforova (1960, p. 202) and Rzhonsnitskaya (1961, p. 39) have proposed to remove the Stricklandiidae from the Pentameracea and place them in the Camerellacea (these authors include *Virgiana* and *Holorhynchus* in the Pentameridae). This group of shells are, however, essentially pentameracean in all respects except for their abbreviated plates, and are believed to be more closely related to the Pentameridae than to the Camerellidae. Nikiforova (1960, p. 211) also removed the Enantiosphenidae from the Pentameracea, referring this family

with question to the Terebratulida. The sole representative of this family is the Middle Devonian genus *Enantiosphen*, which has a typically pentameracean pedicle and brachial internal structure, except for the fact that the processes terminate in a loop (Amsden, 1953, p. 138; Williams and Wright, 1961, p. 164; Cloud, 1942, pp. 144–5). Furthermore, this genus has an impunctate, fibrous shell like that of the Pentameracea, and quite unlike the punctate shell of the Terebratulacea.

Family PENTAMERIDAE M'Coy 1844

This family includes smooth, costate, granulose, or pitted shells with or without interareas. Generally the shells are strongly biconvex. The brachial processes are supported by well-developed inner and outer plates, the latter extending forward far enough to enclose the muscle area. In some genera the outer plates are parallel and discrete, and in others they unite to form a cruralium. The processes are long, rod-shaped or blade-shaped structures with free distal ends. The pedicle valve has a well-developed spondylium, commonly supported on a median septum.

This is the only family of Pentameraceans discussed in the present paper. They are fairly common in the shelly faunas of the late Lower Silurian to Lower Devonian, but range on into the Late Devonian. A single species, *Conchidium munsteri*, is present in Late Ordovician (Ashgillian) strata of Norway. The stratigraphic position of this species is somewhat anomalous because, according to present information, the next younger representative of the Pentameridae does not appear until the latter part of the Lower Silurian; the internal morphology and age of *C. munsteri* is discussed below.

Three subfamilies are here included in the Pentameridae:

Pentamerinae M'Coy 1883

Gypidulinae Schuchert and Levene 1929

Clorindinae Rzhonsnitskaya 1956

In a recent paper Nikiforova (1960, pp. 203–5) divided this group of pentameraceans into four families: Pentameridae, Gypidulinidae, Pentameroidinae Amsden, 1953, and a new family, the Antirhynchonellidae. Nikiforova's diagnosis of Pentameroididae was the same as that given by Amsden in 1953, and the family Pentameridae is essentially the same as the present subfamily Pentamerinae except for the inclusion of *Virgiana* and *Holorhynchus* (these two genera have abbreviated brachial plates and are assigned to the Virgianidae). According to Nikiforova, both the Antirhynchonellidae and Gypidulidae possess a fold and sulcus, the latter having discrete outer plates and the Antirhynchonellidae having the plates united to produce a cruralium.

Rzhonsnitskaya (1961, pp. 42–44) uses a somewhat different classification, recognizing the following families and subfamilies:

Family Pentameridae

Subfamily Pentamerinae

Subfamily? Pentameroidinae

Subfamily Conchidiellinae, new subfamily

Family Gypidulidae

Family Clorindidae

According to Rzhonsnitskaya, the Pentameridae either lack a fold and sulcus or have this structure only weakly developed, and possess long, stalk-like processes. The sub-

family Pentamerinae was defined as including forms having a tripartite brachial apparatus and long, thin processes. Rzhonsnitskaya's diagnosis of this subfamily is similar to the writer's, except that it includes *Virgiana* and *Holorhynchus* (here assigned to the Virgianidae). The Pentameroidinae was accepted, with question, as defined by the writer. A new subfamily, the Conchidiellinae, was proposed for pentamerids with a tripartite brachial apparatus and massive, convex processes. Three genera were included in this subfamily: *Conchidiella* Khodalevich, 1939; *Zdimir* Barrande, 1881; and *Leviconchidiella* Rzhonsnitskaya, 1960. In a forthcoming restudy of Barrande's genus *Zdimir*, Boucot and Siehl (1962) propose to suppress *Conchidiella* as a synonym of *Zdimir*, and refer *Zdimir* and *Leviconchidiella* to the Gypidulinae. According to these authors, these genera have brachial-plate structures basically the same as *Gypidula* and other members of this subfamily. Rzhonsnitskaya restricted the Gypidulidae to those pentamerids with a ventral fold and dorsal sulcus, and massive, stalk-like processes. The Clorindidae were characterized as having a ventral sulcus and a dorsal fold, and a carinate brachial apparatus. These families include about the same genera as they do in the present study (as subfamilies), the principal exception being *Pentamerella* which Rzhonsnitskaya placed in the Clorindidae and which the writer places in the Gypidulinae (see description of *Pentamerella arata*). Also it should be kept in mind that the Gypidulinae of the present work includes genera which Rzhonsnitskaya referred to the Conchidiellinae.

Subfamily PENTAMERINAE Waagen 1883

This group includes smooth, costate or costellate brachiopods, most of which have poorly developed interareas. The shells tend to be larger than most middle Paleozoic brachiopods and some species, such as *Conchidium alaskense* Kirk and Amsden and *C. vogulicum* (Verneuil), are among the largest known brachiopods. They generally lack a fold and sulcus, or if these are present they are poorly developed. The brachial apparatus is tripartite, consisting of inner plates, outer plates, and relatively long, rod-like brachial processes (text-fig. 1A). These plate divisions are commonly clearly marked, both in transverse section (Pl. 42, figs. 1, 2) and in shells split longitudinally to expose one of the brachial plates (Pl. 40, figs. 7, 8). All the genera assigned to this subfamily have discrete outer plates, except for *Pentameroides* in which outer plates are united to form a median septum (the brachial interior of *Pleurodium* is unknown).

The internal structure of *Pentamerus* is quite characteristic of this group of pentamerids (text-fig. 1A; Pl. 40, fig. 4; Pl. 42, figs. 1, 2). The processes are slender rods which served to support at least part of the lophophore. These are supported on long, parallel outer plates which remain discrete throughout their length. The inner plates are well developed, although not quite as long as the outer plates; near their anterior end they are subparallel, but towards the rear they curve outward to meet the lateral walls of the valve, where they form a part of the articulating mechanism.

Shell growth is believed to have taken place in the following manner. In young, immature shells the brachial apparatus was small and confined to the posterior end of the valve. At this stage the apparatus resembled a mature representative of the Stricklandiidae or Virgianidae. As the shell grew larger the inner and outer plates were extended forward, encroaching upon and covering the proximal ends of the brachial processes. To strengthen this part of the shell additional material was deposited over the entire

apparatus (and spondylium), thus to some extent burying the posterior part of the brachial processes (Pl. 41, figs. 6, 7, 12; Pl. 42, figs. 1, 2). Even so, the processes are generally clearly marked in thin sections and parlodion peels of well-preserved specimens.

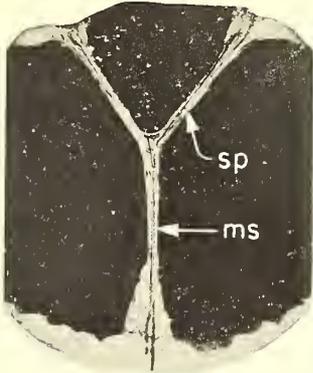
In 1954 the International Commission on Zoological Nomenclature placed *Pentamerus* Sowerby, 1813 (type species *Pentamerus oblongus* Sowerby, 1813) and *Conchidium* Oehlert, 1887 (type species *Anomia bilocularis* Hisinger, 1799) on the *Official List of Generic Names in Zoology*.

The following genera are now assigned to the Pentamerinae: *Pentamerus* Sowerby, 1813; *Brooksina* Kirk, 1922; *Capelliniella* Strand, 1928; *Conchidium* Oehlert, 1887; *Cymbidium* Kirk, 1926; *Harpidium* Kirk, 1925; *Lissocoelina* Schuchert and Cooper, 1931; *Pentameroides* Schuchert and Cooper, 1931 (see below); *Rhipidium* Schuchert and Cooper, 1931. *Pleurodium* Wang, 1955, is provisionally included in this subfamily although the internal structure of the brachial valve is unknown. *Pentamerifera* Khodalevich, 1939, is also assigned questionably to this subfamily, although its internal structure is not clear to the writer. *Aliconchidium* St. Joseph, 1942, may also be appended to the Pentamerinae; however, it differs markedly from the other genera in having a prominent pedicle palintrope. Recently Sapelnikov (1960, pp. 56–62, pls. 5, 6, text-figs. 1–3) described a new genus of Pentameridae, *Jolvia*, which is unusual in having a cardinal process; Sapelnikov's photographs (pl. 6, figs. 5, 6) suggest that this structure is

EXPLANATION OF PLATE 40

- Figs. 1, 2. *Sieberella roemeri* Hall and Clarke, 1892. Henryhouse Formation, Pontotoc Co., Okla. 1, Photomicrograph of a thin section showing the complete spondylium and supporting septum ($\times 15$). 2, Enlarged detail of the same ($\times 75$). Okla. Univ. 5173.
- Fig. 3. *Conchidium munsteri* St. Joseph, 1938. Late Ordovician (zone 5b), Vestre Svartoy, Ringerike, Norway. Parlodion peel showing brachial-plate structure ($\times 10$). See text-fig. 4(3). Paleont. Mus., Oslo, 16668A.
- Fig. 4. *Pentamerus* cf. *P. Oblongus* Sowerby, 1813. Reynales Limestone, near Rochester, N.Y. Photomicrograph of a thin section showing part of spondylium and supporting septum and deltidium ($\times 10$). Cut near posterior end of valve where spondylium and septum are much thickened by secondary shell material. See text-fig. 2. Okla. Univ. 5174.
- Figs. 5, 6. *Gypidula coeymanensis* Schuchert, 1913. Helderberg Formation, Indian Ladder, Thatcher Park, south of Albany, N.Y. Oblique and vertical views of a silicified valve showing brachial apparatus ($\times 3$). Okla. Univ. 5175.
- Fig. 7. *Brooksina alaskensis* Kirk, 1922. Upper Silurian, Kosciusko Island, south-eastern Alaska. Specimen split longitudinally to show the ventral spondylium (left) and brachial apparatus (right) ($\times 1\frac{1}{2}$). U.S. Nat. Mus. 142774.
- Fig. 8. *Harpidium insignis* Kirk, 1925. Upper Silurian, Kosciusko Island, south-eastern Alaska. Specimen split longitudinally to show ventral spondylium (right) and brachial apparatus (left) ($\times 1$). U.S. Nat. Mus. 142775.
- Figs. 9–15. *Pentamerella arata* (Conrad), 1841. Specimens figured by Hall, 1867, *Paleont. N. Y.*, vol. 4, pl. 58, figs. 2–4, 13–17. 9, Silicified dorsal interior ($\times 3$) 'Upper Helderberg Limestone' (Onondaga Limestone), Albany Co., N.Y. 10, 11, 15, Ventral, dorsal, and anterior views ($\times 1$), 'Upper Helderberg Limestone' (Onondaga Limestone), Schoharie Co., N.Y. 12–14, Dorsal, anterior, and ventral views ($\times 2$), Schoharie Formation, Schoharie Co., N.Y. All these specimens are at the Am. Mus. Nat. Hist., 2837/4; 2837/3; 2837/2a.

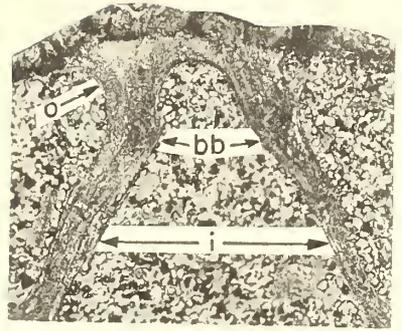
b—brachial process; bb—posterior extension of brachial process; d—deltidium; i—inner plate; ms—median septum; o—outer plate; sp—spondylium.



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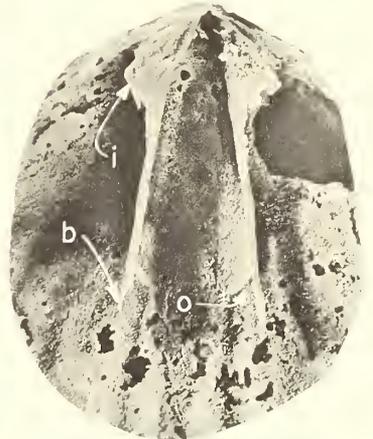
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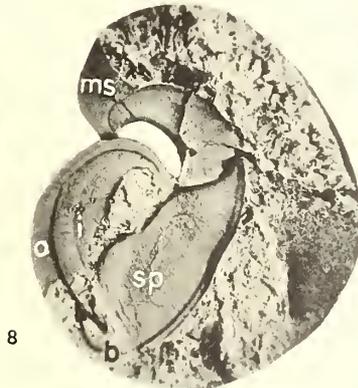
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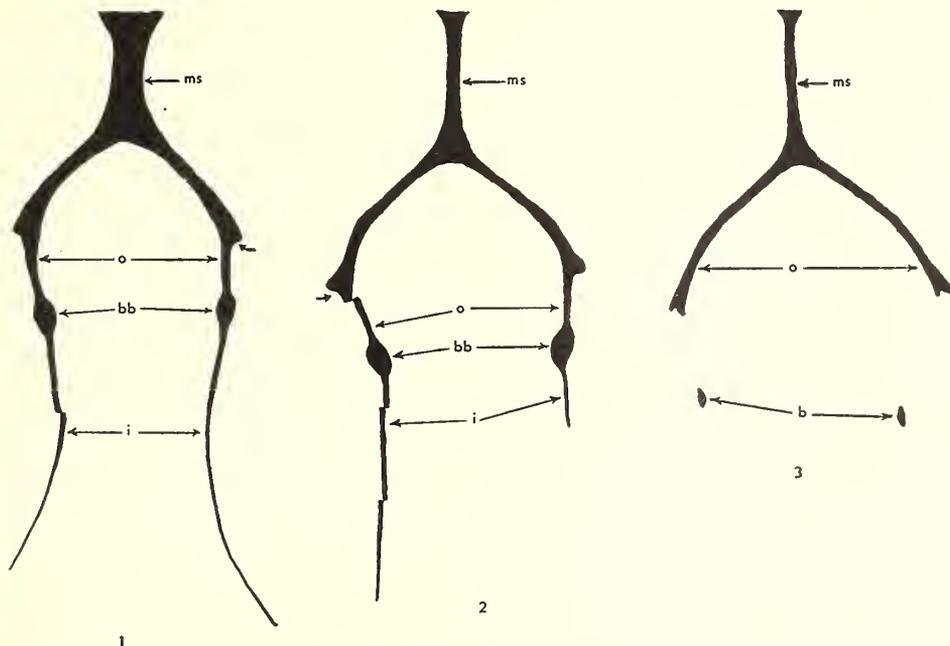
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composed of the secondary fibrous layer. *Subriana* Sapelnikov, 1960, may belong here; the writer has not seen the diagnosis of this genus.

With the exception of a single Late Ordovician species, *Conchidium munsteri*, which is discussed below, the subfamily Pentamerinae appears to be restricted to strata ranging in age from late Lower Silurian to Lower Devonian.



TEXT-FIG. 3. Serial sections of the brachial apparatus of *Pentameroides subrectus* (Hall and Clarke), Niagaran, Jones Co., Iowa. These drawings were made from photomicrographs of thin sections; a photomicrograph of number 1 is shown on Plate 41, fig. 2. The small arrows at the sides of numbers 1 and 2 indicate the position at which the outer plates thin abruptly, presumably due to the termination of the thick, secondary layer (specimen is silicified). Distance from posterior tip of ventral beak: 1: 13.5 mm.; 2: 16.8 mm.; 3: 18.8 mm. Thin sections are at the U.S. National Museum.

b—brachial process; bb—posterior extension of brachial process; i—inner plate; ms—median septum; o—outer plate.

Genus PENTAMEROIDES Schuchert and Cooper 1931

Plate 41, figs. 1–12; text-fig. 3

Pentameroides Schuchert and Cooper, 1931, p. 248; 1932, p. 179, pl. 27, figs. 13, 14, pl. 28, figs. 19, 22, text-fig. 27; Amsden, 1953, pp. 144–6, text-fig. 7.

Type species. Pentamerus oblongus subrectus Hall and Clarke 1894, p. 238, pl. 69, figs. 2, 3, 8–10.

Description. Smooth, elongate, moderately to strongly biconvex shells. The pedicle beak is fairly prominent and hooked over, but not in conjunction with the brachial valve (Pl. 41, figs. 3–5, 11). The pedicle valve bears a long, narrow, and deep spondylium supported on a high septum (Amsden, 1953, fig. 7). The brachial apparatus is tripartite, consisting of rod-shaped brachial processes which are braced at their posterior ends by

inner and outer plates. The outer plates are subparallel for a short distance near their junction with the processes, and then converge to produce a cruralium supported on a median septum. The inner plates are thin and very high (Pl. 41, figs. 1, 2; text-fig. 3). Both the inner and outer plates are long, extending forward for more than half the length of the valve (Pl. 41, figs. 3; Amsden, 1953, fig. 7).

Discussion. The present diagnosis is based on a study of topotypes of *Pentameroides subrectus* from the Niagaran strata, Jones County, Iowa, which were borrowed from the U.S. National Museum and from Peabody Museum, Yale University. Thin sections have been prepared from two of these specimens; these are illustrated by photomicrographs on Plate 41, and by line drawings in text-fig. 3. The internal structures of the specimens sectioned have been replaced by silica, so that the microscopic shell structure is obscure. The writer has also prepared serial sections of specimens of *Pentameroides sp.* from the Merritton Member of the Reynales Limestone near Thorold, Ontario. These specimens are not silicified and the detailed shell structure is well preserved as shown in the photomicrographs on Plate 41. The Reynales specimens are congeneric with *P. subrectus*, although they appear to represent a different species.

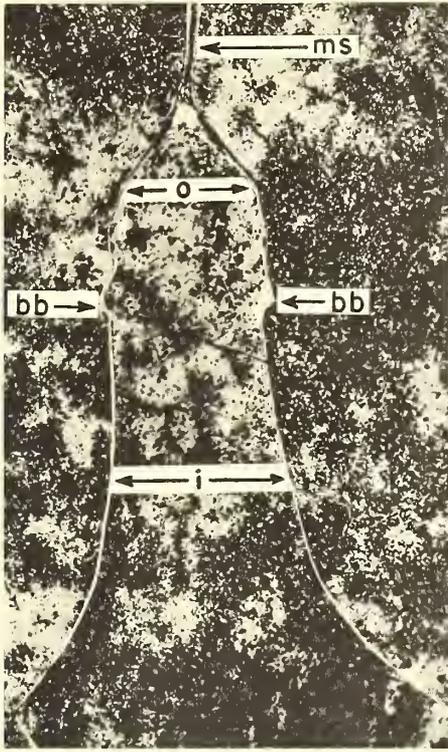
Schuchert and Cooper erected this genus for shells which were externally like *Pentamerus*, but which had a dorsal cruralium. In 1953 the writer redefined this genus and made it the type for a new subfamily, the Pentameroidinae. The genus and new subfamily were thought to be characterized by a fourfold brachial apparatus: inner plates, brachial processes, and outer plates, the latter resting on a fourth set of plates, the septal plates. This diagnosis was based on sections of a topotype of *P. subrectus* from Jones County, Iowa. In this specimen (Pl. 41, fig. 2; text-fig. 3; see also Amsden, 1953, fig. 7) the outer plates thin abruptly at a point about midway between the brachial processes and the median septum. This marked change in thickness was interpreted by the writer as indicating the presence of a fourth element in the brachial apparatus, and was the basis for a new subfamily. This interpretation is now believed to be incorrect. In 1963 a second topotype of *P. subrectus* was sectioned (Pl. 41, fig. 1) and it does not show any trace of this structure, nor does it have any indication of a fourth set of plates. Moreover, serial sections of specimens of *Pentameroides sp.* from Ontario, which appear to have the same internal structure as *P. subrectus* and which are not silicified, give no indication of a fourth plate. These do, however, show that secondary shell material was

EXPLANATION OF PLATE 41

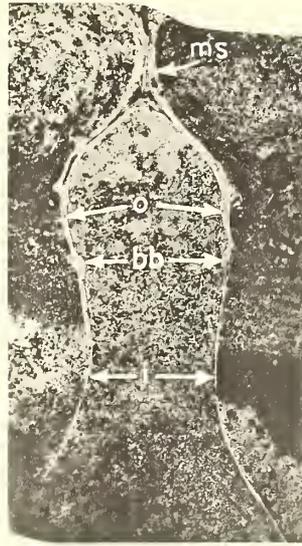
Figs. 1-5. *Pentameroides subrectus* (Hall and Clarke), 1894. Niagaran, Jones Co., Iowa. 1, Photomicrograph of a thin section showing the brachial apparatus approximately 7 mm. in front of the ventral beak ($\times 20$); Peabody Mus., Yale Univ., S-1850. 2, Photomicrograph of a thin section of the brachial apparatus (see text-fig. 3) about 13.5 mm. in front of the ventral beak ($\times 10$); U.S. Nat. Mus. 14776. 3-5, Dorsal, ventral, and posterior views of a steinkern ($\times 1$); Peabody Mus., Yale Univ., S-1850.

Figs. 6-12. *Pentameroides sp.* Reynales Limestone, Merritton Member, Thorold, Ontario. 6-9, Serial sections (6, 7, 8 are parlodion peels, 9 is a thin section) of the brachial apparatus (fig. 6 includes ventral spondylium) ($\times 6$). 10, 12, Enlarged views ($\times 24$) of the sections shown in figs. 8, 9. Distance from ventral beak: fig. 6: 2.7 mm.; fig. 7: 4.2 mm.; fig. 8: 7.3 mm.; fig. 9: 12.9 mm. Okla. Univ. 5176. 11, Dorsal view ($\times 1$); Okla. Univ. 5177.

bb—posterior extension of brachial process; i—inner plate; ms—median septum; o—outer plate; sp—spondylium.



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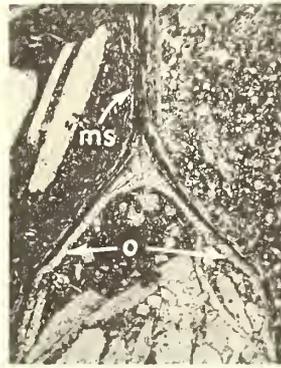
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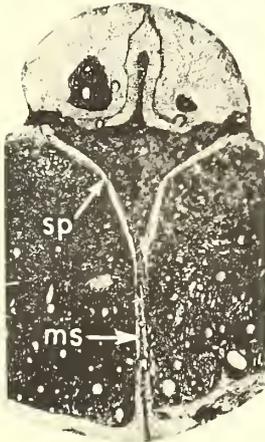
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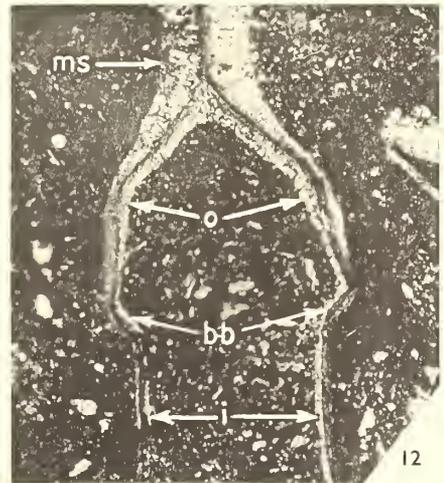
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12

deposited over the posterior part of the brachial apparatus (Pl. 41, figs. 6–10, 12). In all probability the abrupt thinning of the outer plates shown by the first specimen (Pl. 41, fig. 2; text-fig. 3) is the result of a thinning of the secondary material, somewhat more abruptly than is common, with these relations being obscured by later silicification which destroyed most of the wall structure. *Pentameroides* thus differs from *Pentamerus* only in the presence of a cruralium supported on a septum, and, while this is a sound generic distinction, it is not a suitable subfamilial distinction. Accordingly, it is here proposed that the subfamily Pentameroidinae Amsden, 1953 be abandoned.

This genus includes the type species, *P. subrectus*, *Pentameroides* sp. from the Reynales Limestone at Thorold, Ontario, and *Pentameroides* cf. *P. gothlandicus* (Lebedev; see St. Joseph, 1938, pp. 286–90, pl. v, figs. 7–8, pl. vi, figs. 13, 15, text-figs. 1, 8) from zones 7b and 7c of southern Norway. These are the only species of *Pentameroides* definitely known to the writer, although an investigation of the internal structure of species now referred to *Pentamerus* will probably show that some are representatives of *Pentameroides*. According to present information, this genus ranges from late Llandoveryan through the Wenlockian.

Genus CONCHIDIUM Oehlert 1887
Conchidium munsteri St. Joseph 1938

Plate 40, fig. 3; text-fig. 4

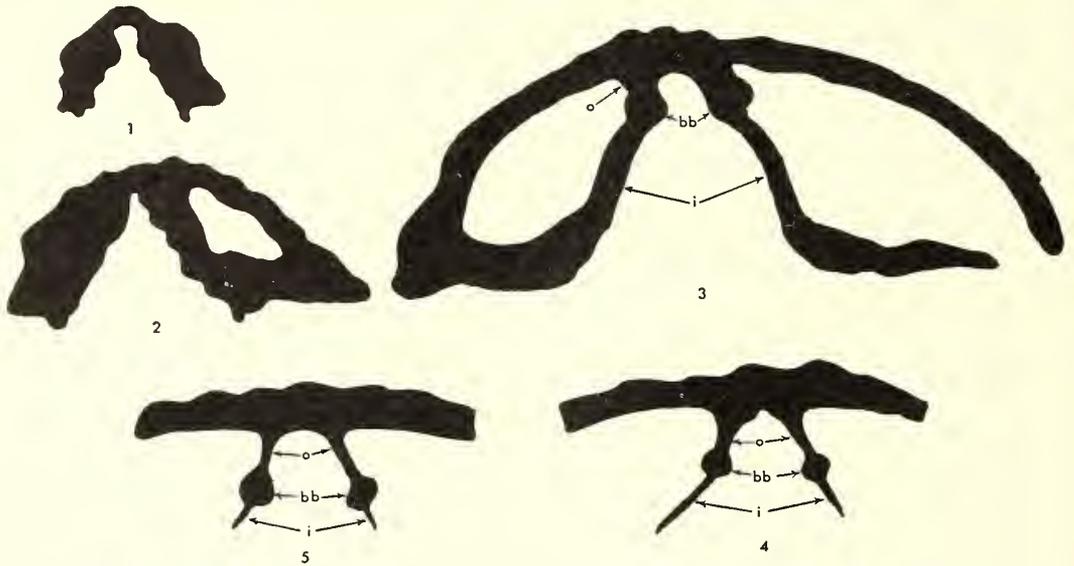
Conchidium munsteri St. Joseph, 1938, pp. 301–4, pl. 5, figs. 9, 11, pl. 6, figs. 10–11, text-figs. 7, 10.

Description. Elongate, biconvex shells without a well-defined fold and sulcus. They are moderately large, with fragmentary specimens suggesting a maximum length of between 40 and 50 mm. The pedicle beak is fairly prominent and the interareas appear to be poorly developed. Both valves are costate, four to five ribs occupying a space of 5 mm. The pedicle valve has a well-developed spondylium supported on a median septum which extends almost the complete length of the valve (St. Joseph, 1938, text-fig. 10, pl. 5, figs. 9, 11). In the brachial valve, the apparatus is tripartite with long, rod-like brachial processes supported on subparallel and discrete outer plates; on the valve illustrated in text-fig. 4, the outer plates extend forward at least 8 mm. The brachial processes are overlain by long inner plates.

Discussion. St. Joseph's description of this species was based upon pedicle valves from zone 5b in southern Norway. He noted that its stratigraphic position was unusual, being separated 'in time from the other representatives of this genus by the whole of the Llandoveryan period', but concluded, on the basis of the internal and external character of the pedicle valve, that it was a true representative of *Conchidium*. In 1963 the writer borrowed a number of topotypes from the Palaeontological Museum at Oslo. This collection includes a number of brachial valves (no articulated specimens), three of which were serially sectioned, one being illustrated herein (Pl. 40, fig. 3; text-fig. 4). These show *C. munsteri* to have a well-developed brachial apparatus with long inner and outer plates. Its internal structure would seem to place it unmistakably in the subfamily Pentamerinae, and its external form relates it to *Conchidium*, or possibly *Rhipidium*. The specimens described by St. Joseph, and the pedicle valves observed by the writer, have

a fairly prominent pedicle beak, indicating that it is a representative of *Conchidium* rather than *Rhipidium*; however, no articulated shells have been observed, and the free pedicle valves observed by the writer are all at least partly embedded in matrix. It is, therefore, difficult to determine the lateral profile, especially the nature of the pedicle beak and umbo with respect to the brachial valve. Possibly a more definitive collection would show it to have the profile of *Rhipidium*.

The stratigraphic position of this species in zone 5b of Late Ordovician (Ashgillian) age is anomalous. Excluding *C. munsteri*, the oldest representative of the subfamily Pentamerinae comes from late Llandoveryan strata; in fact, to the writer's knowledge,



TEXT-FIG. 4. Serial sections of the brachial apparatus of *Conchidium munsteri* St. Joseph, 1938. Zone 5b (Ashgillian), Vestre Svartoy, Ringerike, southern Norway. Drawings made from photomicrographs of parlodion peels; a photomicrograph of number 3 is shown on Plate 40, fig. 3. Distance from posterior tip of brachial valve: 1: 0.8 mm.; 2: 1.4 mm.; 3: 2.2 mm.; 4: 4.1 mm.; 5: 4.8 mm. ($\times 5$). On this specimen the outer plates extend forward at least 8 mm. Parlodion peels at the Paleon. Museum, Oslo, 16668A.

o—outer plate; bb—posterior extension of brachial process; i—inner plate.

there are no other Late Ordovician or early Llandoveryan representatives of the entire family Pentameridae. However, according to information which Dr. Gunnar Henningsmoen kindly supplied to the writer there appears to be no reason to doubt that *C. munsteri* came from zone 5b. The only other Late Ordovician pentameracean is *Holorhynchus* which is also from zone 5b of Norway, but it is a representative of the Virgianidae with abbreviated brachial plates quite unlike the structure of *C. munsteri*. In this connexion it might be pointed out that Late Ordovician and early Llandoveryan pentameraceans (with the exception of *C. munsteri*) appear to be confined to the families Virgianidae and Stricklandiidae, both of which are distinguished by their much abbreviated brachial apparatus. The family Parallelelasmataidae, which is believed to be confined to the Middle Ordovician, has a small pauciplicate shell quite unlike that of *C. munsteri*.

Subfamily GYPIDULINAE Schuchert and LeVene 1929¹

This subfamily includes smooth, costate, pitted or granulose Pentameridae with fairly well-developed interareas. Generally they are strongly biconvex and many species develop a galeatiform shell. Most have a ventral fold and dorsal sulcus, but two genera (*Pentamerella* and *Barrandina*) have a ventral sulcus and dorsal fold, and a few have none. Commonly the shells are of small to moderate size, and only a few species have shells as large as the typical Pentamerinae. The brachial apparatus is well developed and may extend forward as much as half the length of the valve; it is tripartite and non-carinate, consisting of outer plates, brachial processes, and inner plates (text-fig. 1B). The outer plates may be parallel and discrete, or they may unite to form a cruralium.

In such typical genera as *Gypidula*, *Sieberella*, and *Pentamerella*, and probably in all the Gypidulinae, the processes are broad and blade-like. In *Sieberella roemeri* Hall and Clarke (1892, p. 242, pl. 2, fig. 6; Amsden, 1949, pp. 49–50, pl. 2, figs. 1–4; Amsden, 1951, p. 79, pl. 16, figs. 36–40), which is illustrated by photomicrographs on Plate 43, the processes are wide, nearly flat and have their ventral edges canted inward. These processes are supported on long outer plates, which are medially directed and overlain by inner plates which curve outward to meet the lateral edge of the valve; this plate arrangement produces the lyre-shaped cross-section which is so characteristic of the Gypidulinae (Pl. 40, figs. 5, 6, 9; text-fig. 5). Near the anterior end of the brachial apparatus, in the area where the brachial processes become free blades, the junction of the processes with the outer and inner plates may be detected in well-preserved sections (Pl. 43, figs. 4, 5). Further back, however, the plates lose their identity and are fused into what appears to be a single piece. Near the posterior end, in the area around the hinge, it is common for the entire brachial apparatus to be thickened by secondary shell material which serves to strengthen the articulating mechanism (Pl. 43, figs. 1–3). The gypidulinid structure is also well displayed in the etched brachial valve of *Gypidula coeymanensis* illustrated on Plate 40, fig. 5, 6. This is an unusually fine specimen, which shows the blade-like brachial processes and their relationship to the inner and outer plates. The structure is basically the same as that of *Clorindella* (Pl. 42, figs. 3–5) and other members of the Clorindinae, except that in the Clorindinae the brachial processes extend inside of the inner plates as carinae (text-fig. 1C). The external form of the Clorindinae is also similar to the Gypidulinae and the two subfamilies are believed to be closely related; in fact, until recently the genera which comprise the Clorindinae were included in the Gypidulinae. On the other hand, the brachial structure of *Sieberella* differs from that of *Pentamerus* and other members of the subfamily Pentamerinae which have slender processes that retain their identity well back towards the beak (Pl. 42, figs. 1, 2; Pl. 40, figs. 7, 8).

The subfamily Gypidulinae has been variously defined since it was introduced by Schuchert and LeVene in 1929. Schuchert and Cooper (1932, p. 171) used it for more or less galeatiform shells with small ventral interareas, and included six genera: *Clorinda* (*Barrandina* Booker, 1926 was regarded as a synonym), *Barrandella*, *Gypidula*, *Sieberella*, *Pentamerella*, and *Zdimir*.

Barrandella is a synonym of *Antirhynchonella*. In 1955 the International Commission on Zoological Nomenclature, Opinion 374, placed *Antirhynchonella* Oehlert, 1887 (type species *Atrypa linguifera* J. de C. Sowerby, 1839) on the *Official List of Generic Names in*

Zoology, and placed *Antirhynchonella* Quenstedt, 1871 (nomen nudum), and *Barrandella* Hall and Clarke, 1894, on the *Official Index of Rejected and Invalid Generic Names in Zoology*.

The writer would restrict the diagnosis of Schuchert and Cooper by removing genera like *Clorinda* and *Antirhynchonella* (= *Barrandella*), which have a carinate brachial apparatus to the subfamily Clorindinae. The group of shells which here comprise the Gypidulinae and Clorindinae were assigned by Nikiforova (1960, pp. 204–5) to two families: the Gypidulidae with discrete outer plates, and the Antirhynchonellidae with united outer plates. The writer does not believe this is a sound basis for distinguishing these two groups. The distinction between discrete and coalesced outer plates is not as sharply defined at the generic (or even specific) level as sometimes indicated, and in some species of *Sieberella* the outer plates may be separated slightly towards the front, and in some species of *Gypidula* these plates are almost joined. The type genus of Nikiforova's family Antirhynchonellidae is a representative of the Clorindinae, and therefore Antirhynchonellidae Nikiforova, 1960, should be suppressed as a synonym of Clorindinae (or Clorindidae) Rzhonsnitskaya, 1956. Rzhonsnitskaya (1961, p. 42) divided this group of pentamerids into two subfamilies: Gypidulinae, characterized by a ventral fold and dorsal sulcus and massive processes, and the Clorindinae with a ventral sulcus and dorsal fold and carinate brachial apparatus. The present writer assigns the uniplicate genus *Pentamerella* to the Gypidulinae because it does not have a carinate brachial apparatus, and this feature is believed to be of more fundamental importance than the position of the fold and sulcus. Actually, the development of a fold and sulcus in the Gypidulinae and Clorindinae is variable and some genera have none. Moreover, on some specimens belonging to species which normally develop a fold and sulcus this structure may be faint or absent.

The following genera are here assigned to the Gypidulinae: *Gypidula* Hall, 1867; *Barrandina* Booker, 1926 (see below); *?Biseptum* Khodalevich and Brievell, 1959 (may be a representative of the Pentamerinae); *Devonogypa* Havlicek, 1951; *Gypidulella* Khodalevich and Brievell, 1959, *Gypidulina* Rzhonsnitskaya, 1956 (synonym *Sieberina* Andronov, 1961); *Ivdelina* Andronov, 1961; *Leviconchidiella* Rzhonsnitskaya 1960; *Levigatella* Andronov, 1961; *Pentamerella* Hall, 1867 (see below); *?Procerulina* Andronov, 1961; *?Schegultania* Andronov, 1961 (no type species designated); *Sieberella* Oehlert, 1887; *Wyella* Khodalevich, 1931; *Zdimir* Barrande, 1881 (emended Boucot and Siehl). Most of these genera have a ventral fold and dorsal sulcus, but *Pentamerella* and *Barrandina* have a ventral sulcus and dorsal fold, and *Biseptum*, *Leviconchidiella*, and *Zdimir* generally lack a fold and sulcus. Representatives of this subfamily range from the Lower Silurian into the Upper Devonian.

Genus BARRANDINA Booker 1926

Barrandella (*Barrandina*) Booker, 1926, pp. 131–3.

Type species. *Pentamerus linguifera wilkinsoni* Etheridge, 1892, pp. 52–54, pl. 11, figs. 5–9. *Barrandella* (*Barrandina*) *wilkinsoni* (Etheridge). Booker, 1926, pp. 133–7, pl. 5, figs. 1–4, text-figs. 1, 2.

Discussion. Booker proposed *Barrandina* (as a subgenus of *Barrandella* Hall and Clarke 1894) for smooth, galeatiform shells having a ventral sulcus and dorsal fold. The pedicle

valve has a well-developed spondylium supported on a short septum. The brachial apparatus is tripartite, consisting of inner plates, brachial processes, and outer plates, the latter being subparallel and discrete; the brachial processes are blade-like. Booker treated *Barrandina* as a subgenus of *Barrandella* from which it was distinguished by an 'extra plate at the junction of the septa and crural plates'. As pointed out by Schuchert and Cooper (1932, p. 172), his 'extra plate' is only the brachial process which in *B. wilkinsoni* has a blade-like form (well shown in Booker's text-figs. 1, 2). These authors thought *Barrandina* had essentially the same external and internal structure as *Clorinda* and therefore suppressed Booker's subgenus as a synonym. In its smooth shell, pedicle sulcus and brachial fold, and discrete outer plates, *B. wilkinsoni* is similar to *Clorinda armata* (Barrande; type species). However, Booker's serial sections of *B. wilkinsoni* (figs. 1, 2) clearly show that the brachial processes butted smoothly against the inner plates, with no trace of carinae. In this respect it is unlike the carinate apparatus of *Clorinda* and other members of the Clorindinae. Accordingly, *Barrandina* is here regarded as a distinct genus and assigned to the Gypidulinae.

Booker described a second species, *B. minor*, in the same paper. His serial sections (figs. 3, 4) show the brachial apparatus to have an unusual doubly carinate structure. This is unlike any observed by the writer, and its relationship and significance are unknown. Booker (1926, p. 140, pl. 6, fig. 5, text-fig. 5) also redescribed *Pentamerella molongensis* Mitchell, 1920. This species has a smooth shell with a ventral sulcus and dorsal fold, a carinate brachial apparatus and discrete outer plates. This structure is typical for *Clorinda* and it is suggested that Mitchell's species be transferred to that genus.

B. wilkinsoni came from the 'Barrandella shales, Hatton's Corner, Yass', New South Wales. Booker did not assign an age to these strata, but Etheridge (1892, p. 54) correlated them with the Wenlock. The writer has no information bearing on this point.

Genus PENTAMERELLA Hall 1867
Pentamerella arata (Conrad) 1841

Plate 40, figs. 9-15; text-fig. 5

Atrypa arata Conrad, 1841, p. 55.

Pentamerus aratus (Conrad). Hall, 1857, pp. 120-1, figs. 1-8 [the pedicle valve shown in figs. 9 and 10 is probably a representative of *Conchidium*].

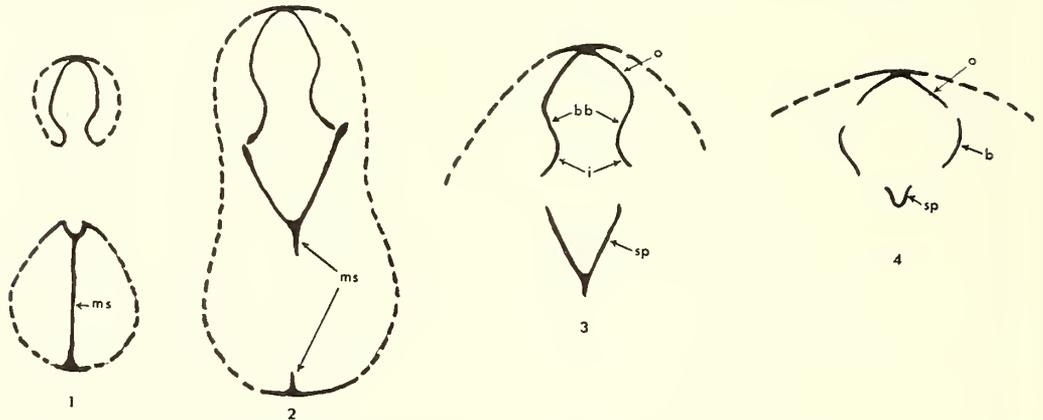
Pentamerella arata (Conrad). Hall, 1867, p. 375, pl. 58, figs. 1-10, 13-21 [the pedicle valve shown in figs. 9 and 10 is probably a representative of *Conchidium*]; Hall and Clarke, 1894, p. 71, figs. 21-29; Schuchert and Cooper, 1932, p. 176, pl. 26, fig. 20.

Description. This species has a biconvex shell with a swollen pedicle valve and a sub-galeatiform profile. The width is about equal to the length; length/width ratio ranges from 0.9 to 1.1. All the specimens examined have a ventral sulcus and dorsal fold, but this varies considerably in its development. The fold and sulcus on specimens from the Schoharie Formation are clearly marked, although never deep (Pl. 40, figs. 12-14; Hall and Clarke, 1894, pl. 71, figs. 24-27); however, on some of Hall's type specimens from the 'upper Helderberg Limestone' (Onondaga Limestone), the fold and sulcus are deeper and better defined at the front (Pl. 40, figs. 10, 11, 15). The umbos of both valves are smooth or only faintly ribbed, but toward the front the shell develops strong

plications which commonly increase by bifurcation; three or four ribs occupy a space of 5 mm.

The specimen from the Schoharie Formation (Pl. 40, figs. 12–14) measures 13.4 mm. long, 14.3 mm. wide, and 10 mm. thick. The largest specimen in the Hall collections from the 'upper Helderberg Limestone' (Onondaga Limestone) of New York is 24.6 mm. long, 22.8 mm. wide, and 14.1 mm. thick. A complete shell from the 'upper Helderberg Limestone' at Waterloo, Iowa, measures 20.5 mm. long, 20.0 mm. wide, and 14.6 mm. thick.

The pedicle valve has a long, deep spondylium supported on a relatively short septum (text-fig. 5; Hall and Clarke, 1894, pl. 71, figs. 21, 22). The brachial apparatus is well



TEXT-FIG. 5. *Pentamerella arata* (Conrad). Transverse serial sections ($\times 6$) of one of Hall's unfigured paratypes from the Schoharie Formation (Lower Devonian), Albany Co., N.Y. (only the brachial apparatus is shown in figs. 3 and 4). Approximate distance from the posterior tip of ventral beak: 1: 0.5 mm.; 2: 2.1 mm.; 3: 3.0 mm.; 4: 3.9 mm. The parlodion peels from which these drawings were made are at the American Museum of Natural History, No. 2837/2.

b—brachial process; bb—posterior extension of brachial process; i—inner plate; o—outer plate; ms—median septum; sp—spondylium.

developed and extends forward almost half the length of the valve. The brachial processes are broad, blade-like structures braced by inner and outer plates, the latter uniting just at the valve floor to produce a cruralium (Pl. 40, fig. 9; text-fig. 5). Hall's unfigured paratype, which was serially sectioned, has a typical gypidulinid structure; the dorsal edge of the brachial process abuts against the ventral edge of the inner plate to produce a smooth junction with no trace of carinae. The silicified interior (Pl. 40, fig. 9) shows a low ridge at the posterior end of the cruralium, but this is the result of secondary shell deposition (common in mature pentamerid shells), accentuated by incomplete silicification at the posterior tip (compare Pl. 43, figs. 2, 3).

Discussion. Hall proposed the genus *Pentamerella* (type species *Atrypa arata* Conrad) for plicate pentamerids with a ventral sulcus and dorsal fold, and a cruralium. *Pentamerella* has generally been assigned to the Gypidulinae, but in 1956 Rzhonsnitskaya referred this genus to a new family, the Clorindidae, on the basis of its ventral sulcus and dorsal fold, and presumed carinate brachial apparatus. This last feature has never been

described in print and, in order to get precise information on its internal plate structure, the type species, *P. arata* (Conrad), has been restudied. Conrad's description of this species is believed to have been based upon specimens from the Schoharie Formation of New York. The writer has not examined Conrad's types, but, through the courtesy of Dr. Roger Batten of the American Museum of Natural History, he was able to study Hall's types (1867, pl. 71, figs. 11-21) which include specimens from the Schoharie Formation, Schoharie County, New York; the 'upper Helderberg Limestone' (Onondaga Limestone), the Helderbergs, Albany County, New York; the 'upper Helderberg Limestone' at the falls of the Ohio and at Waterloo, Iowa. Excluding one large pedicle valve from the Schoharie Formation (Hall, 1867, pl. 71, figs. 11, 12), which may be a species of *Conchidium*, these all appear to be congeneric. There is, however, some variation in the development of the fold and sulcus, and the specimens from the 'upper Helderberg Limestone' (Onondaga Limestone) of New York show a much stronger fold and sulcus than do the others. Whether this represents intraspecific variation or a distinct species cannot be determined without access to larger and more definitive collections. The internal structure can, however, be clearly determined on the basis of Hall's material. The silicified interior and the specimen sectioned, both of which are from the Schoharie Formation and presumably are topotypes, have a characteristic gypidulinid brachial structure with no trace of carinae. Accordingly the genus *Pentamerella* is here retained within the Gypidulinae.

Distribution. Conrad's specimens are believed to be from the Schoharie Formation of late Lower Devonian (Esopusian) age. Hall's collections include specimens from the 'upper Helderberg Limestone' (Onondaga Limestone) of New York, and the 'upper Helderberg Limestone' of Ohio and Iowa, although, as noted above, there is some question whether these are all conspecific. Oliver (1956, p. 1469) records *P. arata* from all four members of the Onondaga Limestone in New York.

The genus *Pentamerella* ranges from the Lower Devonian into the Upper Devonian. In 1953 (p. 143) the writer assigned the Silurian species *Barrandella areyi* Hall and Clarke to *Pentamerella*, but in the present report this species is made the type of a new genus, *Clorindella*.

Subfamily CLORINDINAE Rzhonsnitskaya 1956

This subfamily comprises small to medium sized, smooth to costate Pentameridae, with biconvex shells which tend to have a geleatiform profile. In the pedicle valve the spondylium and supporting septum are well developed. The brachial apparatus is also well developed and consists of inner plates, brachial processes, and outer plates. The inner plates, which are shorter than the outer plates, abut against the outside of the brachial processes, rather than against the upper or ventral edge of the processes; this causes the ventral edge of the processes to extend into the crural cavity as ridges or carina (text-fig. 1c; Pl. 42, figs. 3, 4).

The genera assigned to this subfamily are externally and internally similar to the Gypidulinae and, in fact, were until recently included in that subfamily. They are distinguished from the Gypidulinae primarily on the basis of their carinate brachial apparatus. This structure was first noted by Kozłowski (1929, p. 137, text-figs. 40, 41) in *Clorinda pseudolinguifera* Kozłowski and *Barrandella linguifera* (Sowerby) (*Antirhynchonella linguifera*). Kozłowski described it as a 'carena à la limite des plaques crurales

et des septums cruraux'; actually these ridges are produced by the ventral edge of the brachial process extending inside the inner plates (Pl. 42, figs. 3, 4). The brachial processes in *Clorindella* and *Clorinda* are relatively broad, blade-like structures, and this is probably also true of the other genera assigned to the Clorindinae.

Rzhonsnitskaya proposed this taxa (as a family) to include pentamerids with a ventral sulcus and dorsal fold, and a carinate brachial apparatus. Four genera were included: *Clorinda*, *Antirhynchonella* (as *Barrandella*), *Clorindina*, and *Pentamerella*. As noted above, the writer retains *Pentamerella* in the Gypidulinae and assigns the following four genera to the Clorindinae: *Clorinda* Barrande, 1879; *Antirhynchonella* Oehlert, 1887; *Clorindina* Khodalevich, 1939; *Clorindella* Amsden, gen. nov. All these genera have a ventral sulcus and dorsal fold (but not all of the Gypidulinae have a ventral fold and dorsal sulcus). This group range from the Silurian into the Middle Devonian.

Genus CLORINDELLA gen. nov.

Type species. Barrandella areyi Hall and Clarke, 1894, p. 368, pl. 71, figs. 14-16.

Description. Small, paucicostate shells with a ventral sulcus and dorsal fold. In the ventral interior there is a well-developed spondylium and supporting septum. The

EXPLANATION OF PLATE 42

Figs. 1, 2. *Pentamerus* cf. *P. oblongus* Sowerby. Reynales Limestone near Rochester, N.Y. Photomicrographs of two thin sections showing the brachial apparatus ($\times 10$). Sections cut from the same specimen. 1, Near posterior end. 2, At a point where the inner plates have disappeared, and near the termination of the outer plates. Note that the posterior extension of the brachial process (bb) is well defined in both sections; in fig. 1 the apparatus is considerably thickened by a deposit of secondary shell material. Okla. Univ. 5178.

Figs. 3-5. *Clorindella areyi* (Hall and Clarke), 1894. Irondequoit Limestone near Rochester, N.Y. Photomicrographs of parlodion peels showing the brachial apparatus ($\times 27$). In this species the outer plates unite to produce a low median septum; note well-marked carinae in fig. 3 (carinae also well defined on left side of fig. 4, although partly obscured by an air bubble). These peels (including the pedicle valve) were illustrated by line drawings in Amsden, 1953, fig. 5 (as *Pentamerella areyi*; incorrectly stated to be from Clinton, N.Y.). Distance from posterior tip of ventral beak: fig. 3: 2.5 mm.; fig. 4: 3.1 mm.; fig. 5: 4.5 mm. Parlodion peels at U.S. National Museum.

Figs. 6-10. *Clorindella areyi* (Hall and Clarke), 1894. Hall and Clarke's type specimen figured in *Paleontology of New York*, vol. 8, part 2, pl. 71, figs. 14-16; Clinton Formation, Rochester, N.Y. Posterior, ventral, anterior, lateral, and dorsal views of the type ($\times 2$). N.Y. State Museum 1146.

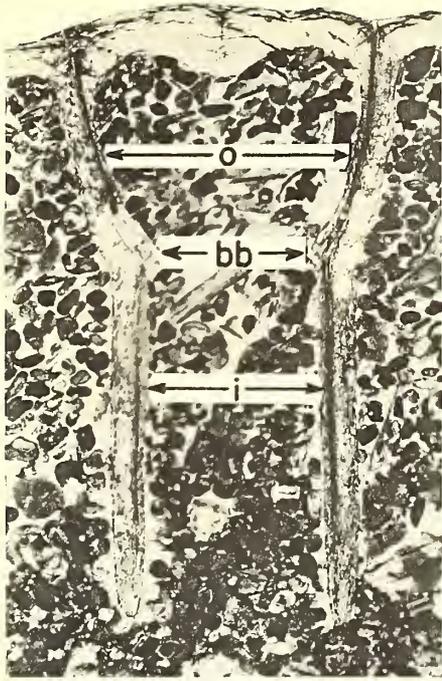
b—brachial process; bb—posterior extension of brachial process; c—carinae; i—inner plate; ms—median septum; o—outer plate.

EXPLANATION OF PLATE 43

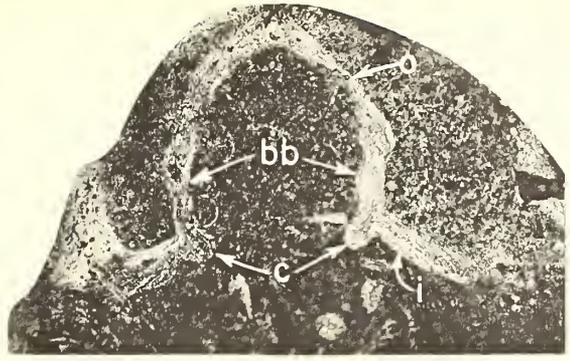
Figs. 1-8. *Sieberella roemeri* Hall and Clarke, 1892. Henryhouse Formation, Henryhouse Creek, Carter Co., Okla. Photomicrographs of serial sections showing the brachial apparatus; fig. 4 is a thin section ($\times 16$), and the others are parlodion peels ($\times 8$). In fig. 4 the shell layers are visible. Distance (in mm.) from posterior tip of beak: fig. 1: 0.7; fig. 2: 1.6; fig. 3: 1.9; fig. 4: 3.3 (thin section); fig. 5: 4.1; fig. 6: 5.1; fig. 7: 5.9; fig. 8: 6.1. Okla. Univ. 5179.

Fig. 9. *Sieberella roemeri* Hall and Clarke, 1892. Henryhouse Formation, Pontotoc Co., Okla. Photomicrograph of a transverse thin section showing brachial apparatus and spondylium; section slightly oblique, the left side being in the zone of articulation and the right slightly in front ($\times 9$). Okla. Univ. 5180.

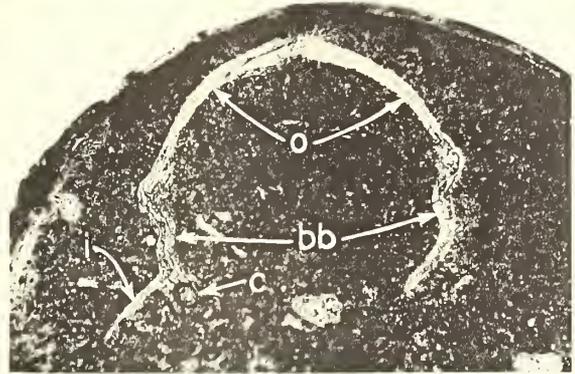
b—brachial process; bb—posterior extension of brachial process; i—inner plate; ms—median septum; o—outer plate, sp—spondylium; t—tooth.



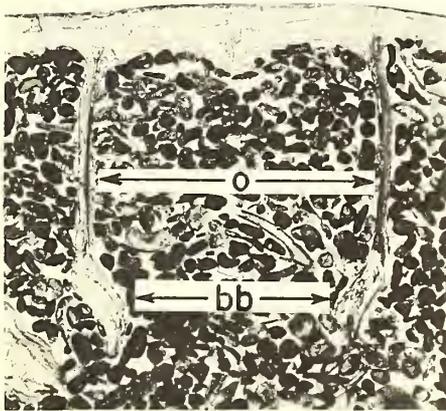
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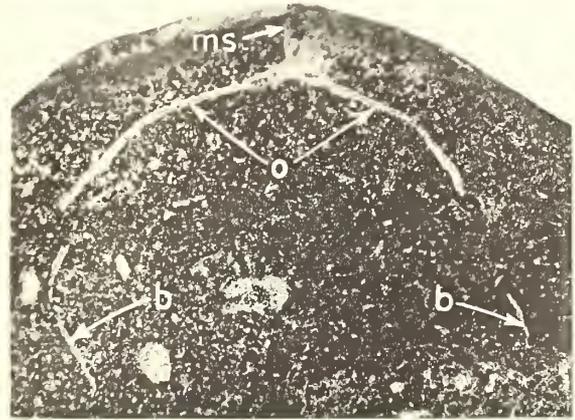
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2



5



6



7



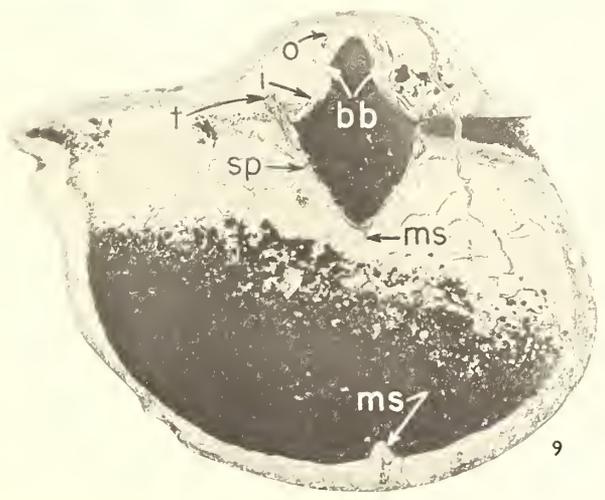
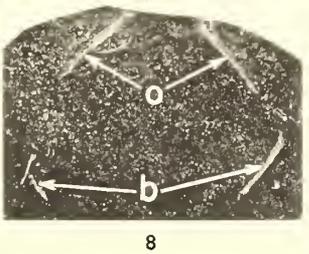
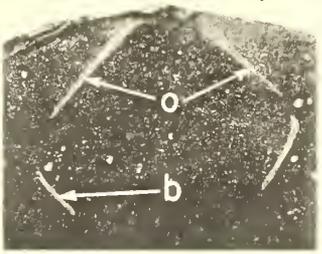
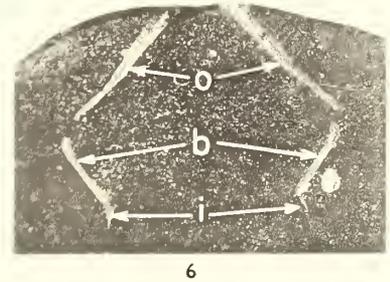
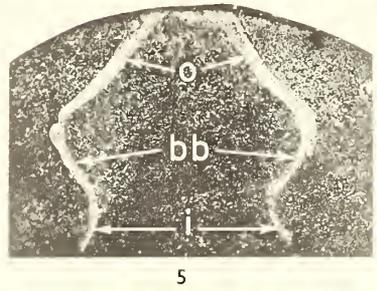
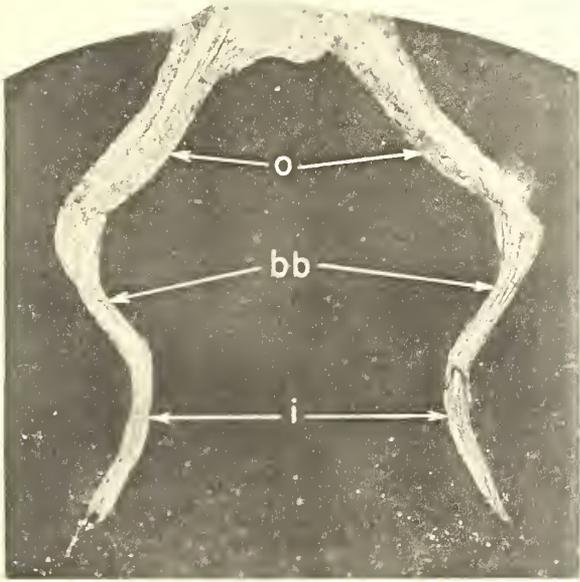
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9



10



brachial apparatus is relatively long and consists of inner plates, brachial processes, and outer plates, the latter uniting above the valve floor to produce a low septum. The inner plates abut against the outside of the processes, allowing the upper or ventral edge of the processes to extend into the cruralial cavity as a ridge. The brachial processes are broad and blade-like (Pl. 42, figs. 3–10).

This genus is characterized internally by its brachial cruralium with carinae, and externally by its paucicostate uniplicate shell. *Clorindella* is internally similar to *Antirhynchonella* Oehlert, 1887 (synonym *Barrandella* Hall and Clarke, 1894), the main difference being that *A. linguifera* (Sowerby) has a sessile cruralium whereas in *Clorindella areyi* the cruralium is elevated on a septum. Both have a ventral sulcus and dorsal fold, but *A. linguifera* has a smooth exterior while *C. areyi* is costate and it is on this feature that the two genera are distinguished. *Clorindina* Khodalevich, 1939, has a costate exterior, but the outer plates are discrete. *Clorinda* Barrande, 1879, has a smooth exterior and discrete brachial plates.

The only representative of this species known to the writer is the type species, *C. areyi*.

Clorindella areyi (Hall and Clarke) 1894

Plate 42, fig. 3–10

Barrandella areyi Hall and Clarke, 1894, p. 368, pl. 71, figs. 14–16.

Pentamerella areyi (Hall and Clarke). Amsden, 1953, p. 143, fig. 5.

Description. This species has a small, strongly biconvex shell. The pedicle valve is deeply arched in the umbonal region and the beak extends over the brachial valve. The pedicle valve has a shallow sulcus and the brachial valve, which is not quite as deep as the pedicle, has a moderate fold. The costae begin just in front of the beaks and become rather high and subangular towards the front. The holotype has one rib in the sulcus and one in the fold.

The internal characters are discussed above and are illustrated on Plate 42, figs. 3–5 (see also Amsden, 1953, fig. 5).

Discussion. Hall and Clarke based their description of this species on a specimen from the Clinton Group (?Irondequoit Limestone) at Rochester, New York. In 1953 the writer (Amsden, 1953, fig. 5) illustrated serial sections of a specimen from the Irondequoit Limestone at Rochester, New York (in the 1953 paper this was erroneously stated to be from Clinton, N.Y.). These parlodion peels from which these illustrations were made were borrowed from the U.S. National Museum in 1963, and photomicrographs of three of them are illustrated on Plate 42, figs. 3–5. In addition, Hall and Clarke's type specimen of *Barrandella areyi* was borrowed from the New York State Museum; this is the specimen illustrated by these authors on Plate 71, figs. 14–16 (and reillustrated here on Pl. 42, figs. 6–10); it is the only one in their collection and therefore the holotype.

In 1953 the writer assigned *Barrandella areyi* to the genus *Pentamerella* on the basis of its costate exterior and brachial cruralium; however, it differs from that genus in having a carinate brachial apparatus and is here assigned to a new genus and included in the Clorindinae.

C. areyi is present in the Irondequoit Limestone (?late Llandoveryan) near Rochester, New York. The writer has also examined U.S. National Museum specimens from

Lockport, New York, which are externally very much like the Irondequoit specimens, although internally they differ slightly in having a sessile cruralium.

Acknowledgements. The writer is indebted to Dr. Arthur J. Boucot who has generously furnished information and access to manuscripts in advance of publication. The present study has been aided by the loan of a number of specimens: Dr. G. Arthur Cooper of the U.S. National Museum loaned topotypes of *Pentameroides subrectus* and *Clorindella areyi*; Dr. A. Lee McAlester of Yale University loaned topotypes of *Pentameroides subrectus*; Dr. Roger L. Batten of the American Museum of Natural History loaned Hall's types of *Pentamerella arata*; Dr. Gunnar Henningsmoen of the Paleontologisk Museum at Oslo loaned specimens of *Conchidium munsteri*; Mr. William Kilgour furnished specimens of *Pentameroides sp.* from the Reynales Limestone, Thorold, Ontario. The writer also wishes to thank Dr. William A. Oliver, Jr., of the U.S. Geological Survey for supplying information on the stratigraphic range of *Pentamerella arata*.

Publication of this paper was authorized by the director of the Oklahoma Geological Survey.

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A MIOSPORE ASSEMBLAGE FROM THE PERMIAN OF IRAQ

by H. P. SINGH

ABSTRACT. A dispersed miospore assemblage comprising 32 genera and 49 species is described from a shale core sample. Two miospore genera, *Iraqispora* and *Mosulipollenites*, and 27 species are new. The material is from Atshan well in the Chia Zairi formation near Mosul in northern Iraq. The miospore flora described here is compared with comparable spore floras of Permian age. On the basis of this study, it is suggested that this spore composition corresponds to an Upper Permian age.

THE miospore flora described in this paper was obtained by macerating a shale core sample from the Chia Zairi formation (Permian) 801 feet below the top of the Atshan well which lies at a distance of about 12 miles west of Mosul in northern Iraq. The lithological sequence of this formation, as reported by Wetzel (1956), shows that the Chia Zairi formation overlies the Harur limestones (Lower Carboniferous) unconformably, but is in turn conformably overlain by the Mirga Mir formation which is of Lower Triassic age.

This miospore assemblage is referred to 32 genera and 49 species, of which 2 genera, *Iraqispora* and *Mosulipollenites*, and 27 species are new. Two miospore genera, *Vestigisporites* (Balme and Hennelly) Hart and *Fimbriaesporites* Leschik, are critically examined. The spore assemblage is described, illustrated and arranged according to the artificial system of classification proposed by Potonié and Kremp (1954) and subsequently modified by Potonié (1956, 1958, and 1960).

A comparison of the Iraqi miospore assemblage has been made with the miospore floras described by Jansonius (1962), Jizba (1962), Wilson (1962), Imgrund (1960), Høeg and Bose (1960), Hart (1960), Bharadwaj (1960), Piérart (1959), Leschik (1956 and 1959), Balme and Hennelly (1955 and 1956*a, b*), Potonié and Klaus (1954), and Samoilovich (1953). On this basis, it is contended that the Iraqi spore assemblage more closely resembles those assemblages from the northern hemisphere than those from the southern hemisphere. However, the Iraqi assemblage differs from both Northern and Southern Permian assemblages, by possessing such genera as *Iraqispora*, *Mosulipollenites*, *Schopfites*, and *Kraeuselisporites* which are not known from any other Permian strata as yet.

Method of spore preparation. The miospores were extracted by macerating the shale sample in cold commercial hydrofluoric acid for 24 hours. The residue was thoroughly washed with water, centrifuged and then warmed with 50 per cent. nitric acid for 5 minutes. After this, the acid was decanted off and the washed acid-free material was further digested with a dilute solution of ammonia. The macerate was thoroughly washed with acetone and centrifuged in a solution of bromoform, diluted with acetone (1/6 volume). The float was washed free of bromoform with acetone and stored in a vial containing glycerine jelly. For the analysis of miospores, single spore mount preparations as well as general slides were made in glycerine jelly medium. All the slides, numbering from V.44220-V.44276, have been deposited in the Palaeontology Department of the British Museum (Natural History).

Acknowledgements. I am deeply grateful to Dr. W. G. Chaloner for valuable suggestions and helpful advice. I am also grateful to the Iraq Petroleum Company for making available the sample which forms the subject of this paper and to Dr. J. M. Pallot who carried out the maceration. My thanks are due to the authorities of the Commonwealth Technical Co-operation scheme for awarding me the Colombo Plan Scholarship during the tenure of which this work was started in the Botany Department, University College London, and to the authorities of the Birbal Sahni Institute of Palaeobotany for the grant of study leave.

DESCRIPTION OF DISPERSED SPORES

Anteturma SPORITES H. Pot. 1893

Turma TRILETES (Reinsch) Pot. and Kr. 1954

Subturma AZONOTRILETES Luber 1935

Infraturma LAEVIGATI (B. and K.) R. Pot. 1956

Genus LEIOTRILETES (Naum.) Potonié and Kremp 1954

Leiotriletes atshanensis sp. nov.

Plate 44, figs. 1, 2

Holotype. Plate 44, fig. 1; slide V.44225.

Diagnosis. Size 35–45 μ (15 specimens), Y-rays two-thirds to three-quarters the radius, exine 1.5–2 μ thick, strongly intrapunctate.

Description. Holotype 42 μ , triangular with broad angles and straight to slightly concave sides. Trilete mark distinct, Y-rays simple, equal, usually three-quarters the radius, ray-ends occasionally bifurcating. Exine 1.5 μ thick, finely but densely intrapunctate. Margin of the spore smooth. Secondary folds rare.

Comparison. *Leiotriletes gracilis* Imgr. and *L. directus* Balme and Henn. differ in having elevated and sinuous Y-rays. Apparently, *L. sphaerotriangulus* (Loose) Pot. and Kr. is comparable with *L. atshanensis* but it differs by virtue of its thinner exine and longer Y-rays. Other species do not compare closely.

Leiotriletes magnificus sp. nov.

Plate 44, figs. 3, 4

Holotype. Plate 44, fig. 3; slide V.44220.

Diagnosis. Size 22–33 μ (15 specimens), triangular with straight-convex sides. Y-rays more than three-quarters of the radius, exine 0.5–1.0 μ thick, very finely intrapunctate.

Description. Holotype 30 μ , triangular with straight to convex sides and rounded corners. Trilete mark distinct, Y-rays long, simple, ray-ends hair thin. Exine about 1 μ thick, finely intrapunctate, rarely folded. Margin of the spore smooth.

Comparison. *Leiotriletes atshanensis* differs from this species by having a greater size and thicker exine. *L. sporadicus* (Imgr.) Pot. & Kr. has a laevigate exine, and longer Y-rays with apparently raised apex and smaller size (20–26 μ). *L. gracilis* Imgr. differs in possessing thicker exine and distinct labra. *L. subadnatoides* Bhard. has broader angles and thicker exine. *L. adnatus* (Kos.) Pot. & Kr. is different in being larger.

Leiotriletes cf. *gracilis* Imgrund 1960

Plate 44, fig. 5

Description. Miospore triangular with straight to slightly concave sides and round angles. Trilete mark distinct, Y-rays ending slightly before the equator. Exine $\pm 1 \mu$ thick in optical section, intrapunctate, secondary folds apparent.

Comparison. In size, thickness of exine, and the length of Y-rays the specimen referred here as *L.* cf. *gracilis* compares well with the illustration of the holotype of *L. gracilis* Imgr., but it does not show distinctly the broad labra of the holotype.

Leiotriletes rarus sp. nov.

Plate 44, fig. 6

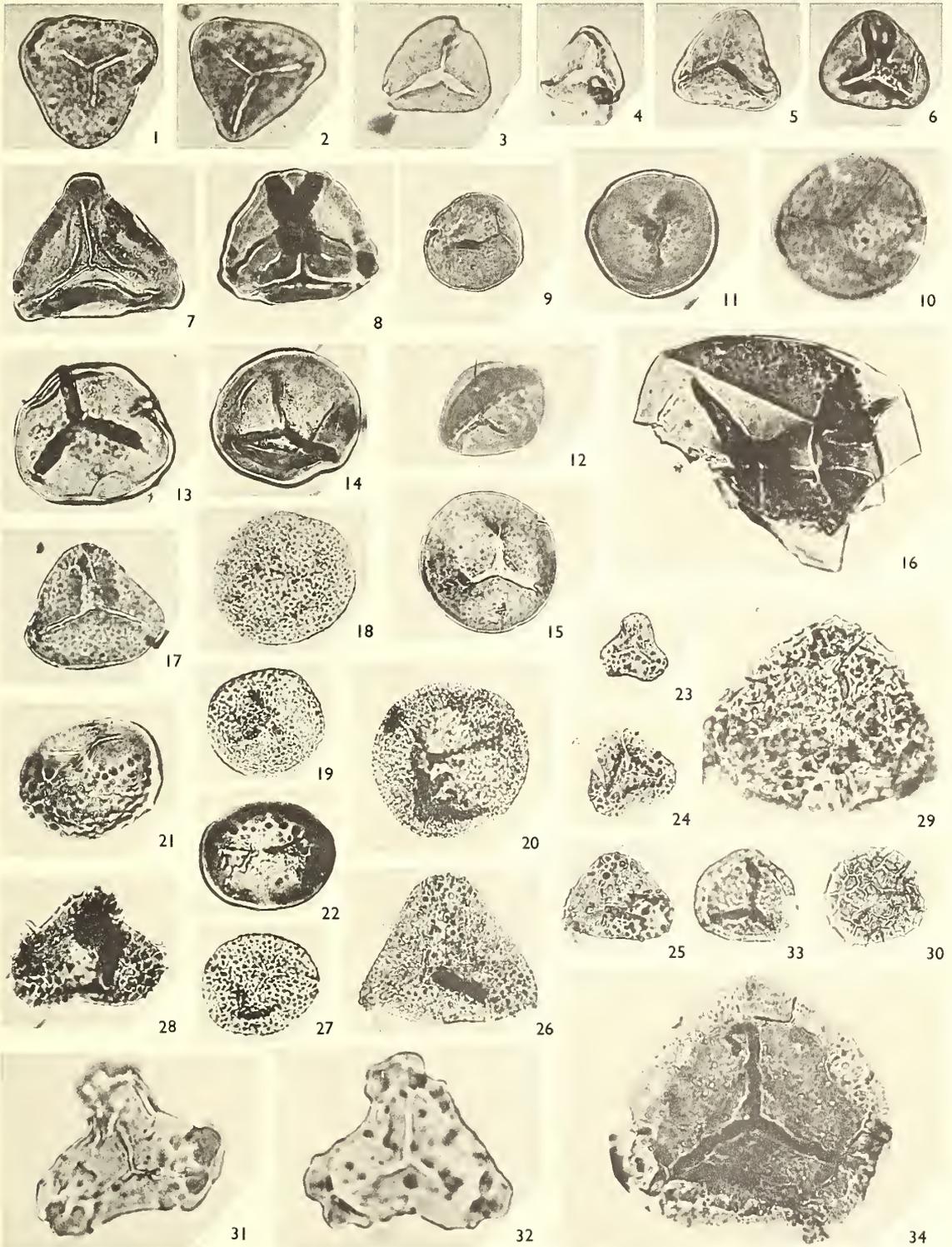
Holotype. Plate 44, fig. 6; slide V.44235.

Diagnosis. Size 25–35 μ (10 specimens), Y-rays three-quarters the radius, bounded by concave, darker, thicker, and about 3 μ broad, bands of interradian exine; exine approximately 1 μ thick, intrapunctate, sometimes folded.

Description. Holotype 30 μ , triangular with broadly rounded corners and straight to slightly convex sides. Trilete mark conspicuous, Y-rays extending up to three-quarters

EXPLANATION OF PLATE 44

- All figures are from unretouched negatives and unless otherwise stated are $\times 500$.
- Figs. 1–6. *Leiotriletes* spp. 1–2, *L. atshanensis* sp. nov. 1, Proximal face; V.44225. 2, Proximal face; V.44223. 3–4, *L. magnificus* sp. nov. 3, Proximal face; V.44220. 4, Proximal face; V.44275. 5, *L.* cf. *gracilis* Imgr., proximal face; V.44220. 6, *L. rarus* sp. nov., proximal face; V.44235.
- Figs. 7–8. *Iraqispora labrata* gen. et sp. nov. 7, Proximal face; V.44256. 8, Laterally compressed; V.44223.
- Figs. 9–14. *Punctatisporites* spp. 9, *P. obliquus* Kos., laterally compressed; V.44249. 10, *P. pyramidicus* sp. nov., proximal face; V.44237. 11–12, *P. spathulatus* sp. nov. 11, Distal face; V.44223. 12, Proximal face; V.44224. 13–14, *P. sp.* 13, Proximal face; V.44220. 14, Proximal face; V.44226.
- Fig. 15. ? *Retusotriletes* sp., proximal face; V.44236.
- Fig. 16. *Calamospora* sp., proximal face; V.44226.
- Fig. 17. *Granulatisporites parvus* (Ibr.) Pot. and Kr., proximal face; V.44228.
- Figs. 18–20. *Cyclogranisporites varius* sp. nov. 18, Distal face; V.44251. 19, Proximal face; V.44223. 20, *C.* cf. *parvipunctatus* (Kos.) Bhard., proximal face; V.44239.
- Figs. 21–22. *Schopfites lateralis* sp. nov. 21, Laterally compressed, proximal face smooth; V.44235. 22, Proximal face; V.44222.
- Figs. 23–26. *Lophotriletes* spp. 23, *L. sparsus* sp. nov., Proximal face; V.44220. 24–25, *L. novicus* sp. nov. 24, Proximal face; V.44220. 25, Proximal face; V.44221. 26, *L. sp.*, proximal face; V.44260.
- Fig. 27. *Apiculatisporis decorus* sp. nov., proximal face; V. 44261.
- Fig. 28. *Neoraistrickia pilata* sp. nov., proximal face; V.44224.
- Fig. 29. *Campotriletes* sp., proximal face; V.44220.
- Fig. 30. *Lycopodiumsporites* sp., distal face; V.44221.
- Figs. 31–32. *Triquitrites iraqiensis* sp. nov. $\times 1,000$. 31, Proximal face; V.44222. 32, Proximal face; V.44247.
- Fig. 33. *Anguisporites minutus* sp. nov., proximal face; V.44252.
- Fig. 34. *Cirratriradites surangei* sp. nov., proximal face; V.44224.



the radius but not reaching the equator; interrarial thickening of the exine prominent and dark. Exine intrapunctate and folded. Margin of the spore smooth.

Comparison. *L. atshaneusis*, *L. magnificus*, and *L. cf. gracilis* lack the prominent inter-radial thickening of the exine of *L. rarus* and hence do not compare with the latter.

Genus IRAQISPORa gen. nov.

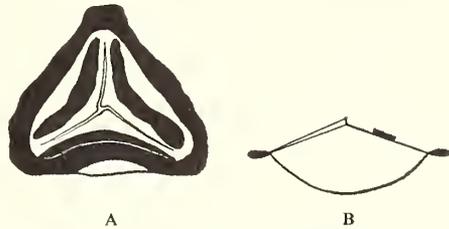
Text-fig. 1a, b

Type species. *Iraqispora labrata* gen. et sp. nov.

Generic diagnosis. Miospores triangular to subtriangular, angles sharply to broadly rounded. Trilete mark always prominent, Y-rays reaching up to or ending just before the equator, characteristically bent near the apex, interrarial thickening broad near the Y-mark. Exine thicker at the equator, sometimes even thicker at the angles, thinner and lighter elsewhere, perceptibly sculptured.

Comparison. *Dictyophyllidites* Couper and *Paraconcavisporites* Klaus are similar to *Iraqispora* in having comparable types of Y-mark and inter-radial thickening near the Y-mark but both of these form genera differ widely from the latter in lacking thickened exine near the equator.

Other genera such as *Gleicheniidites* (Ross) Delc. & Sprum., *Concavisporites* (Pflug) Delc. & Sprum., and *Ahrensispores* Pot. & Kr. differ from *Iraqispora* in usually having concave sides, straight Y-rays and exine with a different distribution of thickening.



TEXT-FIG. 1. A, *Iraqispora labrata* gen. et sp. nov. in polar view, proximal face; B, the same in median section. V.44256, $\times 500$.

Iraqispora labrata sp. nov.

Plate 44, figs. 7, 8

Holotype. Plate 44, fig. 7; slide V.44256.

Diagnosis. See generic diagnosis.

Description. Holotype $48 \times 42 \mu$, dark brown, triangular in polar view with convex sides and round (or more or less flat) corners. Trilete mark conspicuous, Y-rays long, reaching or ending just before the equator, labra thick, elevated, characteristically bent at the apex, interrarial thickening of the exine near the vicinity of trilete apparatus arcuate, $4-7 \mu$ broad, darker and thicker. Equatorial exine about 5μ thick or more so at the angles, lighter and thinner elsewhere; finely intrapunctate to punctate proximally and distally. Margin of the spore smooth.

Genus *Punctatisporites* (Ibrahim) Potonié and Kremp 1954

Punctatisporites obliquus Kosanke

Plate 44, fig. 9

Remarks. The specimen figured here (5 specimens examined) appears to have a thicker exine as compared to the illustration of the holotype of *P. obliquus*. But its other

morphographic characters such as size, shape, triradiate mark, length and nature of the Y-rays and exine ornamentation are the same as that of *P. obliquus*.

Punctatisporites pyramidicus sp. nov.

Plate 44, fig. 10

Holotype. Plate 44, fig. 10; slide V.44237.

Diagnosis. Size 40–60 μ (10 specimens), circular to subtriangular, Y-rays reaching the radius, exine 2.5 to 3.5 μ thick, dark brown, laevigate, proximal surface deeply convex, distal surface \pm flat.

Description. Holotype 44 μ across, \pm circular in polar view. Triradiate mark apparent, Y-rays long and extending up to the full length of the radius, simple, ray-ends bifurcating. Exine 2.5 μ thick in optical section, laevigate. Spore surface proximally convex, distally flat. Margin of the spore smooth.

Comparison. *Punctatisporites gretensis* Balme and Henn., occurring in the Permian of Australia (Balme and Henn. 1956) and Tanganyika (Hart 1960), differs from *P. pyramidicus* by having an apparently ornamented exine, and shorter Y-rays. In *P. punctatus* Ibr. Y-rays extend up to the equator and the exine is thinner. Other species of *Punctatisporites* do not compare closely.

Remarks. From the description of *Punctatisporites pyramidicus*, it might seem that it could as well either be referred to *Stenozonotriletes* (Naum.) Pot. 1956, or *Asterocalamotriletes* (Luber) Pot. 1958, if the thickening of the exine be interpreted in terms of a cingulum. The presence of a wide suture and the type of bifurcation of the ray-ends before the equator, as illustrated by Potonié (1958, pl. 2, fig. 17) for the emended diagnosis of the type species of *Asterocalamotriletes* and the union of the Y-rays with the central body and cingulum, is not apparent in the specimens which I have referred to *P. pyramidicus*. The other genus *Stenozonotriletes* has a distinct cingulum and apparently shorter Y-rays and thus it cannot accommodate such spores as those described here under *P. pyramidicus*.

Punctatisporites spathulatus sp. nov.

Plate 44, figs. 11, 12

Holotype. Plate 44, fig. 12; slide V.44224.

Diagnosis. Size 40–50 μ (10 specimens), circular to subcircular, Y-rays two-thirds to three-quarters the radius, labra thick, exine about 2 μ thick, laevigate.

Description. Holotype 44 μ , miospores assuming different contours due to folding of the exine. Triradiate mark prominent with sinuous and raised Y-rays, reaching nearly three-quarters the radius, labra thick. Exine about 1.5 μ thick in optical section, laevigate. Margin of the spore smooth.

Comparison. In *Punctatisporites pyramidicus* the Y-rays are longer and thinner. *P. obliquus* has a thinner exine. *P. sp.* (below) differs in having longer Y-rays, broader labra, and a thinner exine.

Punctatisporites sp.

Plate 44, figs. 13, 14

Description. Circular in polar view, 48 μ across. Triradiate mark very prominent, Y-rays reaching more than three-quarters the radius, elevated, labra 3.5 μ broad, not flexuose. Exine thin, intrapunctate. Margin of the spore smooth.

Comparison. *Punctatisporites* sp. has a more prominent Y-mark than any other known species of this genus. Only two specimens were found.

Genus RETUSOTRILETES Naumova 1953

? *Retusotriletes* sp.

Plate 44, fig. 15

Description. Size 40–50 μ , circular in polar view. Trilete mark prominent, Y-rays extending up to or more than three-quarters the radius, ray-ends marked by broad contact faces, curvaturae appear to be incomplete. Exine about 1.5 μ thick, thicker at the equator, intrapunctate, lighter at the contact faces.

Genus CALAMOSPORA Schopf, Wilson and Bentall 1944

Calamospora sp.

Plate 44, fig. 16

Description. Size 100–150 μ , originally circular but appears variable in shape owing to secondary folds in the exine. Triradiate mark conspicuous, tecta flexuose and reaches two-thirds of the radius, elevated, slightly sinuous, contact area not apparent. Exine about 1 μ thick in optical section, finely structured, secondary folds large. Margin of the spore smooth.

Comparison. *C. diversiformis* Balme and Henn. is smaller (24–53 μ), with a thicker spore coat and a distinct contact area. *C. breviradiata* Kosanke and *C. minuta* Bhardwaj compare with *C. sp.* in having flexuose tecta but both these species are appreciably smaller.

Infraturma APICULATI (Bennie and Kidston) Potonié 1956

Genus GRANULATISPORITES (Ibrahim) Potonié and Kremp 1958

Granulatisporites parvus (Ibrahim) Potonié and Kremp

Plate 44, fig. 17

Description. Size 36–40 μ (5 specimens), triangular in equatorial contour, sides more or less straight. Y-rays extending up to or slightly more than three-quarters of the radius. Exine about 1.5 μ thick, densely granulose.

Genus CYCLOGRANISPORITES Potonié and Kremp 1954

Cyclogranisporites varius sp. nov.

Plate 44, figs. 18, 19

Holotype. Plate 44, fig. 19; slide V.44223.

Diagnosis. Size 35–50 μ (50 specimens). Y-rays up to or slightly more than two-thirds radius long, exine ornamented with sparsely spaced, small grana and con.

Description. Holotype $36\ \mu$, circular in polar view, Y-rays conspicuous, one Y-arm usually longer than the other two. Exine covered with sparsely spaced grana and coni, grana outnumbering the coni, fifty to eighty in number along the perimeter.

Comparison. The specimens referred here to *C. varius* appear to me to represent a borderline case between the two genera *Cyclogranisporites* and *Planisporites* (Knox) Pot. and Kr. 1954 because these specimens possess both grana and small coni as ornamentation of the exine. In view of this, I have taken into consideration the distribution of grana along the perimeter of the spore and if they are represented by half or more, in comparison to the representation of coni, then I have included these specimens under *Cyclogranisporites*. If the proportion of coni is more than half, then I have described them elsewhere. The coni are extremely small, and can only be made out from the similarly small, neighbouring grana by their pointed ends which usually project beyond the margin of the flattened spores. This character of mixed sculptural elements of grana and coni separates *C. varius* from the other known species of *Cyclogranisporites*.

Cyclogranisporites cf. *parvipunctatus* (Kosanke) Bhardwaj

Plate 44, fig. 20

Description. Circular in polar view, $46\ \mu$ in diameter. Y-rays faintly discernible and extending up to nearly three-quarters the radius. Exine about $2\ \mu$ thick, beset with closely spaced, rounded sculptural elements which are rather longer than broad, giving a velvety appearance to the surface of the exine; about 180 elements are present along the perimeter. Both margin and surface appear rough.

Remarks. In the exine pattern the specimen of *C.* cf. *parvipunctatus* figured is comparable with the illustration of the holotype of *C. parvipunctatus* (Kos.) Bhard. and also with the specimens figured by Bhardwaj (1957, pl. 23, figs. 3–6) from the Saar coals, but it differs from the latter in the presence of longer Y-rays and bigger size.

Genus SCHOPFITES Kosanke 1950

Schopfites lateralis sp. nov.

Plate 44, figs. 21, 22

Holotype. Plate 44, fig. 21; slide V.44235.

Diagnosis. Size 36 – $52\ \mu$ (20 specimens), circular to oval in polar view, usually laterally flattened, Y-rays 10 – $15\ \mu$ long, elevated, distal surface beset with sparsely to closely spaced, rounded warts of variable shape, measuring $2.6\ \mu$ – $4.4\ \mu$ in diameter.

Description. Holotype $38\ \mu$, dark brown, originally circular in equatorial contour but appearing oval due to lateral flattening. Exine about $3\ \mu$ thick, laevigate proximally, and distally covered with rounded rather variable wart-like elements which tend to extend slightly on to the proximal surface. The exine between the warty projections is punctate.

Comparison. *S. dimorphus* Kos. and *S. colchesterensis* Kos. are described by Kosanke (1950) from the Carbondale Formation of the Pennsylvanian of Illinois. Both these species differ from *S. lateralis* in being larger (78 – $115\ \mu$). *S. saarensis* Bhard. has exine ornamentation of coni and in this character it does not compare with *S. lateralis*.

Genus *LOPHOTRILETES* (Naumova) Potonié and Kremp 1954*Lophotriletes sparsus* sp. nov.

Plate 44, fig. 23

Holotype. Plate 44, fig. 23; slide V.44220.

Diagnosis. Size 20–25 μ (10 specimens), triangular, sides concave, Y-rays two-thirds radius in length, exine ornamented with small sparse coni, ten to fifteen in number along the perimeter.

Description. Holotype 22 μ , with concave sides and broadly rounded angles. Triradiate mark clear; sometimes one Y-arm tends to be longer than the other two, and the interradial exine darker than the remainder in some specimens. Exine about 1 μ thick in optical section, ornamented with very sparsely spaced, small coni of irregular size, the space between the adjoining coni often granulose.

Comparison. In size and length of Y-rays *L. commissuralis* and *L. sparsus* are comparable but the ornamentation in the former is denser and thicker.

Lophotriletes novicus sp. nov.

Plate 44, figs. 24, 25

Holotype. Plate 44, fig. 24, slide V.44220.

Diagnosis. Known size 26–32 μ (5 specimens), triangular, sides concave, Y-rays two-thirds of the radius or more, interradial area thickened, exine ornamented with coni, aggregating at the corners, about thirty in number along the equator.

Description. Holotype 25 μ , triangular with concave sides and broadly rounded angles. Y-rays two-thirds the radius in length, interradial exine thickened. Exine bearing small, widely spaced coni, more densely aggregated at the corners, thirty in number along the perimeter.

Comparison. No previously described species of *Lophotriletes* shows this character of large coni, densely aggregated at the corners and thickened interradial exine.

Remarks. In most of the specimens referable to *L. novicus* the exine is ornamented with coni but in some cases (e.g. Pl. 44, fig. 26) in addition to coni, there are elements which are more comparable to baculae than coni.

Lophotriletes sp.

Plate 44, fig. 26

Description. Miospore triangular in equatorial contour, sides \pm straight with broad angles. Trilete mark distinct, Y-rays ending just before the apices. Exine about 1 μ thick, beset with coni of varying sizes, interspersed with fewer, flat-tipped baculae, sculptural elements apparently tend to aggregate more at the apices than elsewhere. Out of fifty-five processes present along the circumference, forty-five are coni and the rest are baculae.

Remarks. The specimen figured here is the only representative of its kind met with in this spore assemblage. As evident from the description and illustration of the specimen, the

exine has a combination of mixed sculptural elements, with more conii than small bacula. On account of this, it has been tentatively assigned to the genus *Lophotriletes* although the presence of bacula suggests its comparison with *Conbaculatisporites* Klaus.

Genus *APICULATISPORIS* Potonié and Kremp 1956

Apiculatisporis decorus sp. nov.

Plate 44, fig. 27

Holotype. Plate 44, fig. 27; slide V.44261.

Diagnosis. Size 35–45 μ (30 specimens), Y-rays two-thirds to three-quarters radius long, two Y-arms usually longer than the third, exine thin, ornamented with sparsely spaced, small conii, forty to sixty in number along the perimeter.

Description. Holotype 38 μ , circular, secondary folds rare. Triradiate mark usually apparent, sometimes faint or obscure, Y-rays simple, unequal, running two-thirds to three-quarters of the radius, ray-ends not bifurcating. Exine about 1 μ thick in optical section, covered with sparsely spaced, small conii; the average space between two conii could accommodate one to two more conii of similar size.

Comparison. *A. decorus* has smaller conii than any other species of *Apiculatisporis*. In this respect, it approaches the genus *Planisporites* (Knox) Pot. and Kr. *A. latigranifer* (Loose) Imgr. has somewhat comparable conii but it is distinctly bigger (55–90 μ) than *A. decorus*.

Genus *NEORAISTRICKIA* Potonié 1956

Remarks. Potonié (1956) has instituted *Neoraistrickia* to accommodate spores which are triangular and have baculate ornamentation, citing *Triletes truncatus* Cookson (1953, pl. 2, fig. 36) as its type species. The figure of the type species of *Neoraistrickia* shows more or less convex sides. The specimens described here, have comparable ornamentation with the type species of *Neoraistrickia*, but they have more or less concave sides. Despite this difference, I have included such forms in *Neoraistrickia*. Similar specimens have been noted by Hart (1960, p. 4) occurring in the East African material but they have not been figured or described by him.

Neoraistrickia pilata sp. nov.

Plate 44, fig. 28

Holotype. Plate 44, fig. 28; slide V.44224.

Diagnosis. Size 40–50 μ (10 specimens), sides more or less concave, Y-rays more than three-quarters the radius, exine baculate, bacula 1–3 μ broad at the base, 2–5 μ long, numbering thirty to thirty-five along the perimeter, tending to aggregate at the angles.

Description. Holotype 48 μ , triangular with more or less concave sides and broad angles. Triradiate mark clear, Y-rays the length of the radius. Exine about 1 μ thick in optical section, baculate, bacula tending to concentrate at the angles, sparsely spaced at the sides.

Comparison. Both *N. truncata* (Cookson) Pot. and *N. neozealandica* (Coup.) Pot. are species of younger horizons occurring in the Tertiary and Jurassic strata respectively.

Both these species differ from *N. pilata* in having bigger bacula. *N. ramosa* (Balme and Henn.) Hart has more or less convex sides and bigger bacula.

Infraturma MURORNATI Potonié and Kremp 1954

Genus CAMPTOTRILETES Naumova 1937

Camptotriletes sp.

Plate 44, fig. 29

Description. Miospore triangular, $64 \times 56 \mu$, sides straight-convex, angles broad. Y-rays three-quarters of the radius in length, simple, open, ray-ends hair-thin. Exine brownish red, about 2.5μ thick in optical section, covered with coni $3-4.5 \mu$ broad, $2-3 \mu$ high and sharply tipped. The bases of the coni are confluent, thus building rudimentary cristae; the proximal exine is intrapunctate.

Comparison. *Camptotriletes biornatus* Balme and Henn. is bigger ($89-127 \mu$) and possesses coarser verrucae.

Genus LYCOPODIUMSPORITES Thiergart 1938

Lycopodiunsporites sp.

Plate 44, fig. 30

Description. Miospore subcircular in equatorial contour, measuring 34μ across. Trilete mark faint but discernible, Y-rays reaching three-quarters the radius. Exine reticulate, proximally as well as distally, meshes polygonal, $5-7 \mu$ broad, four to six in number across the diameter, muri thin and high, fine grana evident both on the proximal and distal surfaces.

Remarks. Only two specimens referable to the genus *Lycopodiunsporites* sp. have been found from this assemblage. Both these specimens show reticulate exine on the proximal as well as distal surface.

Turma ZONALES (Bennie and Kidston) Potonié 1956

Subturma AURITOTRILETES Potonié and Kremp 1954

Infraturma AURICULATI (Schopf) Potonié and Kremp 1954

Genus TRIQUITRITES Wilson and Coe 1940

Triquitrites iraqiensis sp. nov.

Plate 44, figs. 31, 32

Holotype. Plate 44, fig. 32; slide V.44247.

Diagnosis. Size $25-30 \mu$ (5 specimens), Y-rays almost extending up to the angles, angles bearing cushion-like auriculae, projecting beyond the spore margin but limited only to the angles, exine punctate, puncta 0.5 to 1μ in diameter.

Description. Holotype 26μ , triangular in polar view with concave sides having cushion-like auriculae at the angles. Auriculae, irregular in shape, tending to bifurcate. Y-mark clear, Y-rays reaching up to the inner margin of the auriculae. Exine thin, punctate, puncta variable in size, auriculae darkbrown, limited only to the angles, with no equatorial connexion by a flange.

Comparison. *Triquitrites brevipulvinatus* Bhard. is comparable but it differs from *T. iraqiensis* in having a smooth exine. *T. priscus* Kos., reported from the Permian of Gondwanaland by Leschik (1959), does not compare. *T. protensus* Kos. has been reported from the Lower Permian of the Kaiping basin by Imgrund (1960) and it differs from *T. iraqiensis* in having a laevigate exine.

Subturma ZONOTRILETES Waltz 1935
Infraturma CINGULATI Potonié and Klaus 1954
Genus ANGUISPORITES Potonié and Klaus 1954
Anguisporites minutus sp. nov.

Plate 44, fig. 33

Holotype. Plate 44, fig. 33; slide V.44252.

Diagnosis. Size 28–35 μ (15 specimens), central body subtriangular surrounded by an equatorially attached cingulum, Y-mark as long as the radius not extending beyond the central body, exine granulose on both the faces.

Description. Size 28–35 μ (15 specimens). Holotype 30 μ , subtriangular to almost circular with a subtriangular central body, measuring 22 μ in the holotype, surrounded by an equatorially attached cingulum, uniformly about 4 μ broad. Trilete mark prominent, Y-rays as long as the radius, not extending beyond the central body, labra thick and undulating. Exine of the central body granulose proximally as well as distally. Cingulum coarsely granulose. Surface and margin of the spore rough.

Comparison. *A. anguinus* Potonié and Klaus is just double the size of *A. minutus*. Grebe (1957, pl. 1, fig. 10) has figured cf. *A. anguinus* from the Zechstein, Germany, which is not a very clear specimen. However, it falls within the size range of *A. minutus*. *A. intonsus* Wilson also differs from *A. minutus* in being larger (48–55 μ). *A. contortus* Wilson has contorted ornamentation of the body exine.

Infraturma ZONATI Potonié and Kremp 1954
Genus CIRRATRIRADITES Wilson and Coe 1940
Cirratriradites surangei sp. nov.

Plate 44, fig. 34; Plate 45, fig. 1

Holotype. Plate 44, fig. 34; slide V.44224.

Diagnosis. Size 75–100 μ (10 specimens), subtriangular to subcircular, central body subtriangular, about 50 μ , flanged by an equatorial zona, about 9 μ broad, Y-rays raised, long, extending into the zona, labra thick, undulating, exine of the central body finely granulose, having small coni of variable size; one to three circular to triangular distal polar foveolae apparent.

Description. Holotype 80 μ , subtriangular in polar view, having a subtriangular central body, surrounded by an equatorially attached flange. Central body darker in colour as compared to the flange, proximally bearing a conspicuous Y-mark; Y-rays undulating and running over a part of the zona, labra dark, thick and elevated. Exine granulose both on the distal and proximal faces of the central body, interspersed with very widely spaced coni of variable size and form in the same specimen. Distally the central body

has a distinct triangular area composed of a thinner central exine, surrounded by a thicker border. Zona finely structured or sculptured. Margin of the spore irregular.

Comparison. *C. splendens* Balme & Henn. does not show such thick labra and undulating Y-mark and distal foveolae, as does *C. surangei*. In *C. annuliformis* Kos. and Brok., the central body exine is punctate. *C. difformis* Kos. differs in having faintly reticulate exine of the central body. *C. annulatus* Kos. & Brok. is comparable with *C. surangei* but it differs from the latter by lacking grana and coni on its exine.

Turma MONOLETES Ibr. 1933

Subturma AZONOMONOLETES Luber 1935

Infraturma LAEVIGATOMONOLETI Dybova and Jachowitz 1957

Genus LAEVIGATOSPORITES Ibrahim 1933

Laevigatosporites sp.

Plate 45, fig. 2

Description. Miospore $84 \times 62 \mu$, bilateral. Monolete-slit three-quarters the length of the spore or ending just before the poles. Exine appears structured and also corroded. Secondary folds present.

Genus LATOSPORITES Potonié and Kremp 1954

Latosporites intragramulosus sp. nov.

Plate 45, figs. 3, 4

Holotype. Plate 45, fig. 3; slide V.44241.

Diagnosis. Size $88-110 \mu$ (5 specimens), broadly oval to subcircular, monolete mark two-thirds to three-quarters the radius, exine intragramulose, distally strongly arched.

Description. Holotype 90μ , broadly oval to subcircular in polar view having distal surface strongly arched, apparent on lateral flattening of the spores. The monolete mark is usually two-thirds the radius in length, sometimes extending up to three-quarters the radius. Exine about 1μ thick in optical section, densely intragramulose, grana fine. Margin of the spore smooth.

Comparison. This species is larger, and has a longer monolete-slit than any comparable species of *Latosporites*. *L. colliensis* (Balme and Henn.) Bharad. differs from *L. intragramulosus* by having a perfectly smooth exine.

Latosporites ficoides (Imgr.) Potonié and Kremp

Plate 45, fig. 5

Remarks. Only three specimens of this species were found.

Infraturma SCULPTATOMONOLETI Dybova and Jachowitz 1957

Genus PUNCTATOSPORITES Ibrahim 1933

Punctatosporites marattioides sp. nov.

Plate 45, figs. 6-8

Holotype. Plate 45, fig. 7; slide V.44255.

Diagnosis. Size $22-30 \mu$ (50 specimens) oval, monolete-slit three-quarters of the radius or longer, exine granulose, grana very fine.

Description. Holotype 22 μ , yellowish-brown, oval in polar view. Monolete mark prominent, slit straight, usually open, slit-ends not bifurcated. Exine about 1 μ thick in optical section, granulose, grana small and closely spaced. Margin of the spore appears beaded.

Comparison. *P. marattioides* has finer grana and usually a longer monolete mark than *P. minutus* Ibr. *P. scabellus* (Imgr.) Pot. and Kr. and *P. major* Bhard. are larger with coarser grana. *P. rotundus* Bhard. and *P. granulatus* Bhard. differ in having circular shape and a smaller monolete-slit respectively. The equatorial contour of *P. nanulus* (Imgr.) Pot. and Kr. is ellipsoidal while *P. pygmaeus* (Imgr.) Pot. and Kr. differs in having the monolete-slit only half the radius long.

Genus THYMOSPORA Wilson and Venkatachala 1963

Thymospora opaqua sp. nov.

Plate 45, figs. 9–11

Holotype. Plate 45, fig. 11; slide V.44276.

Diagnosis. Size 24–33 μ (50 specimens), circular to subcircular, monolete-slit three-quarters of the radius or longer, exine dark brown, verrucose; verrucae 2–4 μ broad, 1–2.5 μ high, fourteen to twenty-six in number along the perimeter.

Description. Holotype 26 μ , more or less circular. Monolete-slit distinct, straight to curved, thin, labra indistinct, slit-ends not bifurcated. The exine is thick (exact thickness not measurable due to warty exine), verrucose, verrucae of variable size and shape, projecting beyond the spore margin where they tend to bifurcate occasionally; sometimes their bases are confluent. In addition to the verrucae, fine grana are distributed all over the exine.

Comparison. *T. verrucosa* (Alpern) Wilson and Venkatachala has almost the same size range as that of *T. opaqua* but the fainter monolete mark and coarser verrucae with sharper ends differentiates it from the latter. *T. amblyogona* Imgr. possesses a shorter monolete-slit and appears to have fewer verrucae; otherwise, it is very closely comparable to *T. opaqua*. Other Permian species of *Thymospora* reported by Balme and

EXPLANATION OF PLATE 45

All figures are from unretouched negatives and unless otherwise stated are $\times 500$.

Fig. 1. *Cirratiradites surangei* sp. nov., distal face; V.44230.

Fig. 2. *Laevigatosporites* sp., proximal face; V.44226.

Figs. 3–5. *Latosporites* spp. 3–4. *L. intragrammosus* sp. nov. 3, Proximal face; V.44241. 4, Proximal face; V.44259. 5, *L. cf. ficoides* (Imgr.) Pot. and Kr., laterally compressed; V.44231.

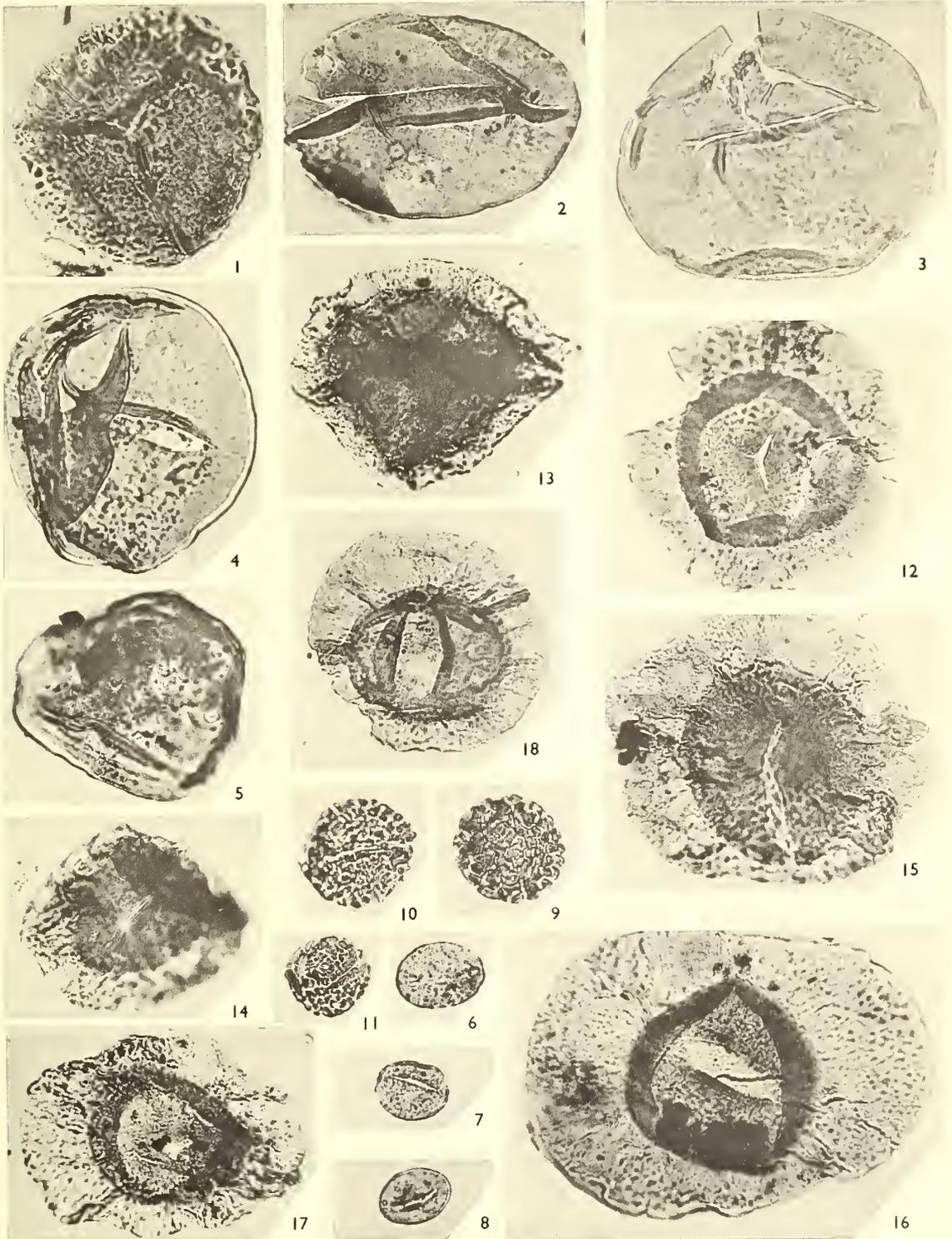
Figs. 6–8. *Punctatosporites marattioides* sp. nov. 6, Proximal face; V.44268. 7, Proximal face; V.44255. 8, Proximal face; V.44245.

Figs. 9–11. *Thymospora opaqua* sp. nov. 9, distal face; V.44225. 10, proximal face; V.44228. 11, Proximal face; V.44276.

Fig. 12. *Nuskoisporites* sp., proximal face; V.44234.

Figs. 13–15. *Mosulipollenites circularis* gen. et sp. nov. 13, Proximal face; V.44222. 14, Distal face; V.44226. 15, Proximal face; V.44222.

Figs. 16–18. *Potonieisporites* spp. 16, *P. bilateralis* sp. nov., proximal face; V.44224. 17, *P. cf. neglectus* Pot. and Lele, proximal face; V.44222. 18, *P. sp.*, proximal face; V.44236.



Hennelly (1956) and Leschik (1959) from Australia and South-west Africa respectively are not closely comparable.

Remarks. The morphographic characters of *T. opaqua* show a wide range of variation. The shape, size and number of verrucae along the perimeter of the miospore are so variable that from the casual observations it appeared that perhaps the population of *Thymospora* represented in this assemblage might consist of two or more distinct species. Therefore, a number of specimens were examined and the number of verrucae along the circumference plotted against the spore size. The resulting distribution diagram gave no indication (in these characters, at least) that the population shows any clear discontinuity.

Anteturma POLLENITES Potonié 1931

Turma SACCITES Erdtman 1947

Subturma MONOSACCITES (Chitaley) Potonié and Kremp 1954

Infraturma TRILETESACCITI Leschik 1955

Genus NUSKOISPORITES Potonié and Klaus 1954

Nuskoisporites sp.

Plate 45, fig. 12

Description. Circular in polar view, 88 μ in diameter, with subcircular central body, surrounded by a sub-equatorially attached saccus. Central body brownish-yellow, exine coarseley granulose, proximally as well as distally, unequally thick, secondary folds evident. Y-rays asymmetric with one Y-arm shorter than the other two. Saccus around the central body about 16 μ broad, intrareticulate. Limbus faintly perceptible.

Comparison. The species described here differs from *N. rotatus* Balme and Henn., in having thicker central body exine and faintly developed limbus. *N. gondwanensis* Balme and Henn. has thinner body exine and coarser saccus, showing radial orientation of the elements. *N. klausii* Grebe has longer Y-rays and coarser body exine. *N. dullhuntyi* Pot. and Kl. differs in having a symmetric Y-mark and well-developed limbus.

Infraturma VESICULOMONORADITES (Pant) Bhardwaj 1955

Genus MOSULIPOLLENITES gen. nov.

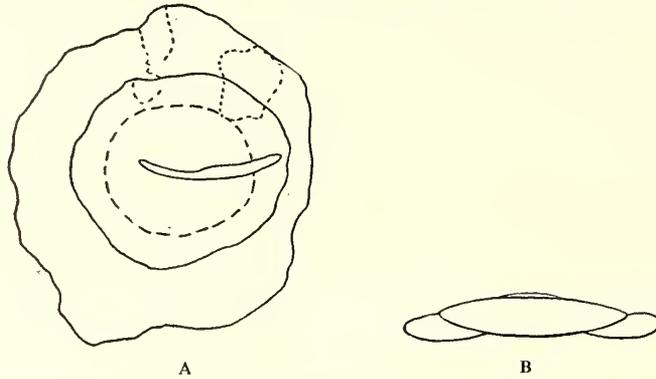
Plate 45, fig. 15; text-fig. 2a, b

Type species. *Mosulipollenites circularis* sp. nov.

Diagnosis. Monosaccate, \pm circular in polar view. Central body circular to oval, usually dark, dense and granulose. Monolete-slit apparent. Saccus usually unequally broad, attached sub-equatorially to the central body, intrareticulate. Secondary folds usually apparent running on or across the central body.

Comparison. *Mosulipollenites* differs from *Potonieisporites* Bhard. in lacking two series of folds which are reported to be characteristic for the latter genus. *Vestigisporites* (Balme and Henn.) Hart is bilateral in symmetry, ranging from monosaccate to bisaccate condition and usually does not have secondary folds on the central body. In *Hoffmeisterites* Wil. the distal attachment of the saccus is below the equator and the compression

folds on the proximal face of the body show a polygonal configuration, demarcating the area of the sulcus distally. *Saturnisporites* Kl. is reported to possess a zona around the central body and the exine in both these is usually finely punctate to granulose, often bearing short hairs. In these characters *Saturnisporites* differs from *Mosulipollenites*.



TEXT-FIG. 2. A, *Mosulipollenites circularis* gen. et sp. nov. in polar view, proximal face; B, the same in median section. V.44223, $\times 500$.

Mosulipollenites circularis sp. nov.

Plate 45, figs. 13–15

Holotype. Plate 45, fig. 15; slide V.44222.

Diagnosis. The same as generic diagnosis.

Description. Holotype about $90\ \mu$, monosaccate, $60\text{--}104\ \mu$ (10 specimens) central body dark brown, broadly oval, about $64\ \mu$ broad, saccus unequally broad, $4\text{--}20\ \mu$, subequatorially attached. Exine of the central body granulose all over, secondary folds usually present on the proximal as well as distal surface, folds irregularly arranged, running to and from the central body and the saccus. Monolete mark discernible, sometimes obscure due to the presence of thick folds, slit-ends usually sinuous, running the full length of the diameter and sometimes entering the saccus region. Saccus less broad as compared to the central body, distally leaving a more or less bladder-free circular area.

Genus POTONIEISPORITES Bhard. 1954

Potonieisporites bilateralis sp. nov.

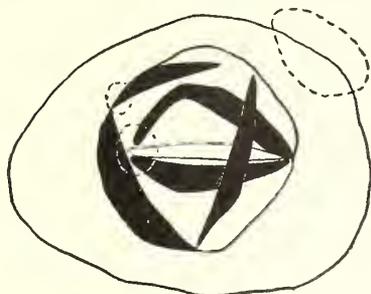
Plate 45, fig. 16

Holotype. Plate 45, fig. 16; text-fig. 3; slide V.44224.

Diagnosis. Size $100\text{--}130\ \mu$ (5 specimens), bilateral, two central body folds crescentic, longitudinal, enclosing a horizontal, monolete-slit. Bladder intrareticulate.

Description. Holotype $124\ \mu$, with a subcircular to oval central body, having a long monolete-slit, running parallel to the longer axis, open, slit-ends not bifurcated. Secondary folds dark, lying perpendicular to the slit-ends near the periphery of the central body. Exine thick, dark brown, indeterminably ornamented. Bladder of variable width, intrareticulate, meshes small.

Comparison. *P. bilateralis* has a dark subcircular to oval central body, and possesses only one set of folds; it is thus not comparable to *P. novicus* Bhard. which has a circular central body and a double set of folds. *P. neglectus* Pot. and Lele differs from *P. bilateralis* in having a trapezoidal central body and finer meshes of the saccus.



TEXT-FIG. 3. *Potonieisporites bilateralis* sp. nov.; proximal face showing the monoete mark and the folding of the central body exine; V.44224, $\times 500$.

Potonieisporites cf. *neglectus* Pot. and Lele

Plate 45, fig. 17

Holotype. Potonié and Lele 1959, pl. 3, fig. 64.

Remarks. The organization of the specimen figured here is comparable to *P. neglectus* but differs from it in having a shorter monoete-slit.

Potonieisporites sp.

Plate 45, fig. 18

Description. Miospore 82μ , bilateral, central body oval to elliptical, having two series of folds (as described by Bhardwaj 1954). Monoete-slit presumably corresponding to a thinner patch of exine in the centre (parallel to the transverse axis of the miospore). Bladder intrareticulate, radially folded, without any recognizable limbus.

Comparison. It differs from *P. bilateralis* and *P. novicus* Bhard. in having an ill-defined monoete mark and radially directed elements of the bladder.

Genus VESTIGISPORITES Balme and Hennelly *emend.* Hart 1960

Remarks. In the diagnosis of *Vestigisporites*, Balme and Hennelly (1955, p. 95) have included both the disaccate and monosaccate forms. The type species of the genus, *V. rudis* (Balme and Henn. 1955, pl. 6, fig. 54), although disaccate, appears to have a lateral connective joining the two sacci. Later Hart (1960) emended the diagnosis of *Vestigisporites* and recognized the monosaccate organization of the forms referable to this genus, suggesting that the disaccate condition could have arisen on account of lateral reduction of the saccus. My observations, on two new species from this assemblage, *V. granulosis* sp. nov., and *V. deusus* sp. nov., support Hart's view.

Vestigisporites granulosus sp. nov.

Plate 46, fig. 1

Holotype. Plate 46, fig. 1; slide V.44240.

Diagnosis. Size 90–110 μ (15 specimens), monosaccate tending to be disaccate, central body horizontally oval, granulose with a monolete mark, bladder attachment sub-equatorial.

Description. Holotype 106 \times 70 μ , bilateral, monosaccate tending to be disaccate. Central body ill-defined, oval, elongated parallel to the overall elongation, granulose proximally as well as distally. Monolete mark present, about 20 μ long, open. Bladder attachment subequatorial, laterally usually confluent, notched at one side, bladder-free-area usually wide, intrareticulate, meshes fine.

Comparison. *V. hennellyi* Hart and *V. dissectus* Hart differ from *V. granulosus* in having either a well-defined central body or a longer monolete mark, or both.

Vestigisporites densus sp. nov.

Plate 46, figs. 2, 3

Holotype. Plate 46, fig. 2; slide V.44225.

Diagnosis. Size about 120 μ , bilateral, monosaccate, tending to be bisaccate, central body dark brown, elongated parallel to the overall elongation, bladder meshes usually radially elongated.

Description. Holotype about 120 μ , bilateral, monosaccate pollen grain with dark brown oval central body bearing a straight to slightly raised monolete mark (presumably on the proximal surface) less than two-thirds radius long measured from the slit-ends. Exine of the central body intragranulose. Bladder much elongated, subequatorially attached and intrareticulate.

Comparison. No other species of *Vestigisporites* has such a dark brown and dense central body as is found in *V. densus*.

EXPLANATION OF PLATE 46

All figures are from unretouched negatives and unless otherwise stated are \times 500.

Figs. 1–3. *Vestigisporites* spp. 1, *V. granulosus* sp. nov., proximal face; V.44240. 2–3, *V. densus* sp. nov. 2, Proximal face; V.44225. 3, Distal face; V.44223.

Fig. 4. *Lueckisporites* sp., proximal face; V.442230.

Figs. 5–8. *Striatites* spp. 5–7, *S. medius* sp. nov. 5, Proximal face; V.44274. 6, Proximal face; V.44263. 7, Proximal face; V.44231. 8, *S. richteri* (Klaus) Pot., proximal face; V.44221.

Fig. 9. *Striatopodocarpites crassus* sp. nov., proximal face; V.44231.

Fig. 10. *Vitreisporites* cf. *signatus* Lesch., proximal face; V.44246.

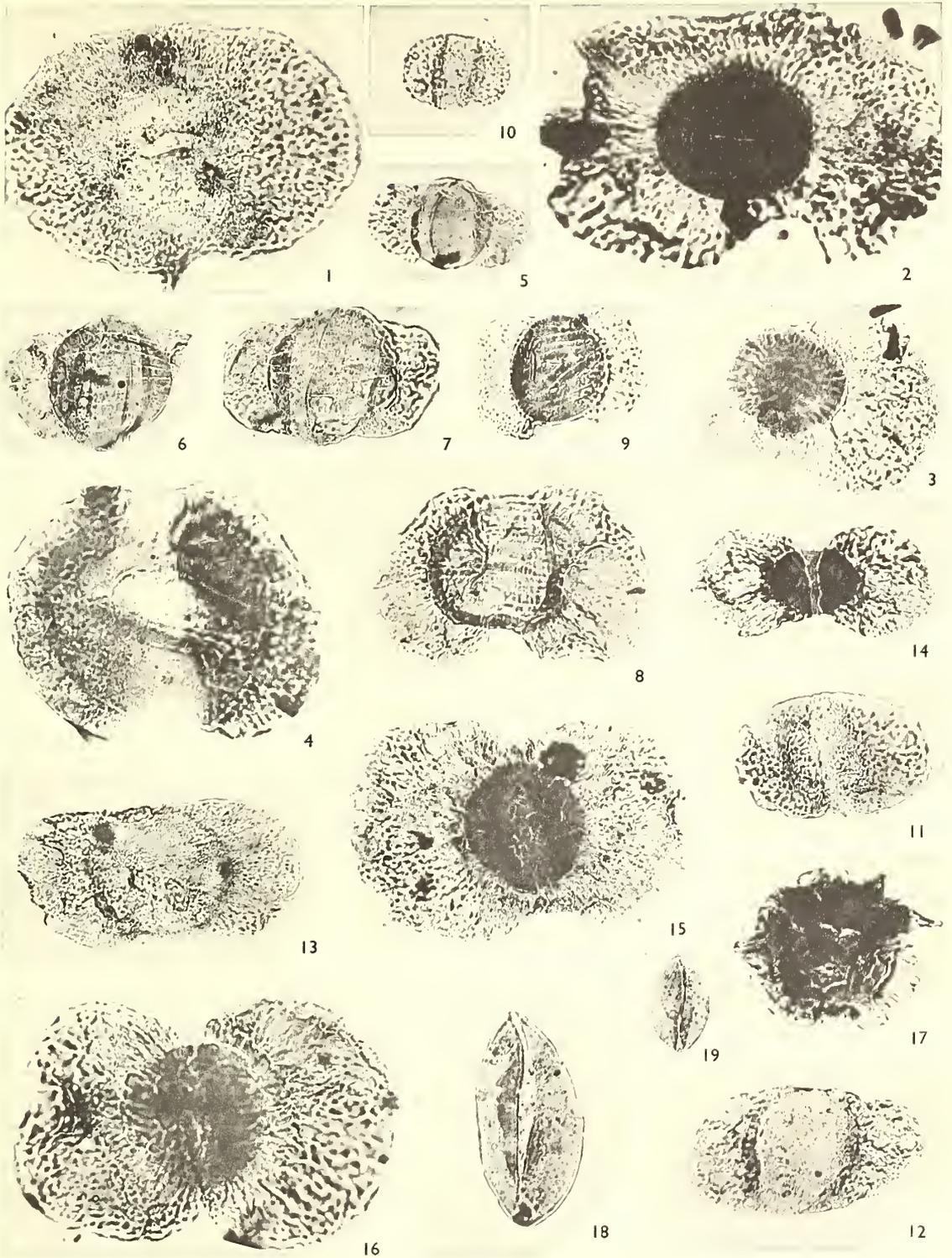
Figs. 11–13. *Vesicaspora* spp. 11–12, *V. obliqua* sp. nov. 11, Proximal face; V.44258. 12, Proximal face; V.44222. 13, *V. sp.*, proximal face; V.44248.

Fig. 14. *Platysaccus papilionis* Pot. and Kl., distal face; V.44258.

Figs. 15–16. *Fimbriaesporites fimbriatus* sp. nov. 15, Distal face; V.44226. 16, Proximal face; V.44226.

Fig. 17. *Kraeuselisporites obscurus* sp. nov., proximal face; V.44221.

Figs. 18–19. *Cycadopites*. 18, Sp. A, proximal face; V.44225. 19, Sp. B, proximal face; V.44221.



SINGH, Permian miospores

Subturma DISACCATES Cookson 1947

Infraturma STRIATITI Pant 1954

Genus LUECKISPORITES Potonié and Klaus emend. Potonié 1958

Lueckisporites sp.

Plate 46, fig. 4

Description. Pollen grain disaccate, diploxytonoid. Central body elongated parallel to the longest axis of the spore, bearing proximally two horizontal stripes, having a single groove between them. Bladders large, distally inclined, intrareticulate.

Remarks. This is the only specimen of its kind met with in this spore assemblage. On account of the poor preservation of the organic matter its identification is tentative.

Genus STRIATITES Pant emend. Bharadwaj 1960

Remarks. Bharadwaj (1960) has emended the diagnosis of *Striatites* stating that the pollen grains referable to it are disaccate with vertically oval to circular central body which bears horizontal striations with or without faint to prominent vertical striations at right angles to them and a microverrucose exine. Jansonius (1962) has also reinterpreted this genus but he makes no mention of the ornamentation of the central body exine. He distinguishes *Striatites* from *Lueckisporites* and *Taeniaesporites* on the basis of number of striations. *Striatites medius* sp. nov. (described below) from this assemblage has six to eight proximal horizontal striations on the central body but its exine ornamentation appears to be matt.

Striatites medius sp. nov.

Plate 46, figs. 5-7

Holotype. Plate 46, fig. 7; slide V.44263.

Diagnosis. Size 52-72 μ (15 specimens), pollen grain bisaccate, \pm haploxytonoid, central body 26-46 \times 22-40 μ , longitudinally oval, \pm narrower on one end. Exine \pm laevigate, bearing six to eight horizontal striations on the proximal surface, distally a longitudinal median suture evident (perpendicular to the longest axes). Bladders equal to, or slightly short of, the body height (perpendicular to the longest axis), intrareticulate, distally inclined.

Description. Holotype 62 μ along the longest axis (including sacci). Exine of the central body appears to be matt, bearing proximally eight horizontal striations, straight to anastomosing (not in the holotype) tending to converge at both the ends. Bladder attachment areas distinct, widely separate laterally as well as distally.

Comparison. *S. richteri* (Klaus) Pot. 1958 has a greater number of striations. *S. cancellatus* (Balme and Hennelly) Pot. 1958 differs in having a circular to subcircular central body.

Striatites richteri (Klaus) Potonié

Plate 46, fig. 8

Remarks. The miospores (10 specimens) referred here to *S. richteri* are somewhat smaller (68-84 μ in the longest axis) in size as compared to its holotype. This species has also been recorded by Jizba (1962) from the Mid-continent area of United States.

Genus STRIATOPODOCARPITES Soritscheva and Sedowa emend. Bharadwaj 1960
Striatopodocarpites crassus sp. nov.

Plate 46, fig. 9

Holotype. Plate 46, fig. 9; slide V.44231.

Diagnosis. Average size about 64 μ , pollen grains bisaccate (10 specimens), diploxytonoid, central body more or less circular, dark brown, horizontal striations eight to eleven, anastomosing, bladders more than semicircular.

Description. Holotype 62 μ , bilateral, bisaccate. Central body more or less circular; exine dense, dark brown, finely structured appearing almost matt, proximally striated, striations usually straight but sometimes anastomosing, particularly the middle ones, ten in number, distal slit not differentiated. Bladders distally inclined, intrareticulate, attachment areas discernible.

Comparison. *S. octostriatus* Hart has eight striations which do not anastomose. *S. fusus* (Balme and Henn.) Pot. differs in being larger and having fewer striations than *S. medius*.

Infraturma DISACCIATRILETI (Leschik) Potonié 1958
 Genus VITREISPORITES Leschik 1955

1950 *Pityopollenites* Reissinger.

1958 *Caytonipollenites* Couper, *vide* Potonié 1960, p. 77.

Remarks. Leschik (1955) established *Vitreisporites*, stating that the pollen grains are bisaccate with a central body less than 20 μ and having a weak Y-mark on it. Recently Jansonius (1962) has emended this genus, rejecting the presence of Y-mark on the central body and a size smaller than 20 μ as characters of the genus. In the figure of the type species of *Vitreisporites* Leschik (1955, pl. 8, fig. 10) and in the specimen figured below as *V. cf. signatus*, a Y-mark has not been observed and this is in accordance with Jansonius's observation. However, the shape of the central body in *Vitreisporites* is variable from subcircular to oval and is not only subcircular as stated by Jansonius.

Vitreisporites cf. signatus Leschik

Plate 46, fig. 10

Description. The specimen figured here measures 32 μ and is bisaccate, more or less haploxytonoid having an elongate central body where height is more than breadth with laterally more or less flat sides. The exine is finely granulose both on the proximal and distal surfaces. No germinal aperture is visible. The attachment of the bladder with the body and other details of my specimen are comparable with those of the specimen figured by Leschik but for its larger size.

Genus VESICASPORA Schemel 1951

Remarks. Hart (1960) has referred three species from the Permian of East Africa to *Vesicaspora*, namely *V. maxima* Hart, *V. ovata* (Balme and Henn.) Hart, and *V. sulcata* Hart. The study of the figure of the holotype of *V. maxima* (Hart 1960, pl. 3, fig. 33) shows that its similarity with *Sulcatisporites* Lesch, is very striking, as it possesses an

indistinctly marked central body with bladders deeply infolded on the distal face. On the other hand *Vesicaspora* differs from *Sulcatissporites* in having a well-defined central body with the bladders continuous around the body. In view of these differences, I suggest that *V. maxima* should be transferred to *Sulcatissporites* as *Sulcatissporites maximus* (Hart) comb. nov.

Vesicaspora obliqua sp. nov.

Plate 46, figs. 11, 12

Holotype. Plate 46, fig. 12; slide V.44222.

Diagnosis. Size 60–90 μ (10 specimens), pollen grain bisaccate, haploxytonoid, central body more or less fusiform, bladders narrowing laterally.

Description. Holotype 90 μ , pollen grains bilateral, distinctly bisaccate with an elongate to fusiform central body, measuring $44 \times 36 \mu$ in the holotype, proximal as well as distal surface finely granulose, appearing microreticulate, striations absent. Bladders converge laterally and usually connected by a thin ledge, distally enclosing a bladder-free area of variable width, the line of attachment with the central body distinct, usually dark, intrareticulate, meshes small.

Comparison. *V. wilsonia* Schemel and *V. ovata* are smaller. *V. sulcata* Hart has a distal sulcus with thickened ends and hence in this respect is not comparable.

Vesicaspora sp.

Plate 46, fig. 13

Description. Size 90 μ , pollen grain bisaccate, haploxytonoid. Central body subcircular 44 μ in diameter, the body wall dark, the exine appearing microreticulate, striations absent, attachment with the body discernible, distal sulcus not differentiated, a narrow lateral connective joins the bladders.

Comparison. *V. obliqua* differs from *V. sp.* in having a fusiform central body.

Infraturma PODOCARPOIDITI Potonié, Thomson, and Thiergart 1950

Genus PLATYSACCUS (Naumova) Potonié and Klaus 1954

Platysaccus papilionis Potonié and Klaus

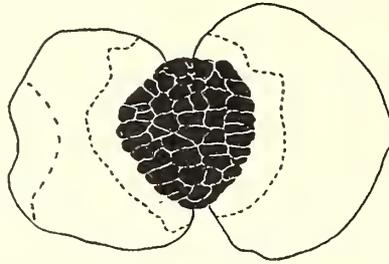
Plate 46, fig. 14

Remarks. The figure of the holotype of *P. papilionis* Potonié and Klaus shows a circular central body whereas in the specimen figured here, it is oval. Jizba (1962) has also recorded this species from the United States, Mid-continent area.

Genus FIMBRIAESPORITES Leschik 1959

Remarks. In its general organization *Fimbriaesporites* is very similar to *Platysaccus* Pot. and Kl., but its proximal exine appears reticuloid (although this is not clear in the figure of the type species of *Fimbriaesporites*) and this feature distinguishes it from *Platysaccus*. This character is very clearly seen in the specimens described here as *F. fimbriatus* sp. nov. In these specimens, it has been observed that the arrangement of rod-like bacula

or irregularly wart-like processes is such that, besides showing a reticuloid pattern, it also simulates striations. These pseudo-striations are distinguishable from the true striations as they are irregular and interrupted (text-fig. 4).



TEXT-FIG. 4. *Fimbriaesporites fimbriatus* sp. nov.; proximal face showing the ornamentation of the body exine; V.44226, $\times 500$.

Fimbriaesporites fimbriatus sp. nov.

Plate 46, figs. 15–16

Holotype. Plate 46, fig. 16, slide V.44226.

Diagnosis. Size 100–120 μ (5 specimens), pollen grains diploxylonoid, central body dark brown, oval to \pm subcircular, exine proximally bearing long, closely packed bacula- to verrucae-like elements, distally laevigate. Bladders large, more than semicircular, distally enclosing a biconvex, bladder-free area.

Description. Holotype 120 μ , bilateral, bisaccate having a conspicuous central body, measuring 48 \times 44 μ . Exine dense, covered with bacula-like or irregular wart-like elements, usually fused with each other producing either a brick-work like pattern, or simulating one to three incipient, horizontal, sinuous, 'striations'; bacula or verrucae-like elements 3.5–9 μ long, usually sixteen at the perimeter, the number varying considerably according to their size. The bladders are large as compared to the central body, leaving a distal, biconvex, bladder-free-intrareticulate area, about 8 μ wide.

Comparison. *F. globosus* Lesch. differs from *F. fimbriatus* in having smaller sculptural elements of the exine.

Turma ALETES Ibrahim 1933

Subturma ZONALETES (Luber) Potonié 1958

Genus KRAEUSELISPORITES Leschik 1955

Remarks. *Krauselisorites* Lesch. has been described as an alete genus by Leschik (1955). Later Jansonius (1962, pp. 46, 47) questioned this and emended the genus stating that, 'A Y-mark, however, is quite distinct in Leschik's photographs, and confusion is hardly possible, in spite of the poor original descriptions'. This statement seems to be hardly acceptable as a restudy of the photographs of the type species of *Krauselisorites* does not clearly show the presence of any Y-mark. Besides this, Jansonius (1962) has much enlarged the circumscription of *Krauselisorites* by including forms which even have punctate or other distinct ornamentation of the central body. I consider that *Krauselisorites* should include only alete forms which have coni or spines as the ornamentation of the central body exine.

Kraeuselisporites obscurus sp. nov.

Plate 46, fig. 17

Holotype. Plate 46, fig. 17; slide V.44221.

Diagnosis. Size 48–60 μ (5 specimens), central body dark and circular, spinose, spines large, 3–4 μ broad, 6–9 μ high, numbering eight to fourteen along the perimeter. Zona of uneven width, transparent about 7 μ broad. Y-mark not visible.

Description. Holotype 58 μ , dark brownish-red, circular in polar view. Central body surrounded by an unequal, equatorially attached transparent flange, bearing large spines with broad bases and tapering ends. Y-mark not discernible. Equatorial zona thin, pale yellow, convoluted.

Comparison. As compared to the other species of *Kraeuselisporites*, *K. obscurus* is distinctive in having larger spines and a denser central body.

Turma MONOCOLPATES Iversen and Troels-Smith 1950

Subturma INTORTES (Naumova) Potonié 1958

Genus CYCADOPITES Wodehouse *emend.* Wilson and Webster 1946*Cycadopites* sp. A

Plate 46, fig. 18

Description. Size 69 \times 33 μ , pollen grain bilateral, more or less oval in polar view. Monosulcate, sulcus long, running the whole length of the longer axis, broader at the centre, with rounded ends. Exine about 1.5 μ thick in optical section, finely punctate. *Extrema lineamenta* appearing smooth.

Comparison. As compared to *Entylissa cymbatus* (18–39 μ) Balme and Henn., *C. sp.* is larger and has a finely punctate and thicker exine. *E. vetus* Balme and Henn. is relatively smaller (18–29 μ).

Cycadopites sp. B

Plate 46, fig. 19

Description. Size 32 \times 20 μ , pollen grain bilateral, more or less oval in polar view. Monosulcate, sulcus running from pole to pole, ends rounded. Exine about 1 μ thick in optical section, finely punctate.

Remarks. The specimen figured here is the only record from this assemblage and hence has been described separately. It is much smaller than *C. sp. A*.

DISCUSSION

The miospore assemblage described above is fairly diversified. In all, it represents 32 spore genera, of which 17 genera are trilete, 3 genera are monolete, 11 genera are saccate, and the remaining genus is a non-saccate pollen grain. Both trilete and monolete spores are well represented (Table 1). Bisaccate pollen grains occur fairly abundantly in this assemblage whereas the representatives of non-saccate pollen grains occur very rarely.

This spore assemblage of Iraq as compared to the spore flora of Kaiping basin from

China (Lower Permian) described by Imgrund (1960) is much poorer in species but it differs from the latter in the presence of some striated disaccate genera such as *Striatites*, *Striatopodocarpites*, and *Lueckisporites* (Table 2).

The comparison of the Iraqi assemblage with the Upper Permian assemblages of the Alpine salt hills, Austria, and Lower Rhein (W. Germany) described by Potonié and Klaus (1954) and Grebe (1957) respectively is interesting and significant. Although the first of these assemblages is much more diversified than the other two, the presence of *Anguisporites*, *Nuskoisporites*, *Lueckisporites*, and *Platysaccus* common to the three

TABLE 1. Composition of miospore assemblage based on a count of 300 specimens

<i>Miospore species</i>	<i>Percentage</i>	<i>Miospore species</i>	<i>Percentage</i>
<i>Leiotriletes atshanensis</i> sp. nov.	0.3	<i>Thymospora opaqua</i> sp. nov.	26.7
<i>L. magnificus</i> sp. nov.	1.3	<i>Nuskoisporites</i> sp.	0.3
<i>Iraqispora labrata</i> sp. nov.	1.0	<i>Mosulipollenites circularis</i> sp. nov.	2.0
<i>Punctatisporites obliquus</i> Kos.	2.7	<i>Potonieisporites bilateralis</i> sp. nov.	0.3
<i>P. pyramidicus</i> sp. nov.	4.0	<i>Vestigisporites granulatus</i>	0.3
<i>Calamospora</i> sp.	0.7	<i>V. densus</i> sp. nov.	0.3
<i>Cyclogranisporites varius</i> sp. nov.	2.7	<i>Striatites medius</i> sp. nov.	3.3
<i>Schlopfites lateralis</i> sp. nov.	1.3	<i>S. richteri</i> (Klaus) Pot.	9.0
<i>Lophotriletes sparsus</i> sp. nov.	1.0	<i>Striatopodocarpites crassus</i> sp. nov.	0.3
<i>L. novicus</i> sp. nov.	1.0	<i>Vitreisporites</i> cf. <i>signatus</i> Lesch.	1.0
<i>Apiculatisporis decorus</i> sp. nov.	14.7	<i>Vesicaspora</i> sp.	7.7
<i>Lycopodiumsporites</i> sp.	0.7	<i>Vesicaspora obliqua</i> sp. nov.	1.0
<i>Anguisporites minutus</i> sp. nov.	0.3	<i>Platysaccus papilionis</i> Pot. and Kl.	0.7
<i>Latosporites intragranulosus</i> sp. nov.	0.7	<i>Fimbriaesporites fimbriatus</i> sp. nov.	1.0
<i>Punctatosporites marattioides</i> sp. nov.	15.7		

assemblages is important. These four genera together with *Striatopodocarpites* and some few additional genera are reported by Leschik (1956) from the Zechstein strata of Neuhoof (near Fulda).

Samoilovich (1953) has investigated the spores of Permian strata of Cis-Urals, U.S.S.R., reporting that the Upper Permian spore complex referred to the Kazanian stage is richer in conifer pollen grains than in pteridophytic and monosulcate forms. On the whole this spore complex appears to be an incomplete representation of the spore flora as is indicated by Samoilovich (p. 23).

Recently Wilson (1962) has described an interesting spore assemblage from the Flowerpot Formation, Oklahoma, U.S.A., and considers that it is closely comparable to the Zechstein (Upper Permian) miospore flora of Germany described by Grebe (1957). The similarity of the Flowerpot spore spectrum with the present one is marked by the presence of such common genera as ? *Nuskoisporites*, *Anguisporites*, *Calamospora*, *Lueckisporites*, *Rhizomaspora* (? = *Fimbriaesporites*), *Strotersporites* (? = *Striatopodocarpites*), and *Potonieisporites*. The number of characteristically Permian genera common to the two assemblages is very significant.

Jizba (1962) has reported bisaccate pollen grains from the United States, Mid-continent area, of which *Striatites*, *Vesicaspora*, and *Platysaccus* are in common with the Iraqi assemblage.

Jansonius (1962) has dealt with the spores and pollen of Permian and Triassic sediments of the Peace River area, Western Canada. The Permian assemblages are reported to

TABLE 2. Comparison of some Permian Spore assemblages. For *Verrucosporites* read *Thymospora* Wilson and Venkatachala 1963.

SPORE GENERA	IMGRUND (1960)	JIZBA (1962)	POTONIE & KLAUS (1954)	GREBE (1957)	LESCHIK (1956)	WILSON (1962)	JANSONIUS (1962)	SAMOILOVICH (1953)	SINGH (PRESENT ASSEMBLY '65)	HART (1960)	HÖEG & BOSE (1960)	PIÉRAAT (1959)	LESCHIK (1959)	BALME & HENNELLY (1955-56)	BHARAD. (1960)
LEIOTRILETES	+	-	-	-	-	-	-	-	+	-	-	-	-	+	+
IRAQISPORIA	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
PUNCTATISPORITES	+	-	-	-	-	-	-	+	+	+	+	+	-	+	+
CALAMOSPORA	+	-	-	-	-	+	-	+	+	-	-	+	-	+	-
GRANULATISPORITES	+	-	-	-	-	-	-	-	+	-	+	+	-	+	-
CYCLOGRANISPORITES	+	-	-	-	-	-	-	+	+	-	-	-	-	+	+
SCHOPFITES	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
LOPHOTRILETES	+	-	-	-	-	-	-	+	+	-	+	-	-	+	+
APICULATISPORIS	+	-	-	-	-	-	-	+	+	-	-	+	+	+	-
MICROBACULISPORIA	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+
MICROFOVEOLATISPORIA	-	-	-	-	-	-	-	-	-	-	-	-	-	+	+
INDOSPORA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
LYCOPODIUMSPORITES	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+
ANGUISPORITES	-	-	+	+	+	+	-	-	+	-	-	-	-	-	+
CIRRATRIRADITES	-	-	-	-	-	-	-	+	+	+	-	+	-	+	+
GONDISPORITES	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
LAEVIGATOSPORITES	+	-	-	-	-	-	-	-	+	-	-	+	-	+	+
LATOSPORITES	+	-	-	-	-	+	-	-	+	-	-	-	+	+	+
PUNCTATOSPORITES	+	-	-	-	-	-	-	-	+	-	-	-	+	+	+
VERRUCOSOSPORITES	+	-	-	-	-	-	-	+	+	-	-	-	+	+	+
NUSKOISPORITES	+	-	+	+	+	+	-	-	+	+	+	+	-	+	+
MOSULIOLLENITES	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-
DENSIPOLLENITES	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
STRIOMONOSACCITES	-	+	-	-	-	-	-	-	-	-	-	-	-	-	+
POTONIEISPORITES	-	-	-	-	-	+	-	+	+	-	-	-	-	-	-
HOFFMEISTERITES	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-
VESTIGISPORITES	-	-	-	-	-	-	+	-	+	+	-	+	-	+	-
LUECKISPORITES	-	-	+	+	+	+	-	-	+	+	-	-	-	+	-
COMPLEXIPOLLENITES	-	+	-	-	-	-	-	-	-	-	-	-	-	-	-
STRIATITES	-	+	-	+	+	-	+	+	+	+	-	+	-	+	+
VERTICIPOLLENITES	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
LAHIRITES	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
HINDIPOLLENITES	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
STRIATOPODOCARPITES	-	-	-	-	+	-	-	+	+	+	-	-	+	+	+
FAUNIPOLLENITES	-	-	-	-	-	+	-	+	-	-	-	-	-	-	+
STROTERSPORITES	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LUNATISPORITES	-	-	-	-	-	-	-	-	-	+	-	+	-	-	+
STRIAPOLLENITES	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
VESICASPORA	-	+	+	-	-	-	+	+	+	+	-	-	-	+	+
PLATYSACCUS	-	+	+	+	+	-	+	+	+	+	+	-	-	-	+
PITYOSPORITES	+	-	+	+	+	-	-	+	+	+	+	+	-	+	+
FIMBRIAESPORITES	-	-	-	-	-	-	-	-	+	-	+	-	+	+	-
RHIZOMASPORA	-	-	-	-	-	+	-	-	-	-	-	-	-	+	-
SULCATISPORITES	-	-	-	-	+	-	-	-	-	+	+	-	-	-	+
LIMITISPORITES	-	-	-	-	+	-	-	-	-	+	-	-	+	-	-
ALISPORITES	-	+	-	-	-	+	+	-	-	-	-	-	-	-	-
CYCADOPITES	-	-	-	+	-	-	-	+	+	-	+	-	-	+	-
GNETACEAEPOLLENITES	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
WELWITSCHIAPITES	-	-	-	-	-	-	-	+	-	-	-	-	-	-	+
VITATINA	-	-	-	-	-	+	+	+	-	-	-	-	-	+	+
MARSUPIPOLLENITES	+	-	-	-	-	-	-	-	-	+	+	+	-	+	-

have abundant *Vittatina*, with *Hamiapollenites* and *Striatites*. *Vittatina* and *Hamiapollenites* are absent from the present assemblage, and *Striatites* is not abundant here.

From the southern hemisphere, Permian strata have been investigated sporologically in Africa (Hart 1960; Høeg and Bose 1960; Leschik 1959; Piérart 1959), India (Bharadwaj 1960) and Australia (Balme and Hennelly 1955, 1956*a, b*). The assemblages of Piérart (Permian of Luena, Katanga), Hart (Lower Permian of Tanganyika), and Høeg and Bose (Permo-Carboniferous of Congo) have little in common with that described here.

The Upper Permian spore floras of Raniganj Stage from India and of Australia appear to be abundantly rich both in quality and quantity and perhaps represent the climax of the Gondwana Upper Permian vegetation. The richness of spore forms, especially with regard to the distribution of the striate disaccate pollen grains along with other forms in these assemblages which can be considered as a characteristic feature of the Upper Permian strata of India and Australia, sharply contrasts with the qualitative paucity of spores and pollen represented in the spore assemblages from western Europe described by Potonié and Klaus (1954), Leschik (1956), and Grebe (1957). However, the Iraqi assemblage is fairly diversified in forms and has the following spore genera in common with the Indian and Australian assemblages: *Calamospora*, *Cyclogranisporites*, *Lophotriletes*, *Punctatosporites*, *Thymospora*, *Nuskosporites*, *Vestigisporites*, some striate bisaccates and *Cycadopites*. Among these assemblages (Iraq, India, and Australia) there are also a number of genera peculiar to one or the other. The presence of *Mosulipollenites*, *Schopfites*, *Kraeuselisporites*, *Iraqispora*, and *Vitreisporites* in the Iraqi assemblages distinguishes it from the other assemblages discussed in this paper.

In conclusion I consider the presence of *Anguisporites*, *Lueckisporites*, *Striatites richteri*, and *Platysaccus papilionis*, which are already known from the Upper Permian of western Europe, as significant in suggesting that the Iraqi assemblage is not older than Upper Permian age. Elliott (1955) has investigated the fossil algae from the same formation and has suggested the same age.

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THE PALAEOECOLOGY OF A TRANSITION ZONE ACROSS AN UPPER CRETACEOUS BOUNDARY IN NEW JERSEY

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ABSTRACT. Sediments and fossils were sampled at one-foot intervals across the Mt. Laurel–Navesink boundary (Upper Cretaceous) at Marlboro, New Jersey; this sequence is of some interest as it contains the *Exogyra cancellata* Zone, which has been traced along the coastal plain from New Jersey to Texas. It is shown that weak bottom currents were present during the time represented by this sequence, that the oysters and sponges examined lived in non-turbid waters of normal salinity in which nutrients were provided in quantity, that water depth increased in the upper part of the sequence, and that an important break in sedimentation, indicated by electron microphotographs of the surface textures of sand grains and the presence of shallow-water crabs, is found at the Mt. Laurel–Navesink boundary and possibly represents a disconformity. Interlocked oyster shells with sponge borings found throughout the section indicate local periods of water turbulence followed by long periods of quiescence. Comparison of sediment and individual size frequency distributions implies that *Guembelina ultimatumida* was probably sorted by water currents after reaching the sea bottom.

THE study of changes in the biological and physical characteristics of sedimentary rock over small stratigraphic intervals has recently received impetus from the work of Carozzi (1958) and Carozzi and Zadnik (1959), who demonstrated that stratigraphic micro-environmental studies of consolidated carbonate rocks are of fundamental importance in the reconstruction of ancient environments, since numerous sedimentation processes are of small scale and therefore commonly overlooked. Relatively unconsolidated deposits of the type discussed below can be similarly studied.

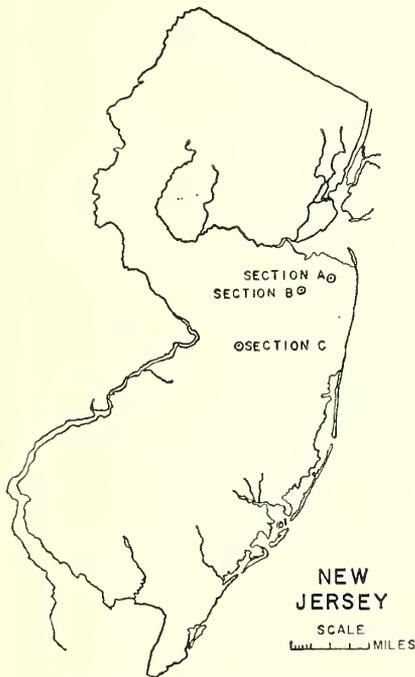
We have attempted to obtain as much environmental information as possible from the megafossils, microfossils, and sediments over an interval of 14 feet in the Cretaceous Navesink and Mt. Laurel greensands at Marlboro, New Jersey. Two other localities at similar stratigraphic horizons were studied to supplement the Marlboro data (text-figs. 1 and 2).

Carozzi (1958) indicated that a fully oriented sample taken every foot vertically appears to be sufficient for investigations of both lithologically uniform and variable sequences. We sampled sediments and fossils at one-foot intervals across the Mt. Laurel–Navesink boundary at Marlboro; the samples near the contact were taken at 6-inch intervals (Table 1). This particular sequence is of interest as it contains the *Exogyra cancellata* Zone, which has been traced along the coastal plain from New Jersey as far west as Texas (Stephenson 1933); it is extremely fossiliferous and contains both mega and microfossils. Weller (1907) pointed out that the entire Upper Cretaceous sequence in New Jersey shows an alternation of two faunal types: the '*Lucina* fauna', considered to be a shallow shelf fauna, and the '*Cucullaea* fauna', considered a deeper water association. The Mt. Laurel–Navesink sequence, dealt with here, was considered by Weller to represent the deeper water '*Cucullaea* fauna'.

Our results indicate that within the stratigraphic interval studied the water probably varied from shallow to deep shelf depth. Four approaches were used in an attempt to

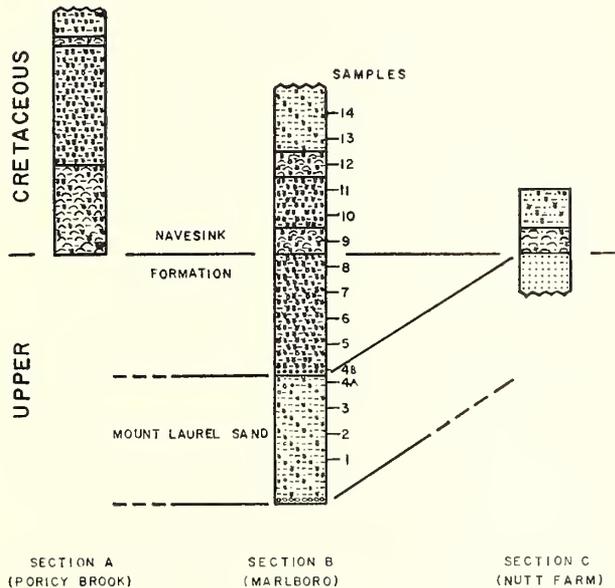
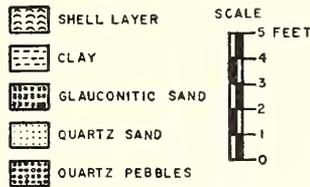
delineate environmental conditions: analyses of megafossils, microfossils, sediments, and electron microscopic sand surface textural studies, all of which are discussed below.

The Mt. Laurel–Navesink sands of New Jersey are Upper Cretaceous unconsolidated greensands containing variable amounts of silt and clay. They dip at very low angles to the south-east and were probably deposited under relatively stable shelf conditions.



TEXT-FIG. 1. Location of sections.

LEGEND



TEXT-FIG. 2. Stratigraphic details of sections.

The Mt. Laurel sand dips 25 feet per mile to the south-east in Monmouth County, New Jersey, and varies in thickness from 5 to 15 feet (Spangler and Peterson 1950). It is a marine glauconitic, medium to coarse, pebbly, buff, red, yellow, or black sand and may locally contain varying amounts of clay. At the Marlboro locality (1-2 miles east of Marlboro, New Jersey, in the south bank of Hop Brook) it consists of 5 feet of grey to olive-green, pebbly, glauconitic, sandy clay with *Belemnitella americana* (Morton), sharks' teeth and crab claws. A good deal of scattered, white crumbly calcium carbonate present represents the remains of shells which have partially gone into solution.

The contact between the Mt. Laurel and the overlying Navesink occurs between our samples 4A and 4B; the boundary is marked by a zone containing crab claws at the very

top of the Mt. Laurel and a large number of small pebbles an inch or two below. The basal contact of the Mt. Laurel with the underlying dark, micaceous Wenonah clay is clearly exposed.

The Navesink sand dips about 20 feet per mile to the south-east where it is best developed in Monmouth County, New Jersey, and locally attains thicknesses of 30 feet (Spangler and Peterson 1950). It is a marine, black to green, glauconitic sandstone containing varying amounts of clay. The lower part of the Navesink at Marlboro contains three fossiliferous zones, a lower *Belemnitella* zone, a middle *Exogyra* zone, and an upper *Gryphaea* zone. At most other localities, the three zones are combined into a single shell layer. The Navesink at Marlboro is about 26 feet thick, but the upper contact is obscure and seemingly gradational. It is overlain by a few feet of yellowish, non-glauconitic sand which may be the base of the Red Bank formation.

At another locality about 7 miles away, on the south bluff of Poricy Brook, $\frac{1}{2}$ mile south of Oak Hill, and about $1\frac{3}{4}$ miles south of Middleton, New Jersey, about 17 feet of Navesink sand are found, including the *Exogyra* and *Gryphaea* layers. The lithology of the Navesink here is very much like that at Marlboro.

The third locality studied, which is in a tributary to Crosswicks Creek, $\frac{1}{3}$ mile north of the C. B. Nutt Farm on Arneytown Road, near Arneytown, New Jersey (about 23 miles south-west of the Marlboro area), consists of a grey, glauconitic sand with numerous fossils. Here the three layers found at Marlboro are combined into one; the material may be considered coquina-like in nature. Lowenstam and Epstein (1954) collected *Belemnitella americana* for their oxygen isotope studies on Cretaceous palaeotemperatures in Crosswicks Creek less than a mile from this locality.

METHODS

A channel was excavated to a depth of 6 inches in the vertical sections sampled. The samples were carefully removed from between $1\frac{1}{2}$ inches above and below every one-foot marker. At Marlboro, sampling began $3\frac{1}{2}$ feet below the Mt. Laurel-Navesink contact and ended 10 feet above it. Samples were taken every foot except near the contact, where 4A and 4B were sampled 6 inches apart. Approximately 500 grams of material was collected at each level; each sample was thoroughly mixed in the laboratory, and quartered until a representative 5-gram sample for foraminiferal examination was obtained. A second 5-gram sample was taken from two of the channel samples and examined for foraminifera as indicated below. There were no significant differences in foraminiferal content in either of the two additional 5-gram samples examined as compared with the original samples.

In order to deflocculate the clay in the sediment and to free the microfossils, each 5-gram sample was soaked in sodium carbonate solution for thirty minutes; the mixture was then heated over a bunsen burner for the same length of time. Clay was removed by wet sieving through a 230-mesh sieve. The remaining material was washed into porcelain evaporating dishes for drying.

Samples 1-14 (Marlboro) were dried over a bunsen burner, while the Poricy Brook and Crosswicks Creek samples were dried in an oven at about 100° C. Poricy Brook samples contained a large amount of non-disaggregated clay after this treatment; they were then placed in sodium carbonate solution, ultrasonically vibrated for about five

minutes, sieved and dried at 100° C. The fossils were floated off on carbon tetrachloride which was poured on to filter paper; the organisms were then transferred from the filter paper to micro-slides ruled into sixty squares. The heavy fraction was examined for additional foraminifera after carbon tetrachloride flotation. No additional foraminifera were noted in samples 1-6 and 14; no more than fifteen foraminifera were found in samples 7-13. It is apparent from Table 1 that the latter number is insignificant when compared with the large number of foraminifera previously obtained in samples 7-13.

TABLE 1

Layer	Total no. of foraminifera in 5-gm. sample	% Plankton	Benthonic-planktonic ratio	Species number		Genera number		Skewness SK	Sorting SO	Max. quartz grain size (inches)	% CaCO ₃ by weight
				P	B	P	B				
14	13	46	1.20	3	4	2	4	0.70	2.75	0.04	7.8
13	27,946	69	0.44	6	13	5	13	1.48	4.85	0.04	10.6
12	22,088	85	0.18	6	16	5	14	1.44	4.84	0.05	27.2 <i>Gryphaea</i>
11	30,516	85	0.18	8	23	5	20	1.42	4.69	0.05	20.9
10	28,993	84	0.20	10	28	5	25	1.01	3.32	0.07	21.3
9	21,135	82	0.23	6	26	4	24	2.29	6.16	0.09	30.0 <i>Exogyra</i>
8	13,460	82	0.22	5	18	4	16	1.48	4.36	0.07	17.4
7	12,172	71	0.40	7	19	5	14	0.64	2.33	0.06	10.2
6	103	54	0.84	4	11	4	9	0.22	1.69	0.06	3.5
5	9	78	0.29	3	2	2	2	0.24	1.76	0.05	1.8
4B	1	0	—	0	1	0	1	0.19	1.73	0.10	5.3 Crabs, Vs
4A	209	70	0.41	7	12	4	11	0.80	2.68	0.18	11.1 No Crabs, no Vs
3	4	25	3.00	1	3	1	3	0.16	1.77	0.12	10.0
2	4	75	0.33	2	1	2	1	0.23	1.85	0.15	12.1
1	22	54	0.83	3	4	2	4	0.00	1.54	0.12	5.9

All samples were taken at one-foot intervals, except 4A and 4B, which are 6 inches apart.

All foraminifera in samples 1-6 and 14 were picked and identified, counted and measured with a micrometer disk attached to a binocular microscope. A sample slide was prepared with representative species from these samples.

The foraminifera in samples 7-13 (5-gram samples) were split to either one-quarter or one-eighth for convenience. Total plankton and benthos in all samples from each locality were counted and recorded. All species were also counted, and two measurements (maximum length and width or, in the case of approximately spherical organisms, maximum diameter of entire organism and of last chamber) were made on individuals of each of the following species: *Guembelina striata* (Ehrenberg), *Guembelina ultimatumida* White, *Globigerina lacera* (Ehrenberg), *Globigerinella aspera* (Ehrenberg), *Guttulina adhaerens* (Olszewski), *Globulina lacrima* Reuss, *Pseudovigerina seligi* (Cushman), and *Buliminella fusiformis* Jennings. The figures were then multiplied by the appropriate factor (4 or 8). Table 3 is a record of the total figures.

The foraminifera in all the samples showed some breakage; a considerable amount of shell debris was present in the residue remaining after carbon tetrachloride filtration. An experiment was planned in which foraminifera picked from untreated sediment were

to be mixed with unfossiliferous material from sample 4B and then subjected to the foraminiferal separation procedure outlined above. However, it was impossible to obtain enough specimens without subjecting the fossiliferous sediment to treatment which might break some of the more fragile specimens. Thus no estimation of breakage due to the techniques used could be made.

PALAEOECOLOGY OF MEGAFOSSILS

The most common oysters at Marlboro are *Gryphaea convexa* (Say), *Exogyra costata* Say, *Exogyra cancellata* Stephenson, *Ostrea mesenterica* Morton, and *Ostrea falcata* Morton. The section examined includes three major shell layers, all in the Navesink formation. The uppermost is known as the *Gryphaea* bed, several feet below is the *Exogyra* bed and about 3 feet below that is the *Belemnitella* bed (Table 1 and text-fig. 1). The beds are separated from each other by sediments which contain fewer fossils. Each of the shell beds contains all the species listed above, but the number of individuals varies from one bed to another.

In the *Exogyra* layer, little evidence of abrasion was noted, although solution was particularly evident. Examination of a layer about 200 yards downstream showed that solution was probably post-depositional; here the oysters were quite fresh and little evidence of solution was present. Nests of *Exogyra* were found with some single valves interlocked, suggesting local turbulence. However, since many larger isolated shells were found with their valves in life position, currents must have been generally aperiodic and very local.

In one of the interlocked nests, the surface of the innermost interlocked shell was found to contain sponge borings; these borings could not have occurred while the shells were interlocked. Thus the bored shell probably lay exposed on the bottom for the length of time necessary to permit boring sponges (*Cliona* sp.) to grow, was moved a short distance and interlocked, which indicates relatively long periods of calm followed by short periods of turbulence. Similar situations were noted in other localities throughout the Navesink formation.

Portions of the *Exogyra* layer were white with high concentrations of calcium carbonate; small *Exogyra* shells were rare and it is possible that solution removed a good deal of the shell material. Although in certain epifaunal marine communities the presence of adults may prevent larvae of the same species from settling, which would cause all specimens taken to be of approximately the same size (see discussion in Thorson 1957, pp. 483-4), this is probably not the case here; at the Crosswicks Creek locality (of roughly equivalent age) adults and young of a presumably living and indigenous population were found together. Fragile specimens of less than half an inch diameter, through a graded series to thick-shelled forms of the same species as large as 6 inches in diameter with both shells together, were found at the latter location.

The size and thickness of both *Exogyra* and *Gryphaea* at all localities examined are rather unusual; specimens over an inch thick and with a maximum diameter of over 6 inches were found. Sponge borings were usually seen only on the larger specimens of *Exogyra* and *Gryphaea*; the frequency of boring was less on the right than left valves and more borings were found on the outsides of both valves than inside. Some valves had borings which started from the interior but did not reach the exterior, indicating that at

least some shells were bored after death; however, many of the borings may have occurred before death, as modern *Cliona* bores living oysters. The surfaces near the margins of the left valves contained the least concentration of borings while the highest concentrations were found in the central portions. Since the left valve was either fastened to the substratum or the oyster was lying free upon it in life, it is assumed that these valves were overturned to permit boring sponges to grow (text-fig. 3). A number of specimens with both valves together, relatively free of sponge borings, were found in living position, indicating probable burial in place.

Belemnitella americana is found in the upper part of the Mt. Laurel and in the lower and middle parts of the Navesink. At Marlboro it occurs scattered through the portion of the sequence represented by samples 1-12 and is well preserved. Usually the rostrum is the only portion of the organism seen and there is no evidence of solution; occasionally, however, portions of the aragonitic phragmacone can be observed in various stages of solution. Cornish and Kendall (1888) believed that the rostrum of belemnites was composed of calcite; Bøggild (1930) showed that the phragmacone of *Atractites*, a projection of the shell that contained the air chambers, was probably composed of aragonite.

In moving water, cones tend to be oriented with their long axes in the direction of maximum current movement (Petřánek and Komárková 1953). Compass orientations of 40 belemnites were made over a stratigraphic interval of one foot directly above the Mt. Laurel-Navesink boundary at Marlboro, New Jersey; no overall preferred orientation was found. Several groups of belemnites with tips pointing in the same direction were found close to casts of numerous pelecypod shells and it is possible that the shells served as obstacles against which belemnites accumulated. The orientation of belemnites around obstacles indicates that currents were present, but lack of overall orientation and the fact that a great deal of bottom scouring did not occur (very few belemnites were uncovered and exposed to boring sponges for any length of time—see below) would tend to show that these currents were extremely weak.

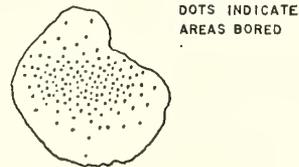
Belemnites were not significantly bored by *Cliona*; only 5 out of 200 specimens observed were so bored and in another group of 8, only one which was oriented with its tip pointing up contained borings on the apical inch of its 6-inch length. The associated non-vertical specimens were not bored. Possibly the tip of the vertical specimen was exposed above the sediment surface for the length of time necessary for boring to occur. This occurrence may be related to the rate of sedimentation.

Belemnites from the Navesink have been used for isotopic temperature determinations since the density of the rostrum precludes much ionic movement. Temperatures at which organisms at the base of the Navesink formation precipitated their shell material

EXOGYRA COSTATA



A. SIDE VIEW OF LEFT VALVE IN LIVING POSITION (DIAGRAMMATIC)



B. BOTTOM VIEW OF LEFT VALVE SHOWING CONCENTRATION OF SPONGE BORINGS (DIAGRAMMATIC)

TEXT-FIG. 3. Borings in *Exogyra costata*.

ranged from 16.4° C. to 20.5° C. (Lowenstam and Epstein 1954). The base of the Navesink at Crosswicks Creek would roughly correspond to samples 7-13 at Marlboro, New Jersey. It is of interest to note that a temperature range of 17° C. to 22° C. at 50 fathoms (300 feet) characterizes bottom waters in the Gulf of Mexico at the present time (Bandy 1956).

In sample 4B a crab-claw layer (*Protocallianassa mortoni*) marks the top of the Mt. Laurel formation. The carapace material found was fragmented; however, a few of the claw segments and pincers were articulated. The segments occur in hard concretionary masses cemented with calcium carbonate; frequently the masses contain a great deal of limonite or goethite which probably originated from the weathering of glauconite. Egg-shaped to irregular in form, the concretions are harder than the surrounding matrix and increase in hardness as the outside layers are stripped away. The segments disintegrate upon soaking in distilled water; high concentrations of calcium carbonate but no glauconite grains are found inside the claws. Occasionally white concretions are observed which are shaped like crab claws except that the segments themselves are missing; this suggests removal after deposition. The claws may be oriented in one direction within a single concretion suggesting movement by currents before formation. Most crab segments are black, but brown patterns which are apparently original can be seen on several specimens.

The claws were probably covered and cemented with calcium carbonate before they could disintegrate or disarticulate and were then transported a very short distance (many concretions can be seen with crab claws exposed and unabraded). The fact that the carapaces are not found whole would suggest that they disintegrated somewhat faster than the claw segments; differential sorting seems unlikely, since the preserved segments are of many different sizes. The sediment in sample 4B, the crab-claw layer, differs considerably from the layer below it in terms of skewness, sorting and maximum quartz grain size (Table 1). It is possible that sample 4B represents a lag deposit, with the fine material having been removed. Crab-claw concretions and one foraminifer are present in addition to a layer of pebbles immediately below; the smallest silt-clay to total weight ratio in all samples examined is also found. We conclude from all the evidence that there is a strong possibility of a disconformity here. Layers with numerous crab claws may represent shoaling even in formations which are generally described as having been deposited in deeper water.

In the Upper Cretaceous *Protocallianassa* has been found in the Merchantville, Wenonah, Mt. Laurel, Navesink, and Tinton formations, all of which are thought to have been deposited in deep water except for the Wenonah, which may have been deposited in shallow water (Henry B. Roberts, *in litt.*). However, in sample 4B numerous claw fragments are found in a sediment which was certainly deposited in shallow water; only one foraminifer was found in this layer and the surface textures of sand grains examined with the electron microscope (see below) indicate beach action. *Callianassa* today occurs generally at depths of 5 to 50 fathoms (De Man 1928) or even less, and lives on sandy or muddy bottoms near the coast. Most modern species tend to live at the minimum rather than the maximum depth. Stevens (1928, 1929) has studied the Callianassidae from the Puget Sound, Washington, area and has shown that several species are destructive to oyster fisheries, as oysters are smothered by material thrown up by the crabs in the process of digging their burrows. It is interesting to note in this connexion

that oyster shells are usually not found with numerous crab remains; at Big Brook the crab-claw layer is barren of oyster shells.

The presence of numerous *Cliona* (class Demospongia) borings in many of the larger oyster shells and several of the belemnites is also interesting, as sponges are good ecological indicators, chiefly with reference to depth, salinity, and lack of turbidity. *Cliona* suggests moderate depths, generally greater than 60 feet but less than 600 feet; it flourishes especially well in areas of sea offshore from mouths of rivers. *Cliona* usually requires clear, silt-free water and full oceanic salinity (De Laubenfels 1953, 1957). De Laubenfels (1936) also believes that if a stratum or horizon contains many fossil sponges it is likely, although not certain, that it was deposited in relatively silt-free water.

All the above would suggest that the water in which the organisms at Marlboro lived was of normal oceanic salinity, and free from turbidity; the oysters were located where nutrients were provided in quantity and lived at depths somewhere between 60 and 600 feet. Other types of information elsewhere in this paper also support these conclusions.

At Poricy Brook, the crab-claw layer is below brook level, while at Crosswicks Creek a few crab claws have been found scattered among the oysters and belemnites. This locality also contains scattered *Belemnitella americana*; the belemnite bed in most places is below brook level. At Crosswicks Creek, belemnites occur in great numbers in a coquina-like layer with numerous oysters.

MICROFOSSILS AND SEDIMENT

Fox and Olsson (1960) have indicated that the Navesink formation represents greater depth than the Mt. Laurel. They believe that the Navesink fauna, containing high percentages of species and individuals of the benthonic foraminiferal families Lagenidae, Buliminidae, Anomalinidae, and Rotaliidae, in addition to floods of planktonic foraminifera, was deposited at neritic depths of from 300 to 600 feet. We believe that the lower figure is more correct and that the water depth fluctuated from very shallow littoral to about 300 feet or less as indicated below.

Fox and Olsson (op. cit.) also infer that the large numbers of individuals present in the Navesink are related to very slow rates of sedimentation. At Marlboro the number of foraminiferal species in the Mt. Laurel is small and greatly increases in the Navesink (samples 7-13). Moreover, the increase in numbers of species is comparable to the increase in the numbers of individuals (Table 1); in some cases the trends correspond. The numbers of genera, species and individuals all change approximately together from sample to sample (Table 1). This probably occurs because a greater abundance of individuals in a sample increases the probability of finding a given species. However, the tremendous increases in individual and species abundance from samples 6 to 7 suggests increase in depth, decrease in the rate of sedimentation, or both; the reverse is true for samples 13 to 14. Bandy and Arnal (1957) reported an increase in the number of species away from shore into progressively more stable environments. Waller (1960) noted that the number of individuals increased with depth, reaching highest values on the outer shelf and decreasing somewhat beyond the break in slope.

The benthonic/planktonic ratio (B/P) is considered to be a depth indicator (Drooger and Kaasschieter 1958; Zalesny 1959; Waller 1960, and others), the lower the ratio the

greater the depth. In samples 1-6, and 14, too few foraminifera are present for the ratio to be significant; however, in samples 7-13 the number of individuals is more than adequate.

The B/P ratio decreases from sample 7 to sample 8, indicating a possible deepening of the water, and increases from sample 12 to sample 13, indicating possible shallowing. In samples 8-12 the ratio is almost constant, which would suggest a relatively constant depth.

Near-shore foraminiferal assemblages frequently include large numbers of agglutinated tests; for instance, Lowman (1949) found the greatest number of *Haplophragmoides* and *Ammobaculites* near shore in the region around the Mississippi delta. Thus these genera may indicate near-shore environments of low salinity and shallow water. The former is most abundant on bottoms between 30 and 120 feet deep. None were found in the Mt. Laurel or Navesink at the localities examined. At the opposite end of the depth range, Lowman found that the Buliminidae are the predominant family below depths of about 300 feet in the infra-neritic and inner bathyal zones. In between these depths, he noted highly diverse populations with many families and genera represented, and locally dominated by the Lagenidae, Buliminidae, and Rotaliidae (or Anomalinidae if *Cibicides* be assigned to this family following Cushman).

Abundant buliminids, lagenids, and rotalids were found in samples 7-13 at Marlboro; assuming that the genera and families found at Marlboro correspond roughly to the above definitions of microfaunal facies, the water depth in these samples could be assumed to have been somewhat greater than 120 feet but less than 300 feet, at least in the samples where foraminifera are common.

Recent work indicates that a large proportion of planktonic individuals (as at Marlboro) is not necessarily unusual in relatively shallow water. Bandy (1956) noted 70 per cent. planktonic foraminifera at slightly over 40 fathoms off St. Petersburg, Florida, and Bandy and Arnal (1957) record 25 per cent. plankton at 10 fathoms at two stations off the west coast of Central America. Burnaby (1962), who has studied the palaeoecology of the Chalk Marl (Cretaceous) in England, also believes that floods of planktonic foraminifera do not necessarily indicate depths of 200 to 300 fathoms or more.

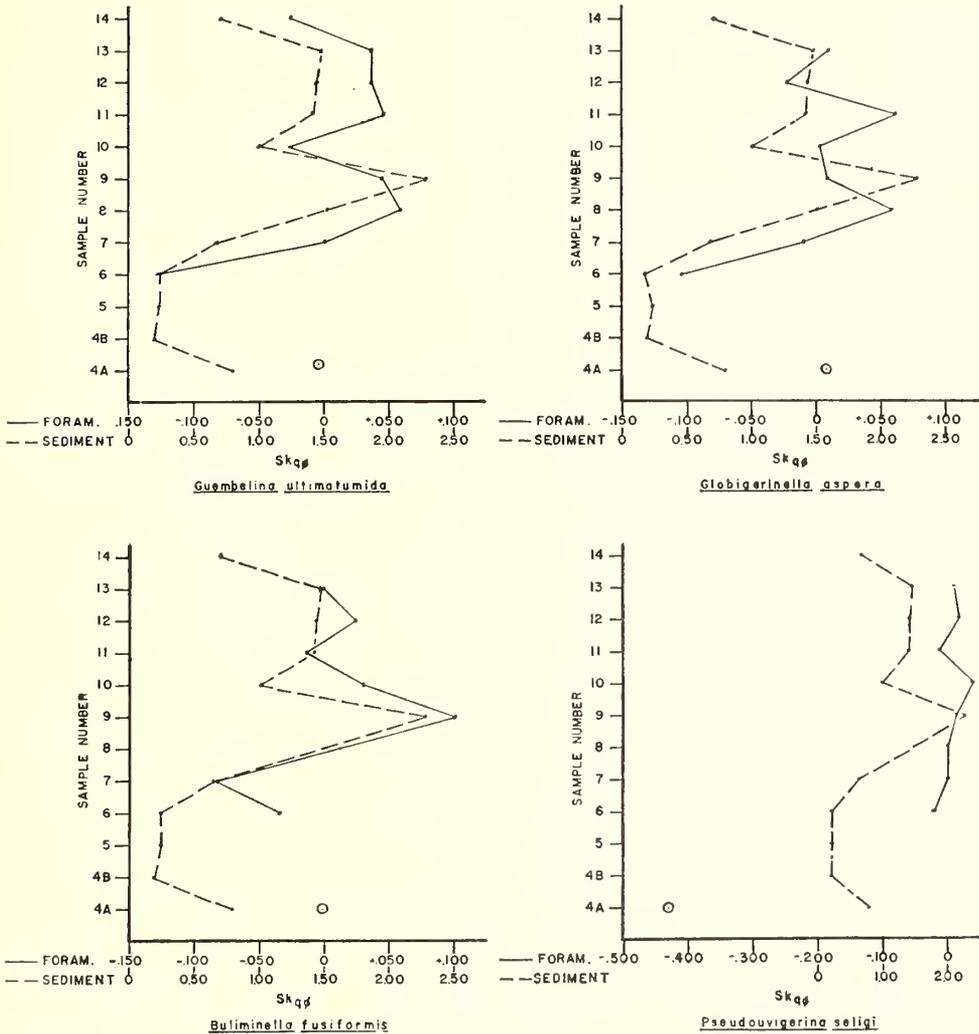
Carter (1951) measured the total number of foraminiferal shells and the total number of individuals of several species in the 30-mesh and 30-60-mesh fractions of a number of unwashed samples from the Coralline Crag of Suffolk. He then plotted each of these measures against stratigraphic position and found that a sudden change in lithology was not reflected in alteration of the constitution of foraminiferal assemblages unless there was also a change in grain size. Neither was there a change in the ratio of foraminiferal tests to sediment. This suggested the work below.

Assuming the presence of bottom currents, any foraminifera on the bottom should be subject to sorting in the same way as other components of the sediment. A comparison of the size-frequency distributions of individual species and sediment in successively higher stratigraphic horizons might therefore show correlation, assuming, of course, that bottom currents were powerful enough to move both fractions. On the other hand, if only the planktonic foraminifera correlate with the sediment, this might suggest (but not prove) that currents were only strong enough to move foraminifera while they were still above the water-sediment interface.

Size frequency determinations were made on four species of foraminifera at the

Marlboro locality: *Guembelina ultimatumida*, *Globigerinella aspera*, *Pseudovigenerina seligi*, and *Buliminella fusiformis*. These species were chosen because upon preliminary examination they appeared to be among the most common and widely distributed. The measurements took a good deal of time and were therefore made on four species only.

PHI QUARTILE SKEWNESS ($Sk_{q\phi}$)
MARLBORO SAMPLES



TEXT-FIG. 4

The Phi quartile skewness $\left(\frac{Q_3 - Q_1 - 2Md}{2}\right)$ was then calculated for each of these species, the same measurements being made for the sediments from which the foraminifera had been collected, and the figures compared (text-fig. 4).

Q_1 First quartile in a size frequency distribution with 75 per cent. of the material coarser than the given Phi diameter.

Q_3 Third quartile in a size frequency distribution with 25 per cent. of the material coarser than the given Phi diameter.

Md The median diameter of the distribution (note that all diameters are in Phi units).

The *Guembelina ultimatumida* (planktonic) and sediment curves correspond rather well and it should be noted that a large number of specimens of this species were measured (Table 2). *G. aspera* and *B. fusiformis* do not correspond so well and *P. seligi* corresponds very poorly to the sediment curve. *G. ultimatumida* was probably sorted after settling to the sea bottom; *G. aspera* and *B. fusiformis* may also have been sorted

TABLE 2. Number of specimens measured for size-frequency studies in each of four species

Layer	1	2	3	4
14	4	0	0	1
13	52	18	26	37
12	66	25	16	18
11	109	41	19	25
10	128	71	34	28
9	126	39	36	13
8	411	35	33	30
7	335	47	42	20
6	23	23	27	6
5	4	0	1	0
4B	0	0	0	0 Navesink
4A	112	21	19	7 Mt. Laurel
3	0	0	0	0
2	0	1	0	0
1	7	0	0	0

1. *Guembelina ultimatumida*

2. *Globigerinella aspera*

3. *Pseudovigierina seligi*

4. *Buliminella fusiformis*

but the number of specimens measured is too small to decide one way or the other. *P. seligi* may not have been sorted, but again the latter argument applies.

The foraminifera in all samples were examined in detail; the maximum size varied somewhat from sample to sample as did the number of solution holes. Much less solution was noted in the foraminiferal shells than in *Gryphaea* and *Exogyra* although both foraminifera and oysters have shells of calcite. In places where large numbers of oysters were observed, the number of solution holes in the foraminifera appeared to decrease; if part of the solution occurred on the sea bottom, it is possible that the oysters served as traps for sediment moved by bottom currents and hence the length of time that a foraminifer spent in direct contact with sea-water would be reduced. Breakage also varied from one sample to another and did not seem to be directly related to solution. The numbers of species and genera also vary in samples 9–12, as do the sorting coefficients (Table 1). Thus, although the depth of water was approximately the same for samples 9–12, environmental conditions varied to some extent.

The important foraminiferal genera and species in this paper are illustrated in Cushman (1946) and Nine (1954); the macrofossils are shown in Richards *et al.* (1958).

TABLE 3. A list of all the Foraminifera found in each 5-gram sample at Marlboro, New Jersey

Layer	1	2	3	4A	4B	5	6	7	8	9	10	11	12	13	14
NAME															
<i>Quinqueloculina</i> sp.									16	14	61	249			
<i>Quinqueloculina</i> sp.								10							
<i>Serpellocammina laevis</i> (Roemer) var. <i>cratosa</i> Cushman															
<i>Serpellocammina semicomplanata</i> (Carsey)				1						14		8	10		
<i>Borbulina</i> sp.										14		21		12	
<i>Bobulius</i> sp.												16			
<i>Lenticulina</i> sp.															
<i>Planularia dissona</i> (Plummer)								10		21					
<i>Margulina</i> sp.				1											
<i>Dentalina</i> cf. <i>D. conobrina</i> D'Orbigny								10				16			
<i>Dentalina basiplanata</i> Cushman			1								14	16			
<i>Lagena lineata</i> (Williamson)															
<i>Lagena sulcata</i> var. (Walker and Jacob)															
<i>Sanitocrinus</i> W. Berry			1							11		16	21		
<i>Gottulina adhaerens</i> (Ostrowski)						1		10		85	14	16			
<i>Gottulina</i> sp.												23	31	12	
<i>Globulina lacrima</i> Reuss			1					5	20	21	114	16	125	145	59
<i>Globulina</i> sp.								1		11		69	10	12	
<i>Paleopolymorphina</i> sp.								1	10		14				
<i>Ramulina ornata</i> Cushman												8			30
<i>Nonionella ansata</i> Cushman												16	21		
<i>Bolivina</i> cf. <i>B. canaliculata</i> (Ehrenberg)												212	291	1298	1943
<i>Guembelina cretacea</i> Cushman						2	7	526	425	543		1297	956	725	771
<i>Guembelina striata</i> (Ehrenberg)	5	2		12							7	16			
<i>Guembelina glabra</i> Cushman			1												
<i>Guembelina ulimatulida</i> White	7			113		4	23	6373	9278	14,744		19,975	22,525	15,941	15,427
<i>Ventilabrella carseyae</i> Plummer															
<i>Bolivina</i> sp.	1			1			2	182	106	86		151	83	145	297
<i>Fouquierina hispida</i> Cushman		1						10	21	14		30	21	24	60
<i>Pseudovigierina cretacea</i> Cushman								10		14					
<i>Pseudovigierina solida</i> (Cushman)						1	27	849	701	1058		1090	810	821	1602
<i>Bulimina fusiformis</i> Jennings				19			6	404	701	400		939	1164	918	2314
<i>Bulimina rostrata</i> Jennings				7				222	42	514		454	416	290	1063
<i>Entosolenia orbiculus</i> (Sopenza)	2								5	7		16	21	24	
<i>Entosolenia marginalis</i> (Walker and Jacob)									11	14		42	24	60	
<i>Virgulina navarroana</i> Cushman										14		14			
<i>Bolivina decurrens</i> (Ehrenberg)	1								101	42	143	182	249	290	712
<i>Loxostoma gemmum</i> (Cushman)				4	1										60
<i>Ellogonostaria pseudoscripta</i> Cushman															
<i>Valvulineria</i> sp.				2				1							60
<i>Gyroldina arkadelphia</i> Cushman				1						14		16			
<i>Gyroldina depressa</i> (Alth)	5			19				1234	637	1409	1454	1639	560	1958	
<i>Siphonina grima</i> Plummer				1				162	21	14		23	166	12	178
<i>Altiomorphina tracheloides</i> (Reuss)												16			
<i>Pullenia americana</i> Cushman								1	10	11					
<i>Globigerina lacera</i> (Ehrenberg)	1			1		1	3	586	509	572		615	249	241	415
<i>Globigerinella aspera</i> (Ehrenberg)		1		21			23	991	785	1258		2241	1787	628	1187
<i>Globotruncana formicata</i> Plummer												8	83	24	60
<i>Globotruncana cancellata</i> (Reuss)									20	5		8	21		
<i>Globotruncana arca</i> (Cushman)				1						7		16			
<i>Anomalina ammonoides</i> (Reuss)									10						
<i>Anomalina pinguis</i> Jennings				1						5	14	16	21	12	60
<i>Anomalina</i> sp.				2			1	202							1
<i>Anomalina elementaria</i> (D'Orbigny)															
<i>Cibicides</i> sp.												30			
<i>Cibicides harperi</i> (Sandidge)									10	11		8	21		
TOTAL	22	4	4	209	1	9	103	12,172	13,460	21,135	28,993	30,515	22,088	27,946	13

SAND SURFACE TEXTURES

Studies of the surface textures of sand grains with the electron microscope permit, in some cases, the determination of the environment of their transportation and/or deposition (Krinsley and Takahashi 1962a; in particular, dune and beach sands were distinguished).

Sand grains from Marlboro samples 1, 2, 3, 4A, 4B, 5, 6, and 11 were photographed with the electron microscope at magnifications of about $\times 5000$ using a platinum-palladium replication technique, and show a V-shaped sculpture.

V-shaped topographic patterns are characteristic of modern grains which have been subjected to surf action and have been duplicated experimentally (Krinsley and Takahashi 1962b). Further work (unpublished) has shown that V-shaped patterns are occasionally found on river grains, but other features are also seen which distinguish these from grains acted upon by surf. In Marlboro sample 1, the V-shaped patterns are not very numerous, and the surfaces of the grains appear to be considerably smoother than many modern beach grains (Krinsley and Takahashi 1962b).

The grains from Marlboro samples 2 and 3 (Mt. Laurel formation) are extremely flat; grains from sample 3 look somewhat like grains of crushed quartz etched in a strongly basic sodium hydroxide solution. The grains from sample 4A show two types of features; the large-scale ones may represent mechanical action, but they are unlike the features seen on modern beach grains (Krinsley and Takahashi 1962b); the smaller

features closely resemble grains etched in sodium hydroxide and in places they seem to have overridden and eliminated the larger textures, suggesting that the etched patterns are of later date.

The grains from sample 4B, close to the Mt. Laurel-Navesink boundary, most closely resemble crushed quartz which has been mechanically agitated in water for about 48 hours simulating beach conditions. It can be shown that when pebbles are added to the crushed quartz under the above conditions, larger surface features result, so the features shown by the grains in sample 4B were probably impressed under conditions where few pebbles were present. A background pattern is also present and may be due to chemical etching, either in sea-water or post-depositionally. The surface textures in samples 4A and 4B are completely different, complementing the sedimentary data and again suggesting a break in sedimentation between the two samples.

Sample 5 again suggests etching, but there is no evidence of shallow-water action. The surfaces of the grains in sample 6 were nearly flat, indicating either that no mechanical action had occurred or, more probably, that the features were subsequently removed. The grains in sample 11 show no V-shapes characteristic of surf action; etching patterns are evident.

It is apparent that electron microscopy will be useful in future sedimentary environmental studies; among possible uses are the differentiation of sedimentary environments as indicated above.

CONCLUSIONS

Interlocked, bored pelecypod shells suggest the presence of currents strong enough to move and interlock the valves; *Cliona* borings indicate periods of quiescence, as do specimens with both valves together in living position. Orientation of belemnites around obstacles with no discernible overall orientation indicates weak and localized currents. The presence of relatively few bored belemnites suggests that few of these fossils were uncovered by current action. In summary, the currents at Marlboro locality were weak, local, and aperiodic.

The crab-claw layer, 4B (Table 1), probably represents shoaling; the presence of crab claws, pebbles, only one foraminifer, and electron micrographs of the sand grains suggests this possibility.

Although juvenile *Exogyra* and *Gryphaea* were not found at Marlboro, it is probable that they were present originally and later eliminated by post-depositional solution. This is indicated by the presence of juveniles along with adults at the Crosswicks Creek locality, and a significant number of pelecypods in living position at Marlboro, together with evidences of solution.

The presence of *Cliona*, a good ecological indicator, suggests clear, silt-free water, full oceanic salinity, and a nearby river mouth where nutrients were provided in quantity.

The benthonic/planktonic foraminiferal ratio in layers 7-13, and large numbers of foraminiferal genera, species, and individuals, suggest depths of from 120 to 300 feet. Floods of planktonic foraminifera are not necessarily unusual at shelf depths; a number of workers (Bandy 1956; Bandy and Arnal 1957; Burnaby 1962) have indicated that up to 70 per cent. planktonic foraminifera can be found here. The large number of foraminiferal individuals also suggests that sedimentation was rather slow in layers 7-13.

The technique of comparing sediment and foraminiferal size frequency distributions

has been used to show that *Guembelina ultimatumida* was sorted after reaching the sea bottom. The study of sand surfaces by electron microscopy is also shown to be valuable in palaeoecological interpretation.

It is felt that the use of as many techniques as possible is advisable in palaeoecological studies so that independent checks on hypotheses are available.

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THE DENTITION OF THE DURHAM PERMIAN PELECYPOD *PERMOPHORUS COSTATUS* (BROWN)

by A. LOGAN

ABSTRACT. The all-important Upper Magnesian Limestone specimens of *Permophorus* [formerly *Pleurophorus*] *costatus* (Brown) from Byers's Quarry, Durham, upon which King based his controversial diagnosis of the dentition of *Pleurophorus* King, have been located and re-examined. They confirm the belief of earlier authors that King's original description was erroneous and that there is only one cardinal tooth in each valve. Several other Upper Magnesian Limestone specimens of this species in the Kirkby Collection support these conclusions and have been figured. The essential characters of *Pleurophorus* King (renamed *Permophorus* by Chavan) are redefined in the light of these investigations.

THE well-known and common Permian pelecypod *Permophorus costatus* from the Magnesian Limestone of Durham (and its western representative) and the Zechstein of Germany was first described from the Permian Marls of Newtown, near Manchester, as *Arca costata* by Brown in 1841 (p. 66, pl. 6, figs. 34, 35). It was later described by various authors, who assigned it to several different genera, including *Modiola* (by de Verneuil, 1845), *Cypricardia* (by Geinitz, 1846), *Myoconcha* (by Howse, 1848), and *Cardita* (by Geinitz, 1848). Howse (1848, p. 245) noted that the hinge margin of the right valve 'is furnished with a distinct, oblique tooth or callosity, which fits into the corresponding depression in the left valve'. He was in error in assigning Brown's species to *Myoconcha*, however, for this genus has one oblique cardinal tooth, but no elongate posterior tooth. In addition, the acuminate posterior extremity and the mytiliform shape of *Myoconcha* are quite unlike the typical Durham form of this shell.

In 1848 (p. 11) King described a new genus *Pleurophorus* and his short diagnosis, without figures, was published as follows: 'Form inequilateral: cartilage external: anterior adductor muscular impressions deeply excavated, often bounded posteriorly by a ridge: pallial line entire: dentition cardinal and posterior: cardinal teeth two in each valve, diverging inwardly, and interlocking alternately: posterior teeth linear; the receiving tooth in the left valve.' In 1850 King repeated his diagnosis (p. 180) and described and figured specimens of *Pleurophorus costatus* (Brown), designated by him as type species, from both the Middle Magnesian Limestone of Humbleton Hill and Tunstall Hill, near Sunderland (pl. 15, figs. 13-15), and the Upper Magnesian Limestone of Byers's Quarry, near Marsden (pl. 15, figs. 16-20). King's description of the teeth and muscle scars was presumably based on the complementary valves of a mature individual (figs. 16, 17) and a juvenile (figs. 18, 19). The artist, G. B. Sowerby, Junior, clearly showed the two diverging cardinal teeth in all four valves; there is thus no reason to suspect any printing or lithographic errors on the part of either the author or the artist.

It was not long before students of Permian palaeontology began to express their doubts concerning King's observations. M'Coy (1855, p. 497) could discover in his specimens 'only the most minute traces of the cardinal teeth represented so strongly in Professor King's figures'. Schauroth (1856, p. 229) could discern one or two tooth-like

elevations on the hinge-plate of his specimens from the German Zechstein, but stated that they were never clearly developed as two separate cardinal teeth in each valve, as King had described. Howse (1858, p. 36) denied the existence of a second cardinal tooth, while Geinitz (1861, p. 71) cautiously expressed the view that 'a second cardinal tooth of the type clearly illustrated by King appears to be rare' (free translation).

Waagen (1881, pp. 214–15) discussed this problem and concluded that the Salt Range forms of this genus (*Pleurophorus imbricatus* de Koninck, *P. subovalis* Waagen, *P. complanatus* Waagen, and *P. acuteplicatus* Waagen) did indeed possess the distinctive cardinal dentition of King's specimens.

Boehm's studies (1914) of *Pleurophorus* led him to request the loan of King's original specimens from Dr. F. L. Kitchin of the Geological Survey of Great Britain; a search by Dr. Kitchin, however, failed to uncover them. Boehm reports (p. 554) that Kitchin finally sent him a specimen from Tunstall Hill which Boehm illustrated (pl. 21, fig. 4a, b) to support his conclusion that only one cardinal tooth is present in each valve.

Newell (1940, p. 297), describing *Pleurophorus albequus* Beede from the Permian Whitehorse Sandstone of the American Mid-Continent region, gave an excellent discussion of the generic problem involved. He had also begun a search for King's specimens, but failed to ascertain their whereabouts and concluded, mainly from his study of the North American representative of *Pleurophorus*, that King's original diagnosis was probably incorrect. He was able to distinguish only one cardinal tooth in each valve and his detailed and well-illustrated description of *P. albequus* indicates the remarkable similarity of this form to the English Permian form, from which it is distinguished only by its more elongate shape.

Chavan (1954, p. 200), principally from a consideration of *P. albequus* Beede, believed *Pleurophorus* to have a rudimentary second cardinal tooth in each valve and assigned to this genus the lucinoid dental formula 2 (4b) P II / (3a) 3b P III. He also suggested the name *Permophorus* for King's genus, preoccupied by *Pleurophorus* Mulsant 1842, which is in general use by coleopterists (Cox, private communication). Newell (1957, p. 10)

EXPLANATION OF PLATE 47

Figs. 1–9. *Permophorus costatus* (Brown). 1, Hinge of right valve of a mature specimen, showing single cardinal tooth and socket, and slightly grooved postero-lateral tooth, King Collection, Upper Magnesian Limestone, Byers's Quarry, Durham, $\times 5$. 2, Hinge of a mature left valve, with cardinal tooth, King Collection, same locality and horizon as fig. 1, $\times 5$. 3, Hinge of a mature right valve, with cardinal tooth and socket, anterior ridge, pedal retractor pit and anterior adductor muscle shown, King Collection, same locality and horizon as fig. 1, $\times 5$. 4a, Right valve of a poorly preserved mature individual, King Collection, same locality and horizon as fig. 1, $\times 2$. 4b, Cardinal tooth of previous specimen, illuminated from south-west, $\times 2$. 5, Right valve of poorly preserved juvenile specimen, figured by King, 1850, pl. 15, fig. 18, King Collection, same locality and horizon as fig. 1, $\times 5$. 6, Left valve of a juvenile specimen, figured by King, 1850, pl. 15, fig. 19, King Collection, same locality and horizon as fig. 1, $\times 5$. 7, Internal mould of hinge of a mature right valve, illustrating cardinal tooth and socket, anterior ridge, curved pedal retractor pit, and anterior adductor muscle scar, Kirkby Collection, Middle Magnesian Limestone, Humbleton Hill, $\times 4$. 8, Internal mould of hinge of a mature right valve, showing cardinal tooth and socket, anterior ridge and anterior adductor muscle, Kirkby Collection, Upper Magnesian Limestone, Souter Point, Durham, $\times 5$. 9, Internal mould of a mature left valve, showing cardinal tooth and socket and postero-lateral tooth and socket, Kirkby Collection, same locality and horizon as fig. 8, $\times 5$. Figs. 1–6 are in the King Collection, University College, Galway. Figs. 7–9 are in the Kirkby Collection in the Hancock Museum, Newcastle upon Tyne.



1



2



3



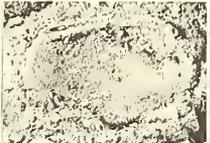
4a



4b



5



6



7



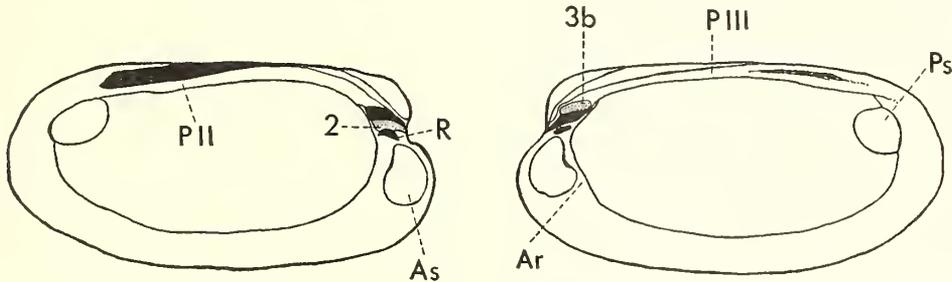
8



9

was unable to confirm cardinal tooth 3a in any of his silicified specimens of *P. albequus* from south-west U.S.A., while 4b and P I were only occasionally present in certain specimens. His dental formula for *Permophorus* was thus: 2 (4b) P II / 3b (P I) P III.

The specimens described and illustrated by King in 1850 from the Upper Magnesian Limestone of Byers's Quarry, Durham, are in the King Collection at University College, Galway, and were kindly loaned by Professor J. L. Mitchell. The shells are rather poorly preserved in the highly calcareous, crystalline facies of the Concretionary Limestone series. In all cases the shells have suffered from partial or complete recrystallization, so that it is often difficult to elucidate the detailed internal structure. King's controversial drawings (figs. 16, 17) are not taken from the two separate valves of a single individual,



TEXT-FIG. 1. Diagrammatic restoration of hinge and musculature of left and right valves of *Permophorus costatus* (Brown), $\times 2$. As, anterior adductor muscle; Ps, posterior adductor muscle; Ar, anterior ridge; R, pedal retractor pit; 2 and 3b, cardinal teeth; P II and P III, postero-lateral teeth. Teeth stippled, sockets black.

but appear to have been reconstructed from several incomplete shells (Pl. 47 figs. 1-4). Similarly, the two juvenile valves illustrated by King (figs. 18, 19) are present on one slab of limestone (although it is not certain that they at one time comprised a single, complete shell), and are so poorly preserved that it is inconceivable that such detail as is depicted in King's figures could possibly be extracted from them (Pl. 47, figs. 5, 6). A single cardinal tooth is well developed in each valve but a close examination of the dentition and musculature in all the specimens available reveals no evidence whatsoever of a second cardinal tooth, however rudimentary, in either valve. The other features, such as the elongate postero-lateral teeth and the small impressions on the anterior ridge (which King attributed to the presence of a visceral or pedal muscle), are easily distinguished, however, and lead one to wonder why the cardinal teeth were so misinterpreted.

A small slab of Upper Magnesian Limestone in the Kirkby Collection, from Souter Point on the Durham coast, about one mile south of Byers's Quarry, showed two internal moulds, one of the left valve and one of the right valve. The shell is no longer present but the hard, fine-grained dolomitic limestone, typical of the Concretionary Limestone series at this locality, has preserved the internal details of these valves to a remarkable degree (Pl. 47, figs. 8, 9). From a study of both King's and Kirkby's specimens (including one well-preserved internal mould from the Middle Magnesian Limestone of Humbleton Hill (Pl. 47, fig. 7)) the dentition of the valves may be elucidated (see text-fig. 1). In the right valve there is a triangular, almost horizontal, ventrally

concave cardinal tooth (3b), with its apex situated just below the beak, which fits into a corresponding socket in the left valve. In the left valve there is a rather smaller, but similarly shaped cardinal tooth (2), situated on the ventral ridge of the large socket, which interlocks with a corresponding socket beneath the cardinal tooth of the right valve. This tooth may be rather indistinct and only slightly developed in some specimens. The sharp, angulated, and, occasionally, grooved dorsal margin of the right valve (Pl. 47, fig. 1) serves as a postero-lateral tooth (P III), fitting against the slightly excavated dorsal margin of the left valve and interlocking posteriorly with the left valve hinge margin where it becomes divided by a narrow, but deep, furrow or socket. This socket is bounded ventrally for three-quarters of the shell length by a narrow postero-lateral tooth (P II) which, however, has no corresponding socket in the opposite valve, merely serving to support the left valve socket and give extra strength to the articulation of the valves at this point (Pl. 47, fig. 9).

SYSTEMATIC DESCRIPTION

Order HETERODONTA Neumayr

Superfamily CARDITACEA Menke

Family KALENTERIDAE Marwick, 1953

Genus PERMOPHORUS Chavan, 1954, p. 200

[*Pleurophorus* King 1848, non *Pleurophorus* Mulsant 1842]

Type species. *Arca costata* Brown 1841 (type specimens missing).

Revised diagnosis. Shell inequilateral, posteriorly elongate, rectangular, with beaks situated at anterior extremity and markedly prosogyral. Ligament external and amphidetic, escutcheon and very small lunule present. A simple cardinal tooth, situated beneath the beak, present in each valve, and a linear postero-lateral tooth in the right valve fits into a corresponding socket in the left valve, the furrow being bounded ventrally by a narrow postero-lateral tooth. Anterior muscle scar small and deep and bounded posteriorly by a well-marked ridge, furnished with a small, curved pedal retractor pit near its junction with the dental plate. Posterior muscle scar large but shallow, and situated near posterior extremity of hinge-line; muscle scars joined by an integripalliate pallial line. Ornament of concentric growth lamellae and radial costae, usually three to six in number and extending diagonally from the beak to the postero-lateral border. Occasional specimens may be non-costate.

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AMMONITES OF THE LIASSIC FAMILY JURAPHYLLITIDAE IN BRITAIN

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ABSTRACT. The genus *Galaticeras* is recorded from the Lower Lias of Britain for the first time. The palaeontology and stratigraphy of *Tragophylloceras* are revised, ten out of fourteen previously described species being placed in synonymy, while one new one, *T. carinatum*, is described. Microconch-macroconch pairs are recognized in *Tragophylloceras* and formally described, this being the first full description of dimorphic pairs in Liassic ammonites.

THE Jurassic members of the ammonite superfamily Phyllocerataceae are well known to have been restricted in their geographical distribution. In Europe, they are abundant in the Mediterranean countries, and spasmodic in their occurrence further north. In the Lower and Middle Lias of north-western Europe they are represented by two genera of the family Juraphyllitidae. One of these, *Galaticeras*, was a straggler from the southern province. The other, *Tragophylloceras*, was peculiar to north-western Europe and is not recorded from the Mediterranean area.

Galaticeras is a new record for the British Lias. It was discovered by Mr. J. F. Jackson in the Flatstones of the Lower Lias near Charmouth, Dorset, and simultaneously recognized by one of us (D.T.D.) in borehole material in the Geological Survey collections. *Tragophylloceras* has been reviewed in the light of all relevant British collections and a systematic description of its species is given for the first time. In three of the five species described dimorphic pairs of microconchs and macroconchs have been found. The pairs are considered to be dimorphic forms of the same species for reasons discussed under the section on the genus *Tragophylloceras*. By referring them to the same species we do not mean to imply that the dimorphism is sexual; this could indeed be the case, but there is not sufficient material of *Tragophylloceras* to throw any light on the subject of sexual dimorphism in ammonites. Such dimorphism has only been recognized in Liassic ammonites in recent years, and this is the first formal description of any Liassic dimorphic pairs.

Acknowledgements. We wish to thank Dr. J. H. Callomon for the gift of two specimens from his collection, and Brigadier G. Bomford, Dr. J. C. W. Cope of Swansea University College, Dr. M. L. K. Curtis of Bristol City Museum, Mr. D. Emlyn Evans of the National Museum of Wales, and Dr. R. J. G. Savage of Bristol University for the loan of specimens under their care. Our thanks are also due to Mr. L. Bairstow for allowing us to quote determinations of ammonites in his collection from Robin Hood's Bay. Specimens in the British Museum (Natural History) are listed under the abbreviation BM, those in the Geological Survey and Museum, London, as GSM, those in the National Museum of Wales, Cardiff, as NMW, and those at the Sedgwick Museum, Cambridge, as SM. Whorl dimensions are quoted in millimetres in the following order: diameter: whorl height, whorl breadth, umbilical width.

SYSTEMATIC DESCRIPTIONS

Family JURAPHYLLITIDAE Arkell 1950

The family comprises eight genera (Arkell 1957, pp. L189-92) which have phylloceratid suture-lines, but which have shells with umbilici larger (commonly between 15 and

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30 per cent. of the diameter) than in contemporary members of the family Phyllocerataidae. Constrictions on the internal mould, due to thickenings of the shell-wall, are present, though sometimes on the inner whorls only. The shell is ornamented by sigmoidal growth-lines. Ribbing of the same form is often present, and is usually developed on the outer whorls only. Modification of the venter may occur, by a keel in *Harpophylloceras*, an interrupted keel in *Meneghiniceras*, or a groove in *Schistophylloceras*.

In Europe, juraphyllitids are common in Lower and Middle Liassic rocks south of the Alpine geosyncline, and they are also found in North Africa. *Galaticeras* is a typical southern genus which seems to have migrated north during the Obtusum Zone. *Tragophylloceras* is known only from north of the Alps, with the exception of records from Portugal (Arkell 1956, p. 242).

Genus *Galaticeras* Spath 1938

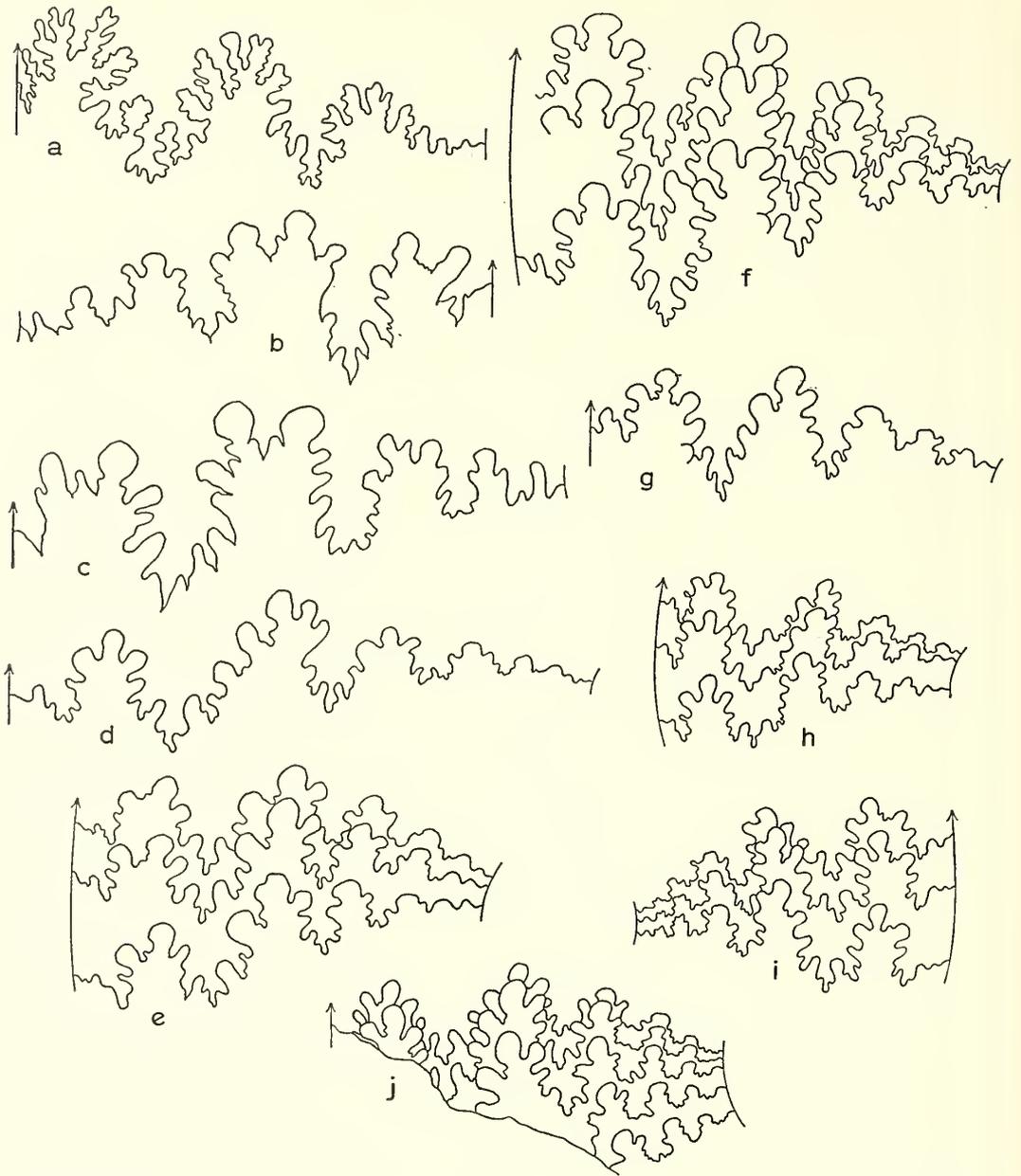
Type species. Amphiceras harpoceroides Gemmellaro 1884.

Synonym. Amphiceras Gemmellaro 1884, non Gray 1847.

This genus is known mainly from the 'Terebratula' *aspasia* Beds at Rocche Rosse, near Galati, Sicily, which are of Jamesoni and Ibex Zone age. Five species were described by Gemmellaro (1884, pp. 192–8): *Galaticeras harpoceroides*, *G. aegoceroides*, *G. flexistriatum*, *G. propinquum* (doubtfully distinct from *G. harpoceroides*), and *G. mariani*. Outside Sicily the genus is rare. There are two specimens in the British Museum (Natural History) (C52815–6) from the High Atlas, Morocco, that can be identified with *G. aegoceroides* (Gemmellaro 1884, p. 192, pl. 4, figs. 28–33, non figs. 26, 27 = *G. harpoceroides*), and show the characteristic low radial folds on the dorsal half of the side of the whorl. The specimen figured as '*Anauroceras?* sp.' by Mouterde (1951, p. 187, pl. 2, fig. 6) from the Ibex Zone of San Pedro de Muel, Portugal, might be another species of *Galaticeras*. This was said by Howarth (1959, p. 27) to be a polymorphitid, possibly *Tropidoceras masseanum* (d'Orbigny) var. *mediterranea* (Gemmellaro 1884, p. 200, pl. 5, fig. 1), but reference to *Galaticeras* seems more likely from the type of ornament. The suture-line was not figured by Mouterde, but was obtained when the specimen was on loan and is now figured here (text-fig. 1a). Although the suture-lines of *T. masseanum* (d'Orbigny 1844, pl. 58, fig. 3; Gemmellaro 1884, pl. 5, fig. 4) and *Galaticeras* (Gemmellaro 1884, pl. 4, fig. 23) do not differ fundamentally, those of *Tropidoceras* have narrow-necked saddles with minor lobes penetrating deeply into the dorsal sides of the second lateral and first auxiliary saddles. Such features do not occur in the Portuguese specimen, which has a suture-line which does not differ significantly from *Galaticeras*. The evidence favours reference of this specimen to *Galaticeras*, but confirmation could only be obtained by sectioning it to reveal the presence or absence of a keel on the inner whorls, for the outer whorl is an internal mould with no keel.

The new species described below from the Obtusum Subzone of Dorset is referred to *Galaticeras*, rather than made the type of a new genus on account of its considerably lower horizon, because of its marked resemblance to *G. mariani* (Gemmellaro), from which it differs only in being more involute.

Galaticeras has been recognized from two recent boreholes in the south of England. Two small specimens from the British Petroleum borehole at Brightling, Sussex (Falcon



TEXT-FIG. 1. Suture-lines of Juraphyllitidae. *a*, ? *Galaticeras* sp., from the Ibez Zone at San Pedro de Muel, Portugal; final suture-line at 90 mm. diameter from specimen figured by Mouterde (1951, p. 17, pl. 2, fig. 6). *b*, *c*, *Galaticeras jacksoni* sp. nov., bed 83, Flatstones, Obtusum Subzone, Stonebarrow, Charmouth, Dorset; *b*, BM C50907, at 26 mm. diameter; *c*, BM C50904, holotype, at 30 mm. diameter. *d*, *e*, *Tragophylloceras undulatum* (Smith), Valdani or Jamesoni Limestones, Radstock, Somerset; *d*, GSM 24430, final suture-line at 34 mm. diameter before adult body-chamber; *e*, BM C49721, Kilmersdon Road, Radstock, final three suture-lines showing crowding at 25 mm. diameter. *f*, *g*,

and Kent 1960, pp. 10, 11), show the characteristic ornament and suture-line of the genus. They are GSM 102186, about 11 mm. in diameter and preserving the beginning of the body chamber, and GSM 102187, retaining one-quarter of a whorl of body chamber at a diameter of 9 mm., preceded by approximated suture-lines. They occurred 17 feet above an asteroceratid ammonite and are probably from the Obtusum Zone, but the upper limit of this zone was not determined, the next ammonite being a Raricostatum Zone form 65 feet higher up the borehole.

The second record is from near Highbridge, Somerset, where small (*c.* 20 mm.) pyritized ammonites with typical *Galaticeras* ornament were collected. Suture-lines are not seen. This occurrence is accurately dated by other ammonites as belonging to the Stellare Subzone of the Obtusum Zone.

Galaticeras is readily distinguished from *Juraphyllites*, which has stronger, straight ribs and is often constricted. *Tragophylloceras* is usually more involute and has phylloid endings to the long monophyllic endings of the suture-lines. The only other genus which can be compared with *Galaticeras*, and particularly the Dorset species described here, is *Bouhamidoceras* Dubar (1962, p. 320). This occurs in the Oxynotum Zone at Ziz, High Atlas, Morocco, and is a compressed, involute and feebly ribbed form with a highly characteristic suture-line, in which the ventral lobe is very shallow, the first lateral saddle asymmetrical, and the first lateral lobe wide and divided by large minor saddles. Another species which should probably be referred to this genus is *Amphiceras kammerkerense* Hahn (1910, p. 358, pl. 16, fig. 3; Lange 1952, p. 87, pl. 18, fig. 5), from the Hettangian (Liasicus or Angulata Zones) of the northern Alps. This species has a more evolute body chamber which shows adult characters near the aperture. Lange referred it to *Galaticeras*, and it shows some resemblance to *G. propinquum* (Gemmellaro 1884, pl. 6, figs. 10–12), but it is better placed in *Bouhamidoceras* on account of its suture-line. The Dorset species has stronger ribs than *Bouhamidoceras* and a different suture-line.

Galaticeras jacksoni sp. nov.

Plate 48, figs. 1–4; text-figs. 1*b*, *c*

Material. Nine specimens collected by Mr. J. F. Jackson.

Holotype. BM C50904 (Pl. 48, figs. 1*a*, *b*). *Paratypes.* BM C50905–6, BM C50907 (Pl. 48, fig. 2), BM C71099 (Pl. 48, fig. 3), BM C71100, NMW 60.510 G1714, G1887 (Pl. 48, fig. 4), G2202.

Horizon and locality. The Flatstones, bed 83h (possibly also bed 83d), Black Marl, of the Obtusum Subzone, Obtusum Zone. Stonebarrow cliff, Dorset (Lang 1926, p. 160).

Diagnosis. A relatively involute species, in which the sigmoidal striae increase in strength on the venter to form forwardly projected chevrons on the keel. The whorl section is

T. loscombi (J. Sowerby), Stokesi Subzone, Eype Nodule Bed, Dorset; *f*, SM J44818, Eype Mouth, Dorset, final three suture-lines showing crowding at 25 mm. diameter; *g*, GSM 102185, Golden Cap, Seatown, Dorset, final suture-line at 21 mm. diameter. *h–j*, *T. carinatum* sp. nov.; *h*, BM C56679, holotype, Ibex or Davoei Zone, Stonebarrow, Charmouth, Dorset, final three suture-lines showing crowding at 16 mm. diameter; *i*, BM C28222, Ibex Zone, Battledown brickworks, Cheltenham, final three suture-lines at 17 mm. diameter; *j*, BM C71121, Luridum Subzone, brickpit at Blockley Station, Gloucestershire, final five suture-lines showing crowding at 21 mm. diameter.

Fig. 1*a*, $\times 1.7$; remainder $\times 5$.

nearly flat sided, has a slightly differentiated ventral keel, and umbilical walls varying between gently sloping and near-vertical. The ornament consists of somewhat irregular striae or fine ribs which are highly sigmoidal or S-shaped on the side of the whorl; towards the venter they are inclined strongly forwards and increase in strength to form marked chevrons on the keel.

Description and remarks. The material consists of nine specimens in which the septate whorls are preserved as solid casts of calcite and have the shell intact in a few places, while the body chambers are crushed flat but retain good preservation of the ornament. The calcite casts have well-preserved suture-lines and these are spaced normally up to the body chamber with no signs of crowding. The body chambers show no adult characters, but all are less than half a whorl and incomplete, and the mouth border is unknown. Dimensions of the septate whorls of the two best-preserved specimens are as follows:

C50904—at 38.5 mm.: 19.8 (0.51), 9.4 (0.24), 7.5 (0.19).

C50907—at 35.0 mm.: 17.0 (0.49), 8.6 (0.25), 7.8 (0.22).

These measurements show the extent to which C50904 is more involute than C50907, a fact which can be readily seen in the figures (Pl. 48, figs. 1*a* and 2*b*). In much larger collections of similar-sized ammonites a difference of this order of magnitude in the size of the umbilicus (19 to 22 per cent. of the diameter) is often well within the variation of the species. C50904 and 50907 also differ in the steep umbilical wall and small chevrons on the venter of the former, compared with the gently sloping rounded umbilical wall and larger chevrons of the latter specimen. All the other specimens are intermediate between these two and form a continuous series; the specimen of Plate 48, fig. 4 has an umbilicus of similar size to that of C50904, but it has sloping umbilical walls and rather larger chevrons, while the example in Plate 48, fig. 3 has large chevrons and a wide umbilicus like C50907, but it has small, steep umbilical walls. To a large extent the size of the chevrons, the size of the umbilicus, and the type of umbilical walls vary independently of each other; this is the normal variation of the species and should not be made the basis of splitting into more than one species.

The suture-lines (text-fig. 1*b*, *c*) are characterized by bifid first and second lateral saddles, which have rounded, slightly phylloid endings. The first lateral lobe is much deeper than the external lobe and has a long pointed central ending. They agree in all respects with the suture-lines of the Sicilian population figured by Gemmellaro (1884, pl. 1, figs. 12, 17; pl. 4, figs. 23, 30, 38; pl. 6, fig. 12; pl. 7, fig. 23).

The closest comparison with the Sicilian species is to be made with *G. mariani* (Gemmellaro 1884, p. 197, pl. 1, figs. 13–17; pl. 4, figs. 34–39, pl. 7, fig. 23). The three medium-sized specimens figured by Gemmellaro differ somewhat amongst themselves, and the original of his pl. 4, fig. 34 is closest to the Dorset specimens. The only significant differences between this specimen and C50907 (Pl. 48, fig. 2) are the smaller umbilicus and lower horizon of the latter. In both the Dorset and Sicilian specimens the ribs are straight and inclined forwards at an angle of about 45° to the venter for some distance before they reach the keel on the mid-ventral line. As in the Dorset specimens the size of the chevrons varies in the three Sicilian examples. The sigmoidal shape of the striate ribs on the whorl side is exactly the same in the two populations. The four other species of *Galaticeras* figured by Gemmellaro (1884) have smooth venters with no chevrons.

Genus TRAGOPHYLLOCERAS Hyatt 1900, p. 568

Type species. The sole definition of the genus given by Hyatt was 'Type *T. (Phyl.) heterophyllus-numismalis*, Quenst. sp.' According to the International Code of Zoological Nomenclature (edition of 1961), Article 68 (a), this is the nominal type species by original designation. In the *Treatise*, Arkell (1957, p. L191) stated the type species to be so by subsequent designation by Buckman (1912, p. viii), but Buckman's designation was superfluous. In accordance with Article 45 (d) (i) of the Code, the name *numismalis* as originally cited by Quenstedt in the combination *Ammonites heterophyllus numismalis* is interpreted as a sub-specific name raised to specific rank by later authors. The type species of *Tragophylloceras* is therefore *A. numismalis* Quenstedt 1845.

Synonym. *Phyllobites* Vadász 1907, p. 352. In proposing *Phyllobites*, Vadász (1907, p. 402) said 'Nachdem wir als Typus des oberwähnten Phyllobites *Ammonites loscombi* Sow. und *Amn. ibex* Quenst. betrachten, . . .' We therefore designate *Ammonites loscombi* J. Sowerby 1817, as the type species. We agree with all other workers in regarding this genus as a subjective synonym of *Tragophylloceras*.

Characters of genus. *Tragophylloceras* is a phylloceratid genus with open umbilicus. The whorl is strongly compressed, with parallel or convergent sides. The first whorl after the protoconch is always smooth. On the second or third whorl, constrictions appear on the internal mould due to thickening of the shell wall on its inner side; they are not seen in specimens with the shell preserved. The constrictions persist for one or two whorls only, except in *T. numismale*, in which they may continue up to a diameter of over 20 mm. Sigmoidal ornament is present throughout. This may remain as growth-lines or be developed as ribs. It is usually strongest over the venter, as in *Galaticeras* and *Juraphyllites*. The early sutural development has been worked out by Spath (1914) for *T. loscombi* and by Schindewolf (1961, pp. 711, 713) for *T. ibex* and *T. undulatum*. At an early stage (by 20 mm. diameter in *T. loscombi*) the saddles bear inflated folioles of typical phylloceratid type. The adult external suture-line has six or seven saddles; the first lateral saddle is monophyllic and roughly symmetrical. The second lateral saddle, however, changes during development from a monophyllic state to one described by Spath (1914, p. 346) as subdiphyllic, with two terminal leaflets, of which the one nearer the venter is usually slightly larger than the other.

Three out of the five species show adult shells of two different sizes. These correspond to the microconchs and macroconchs recognized in Upper Jurassic ammonites by Callomon (1955, p. 238) in that the smaller forms have apertures with constrictions and lappets, while the larger have plain apertures. The observations may be tabulated as follows:

<i>Species</i>	<i>Approximate diameter of microconchs</i>	<i>Approximate diameter of macroconchs</i>
<i>carinatum</i>	3 cm. Rare.	Not known.
<i>loscombi</i>	3-4 cm. Common at two horizons only.	9-15 cm. Common.
<i>undulatum</i>	4-5 cm. Common.	Over 8 cm. A few.
<i>ibex</i>	5 cm. A few.	13-14 cm. Common.
<i>numismale</i>	Not known.	20-22 cm. Common.

We conclude that dimorphism existed in *Tragophylloceras*, but the material available does not add anything to our knowledge of this phenomenon. The disparity in relative abundance and in stratigraphic horizon between the microconchs and macroconchs of each species is no greater than in many other cases of dimorphism.

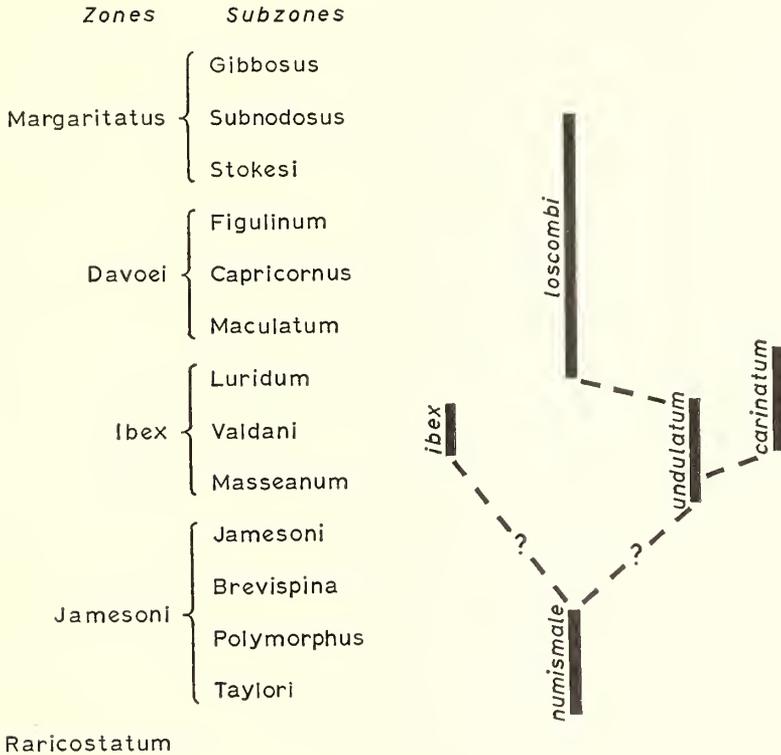
In each case the microconch differs from the macroconch only in those characters associated with the attainment of the complete adult microconch shell. At all growth stages before the final half whorl the microconch cannot be distinguished from similar-sized inner whorls of the macroconch. For this reason the two forms are referred to the same species. Other scales of classification which could have been adopted are the reference of the two forms to separate species, such as has been done in the case of large collections of closely associated large and small forms obtained in the Upper Lias by one of the authors (Howarth 1962*b*, pp. 412–13), or the reference of the two forms to separate subgenera, such as is commonly adopted in the Upper Jurassic. In the case of the Upper Lias species it has been found that similar-sized inner whorls of the large and small forms are separable by small but distinct differences (other than the adult features of the small forms), and reference to different species seems to be appropriate. On the other hand the large and small forms of *Tragophylloceras* are only separable when the small forms show their adult characters. The reference of many Upper Jurassic pairs to different subgenera follows the scaling down of the original morphological classification in which generic status was given to the small forms with lappets as distinct from the larger forms without lappets. But recent revival of interest into the possibility of sexual dimorphism in ammonites, as a result of careful and accurate collecting, may lead to the eventual adoption of an entirely different classification. *Tragophylloceras* does not add anything of significance to the theory of sexual dimorphism in ammonites. The small numbers and restricted distribution of the small forms found so far are undoubtedly due to the reluctance of collectors to collect what they considered to be inner whorls when larger outer whorls were available. The discovery during unbiased collecting of roughly similar numbers of large and small forms at all horizons and localities is necessary before any contribution can be made to the theory of sexual dimorphism.

Tragophylloceras is currently (e.g. by Arkell 1957, p. L191) placed in the family Juraphyllitidae, and it shows a general resemblance to other members of the family, and difference from the Phylloceratidae, in its open umbilicus and its tendency to have ornamented outer whorls. The Juraphyllitidae, like the Phylloceratidae, are overwhelmingly Tethyan in distribution, and *Tragophylloceras* is the only genus which is common in north-west Europe; it is, in fact, almost restricted to this area. The geographical distribution will be discussed further below.

It would be fruitless, at present, to seek to establish the immediate ancestors of *Tragophylloceras* among the numerous Tethyan phylloceratids and juraphyllitids, in view of the poor stratigraphical dating of many of these. The earliest British species, *T. numismale*, has the longest constricted stage. From purely morphological considerations *Tragophylloceras* could have evolved from *Juraphyllites*, or from one of the numerous constricted phylloceratids (Subfamily Calliphylloceratinae) which abounded in the Tethyan area from the Hettangian onwards.

Tragophylloceras numismale is found in the Inner Hebrides and the north of England, and rarely as far south as Somerset, but it is not known from the Dorset coast. This can hardly be due to collection failure, for the subzones in which it occurs are represented by over 20 feet of strata in Dorset. It is found in Europe, however, in Swabia and on the borders of the Massif Central. The only *Tragophylloceras* from the upper part of the Jamesoni Zone in Britain, from beds 115–118c on the Dorset coast, are not specifically identifiable. *T. ibex* and *T. undulatum*, the two most strongly ornamented species, appear

roughly simultaneously at the beginning of the Ibex Zone. They have a different distribution from *T. numismale*, being common in the south-west of England but absent from Yorkshire and the Hebrides. They do not form an obvious evolutionary development from *T. numismale*, and no transitional forms are known. The third ornamented species, *T. carinatum*, appears later in the Ibex Zone and could have evolved from *T. undulatum* by sharpening of the venter to form a keel.



TEXT-FIG. 2. Stratigraphical ranges and possible phylogeny of species of *Tragophylloceras*.

Tragophylloceras loscombi, which appears late in the Ibex Zone and has a long range, has a similar geographical distribution to *T. ibex* and *T. undulatum*, being common in the south of England and rare in Yorkshire. It could have evolved from *T. undulatum* by weakening of the ornament.

It is clear that the evolutionary history of *Tragophylloceras* is very imperfectly known. The most probable phylogeny is shown in text-fig. 2, but it must be regarded as very tentative.

Previous authors have described fifteen species which are now placed in *Tragophylloceras*. Fourteen of these were described from north-western Europe—France, Germany and Britain—and one (*T. vadaszi* Lóczy 1915) from Hungary. Our revision has reduced the fourteen north-west European species to four, and added one, the rare *T. carinatum*.

T. vadazsi has been recently redescribed by Géczy (1959), but its relationship to the north-west European species remains uncertain.

Stratigraphy of species of Tragophylloceras

The range of *Tragophylloceras* in Britain is from the lowest part of the Jamesoni Zone up to the base of the Subnodosus Subzone, Margaritatus Zone. The horizons of specimens collected from the outcrop between Gloucestershire and the Humber are rarely recorded more accurately than the nearest zone, and even the zone is often inferred from the species themselves. The main exception is in the case of *T. ibex*, which is found in association with *Acanthopleuroceras valdani* (d'Orbigny) at many localities and is therefore known to come from the Valdani Subzone. More accurate stratigraphy is available for the collections from Dorset, Radstock, Yorkshire and Pabay, Inner Hebrides, and it can be summarized here.

Dorset. Collections made by Lang (1928, pp. 189-95; 1936, pp. 431-5) from the Lower Lias and by Howarth (1957, pp. 188-94) from the Middle Lias give the following sequence of species:

		<i>Bed</i>			
Margaritatus Zone	{	Subnodosus Subzone	24	Margaritatus Stone	} <i>Tragophylloceras loscombi</i>
			18	Eype Nodule Bed	
	Stokesi Subzone	11-16			
	{	6-10	Three Tiers		
		1-3			
Davoei Zone		122-130	Green Ammonite Beds		
Ibex Zone	{	Luridum Subzone	121	Belemnite Stone	
		Valdani Subzone	119	<i>T. ibex</i> , <i>T. undulatum</i>	
		118d	<i>T. undulatum</i>		
	{	Masseanum Subzone	118c		
Jamesoni Zone		Jamesoni Subzone	118b	} <i>Tragophylloceras</i> sp. indet.	
		Brevispina Subzone	115		

Bed 121, the Belemnite Stone, is the most probable horizon of the holotype of *T. loscombi*.

Radstock, Somerset. Considerable numbers of well-preserved *Tragophylloceras undulatum* together with some *T. ibex* and *T. numismale* are known from the Radstock area. All are preserved in the same ironshot limestone matrix and Tutcher and Trueman's (1925) stratigraphical description of the Lower Lias in that area shows that this must represent both the Valdani and Jamesoni Limestones. *T. ibex* is recorded from the Valdani Limestone (Valdani Subzone) only, but *T. undulatum* is recorded (as *T. 'wechsleri'*) from both limestones (Tutcher and Trueman 1925, pp. 605, 616), while the horizon of *T. numismale* is not given. Ammonites recorded from the Jamesoni Limestone indicate the presence of the Polymorphus, Brevispina, Jamesoni, and Masseanum Subzones (Tutcher and Trueman 1925, pp. 601, 605) but the position of *T. undulatum* in this sequence is not known. It can only be inferred, therefore, that *T. undulatum* occurs in the Valdani and Masseanum Subzones of the Ibex Zone, with the possibility that it also occurs at lower horizons.

Yorkshire. Detailed collecting at Robin Hood's Bay by Mr. L. Bairstow has yielded the following sequence of species:

	Ibex Zone, ? Luridum Subzone
Bed	
569	<i>Tragophylloceras loscombi</i>
	Jamesoni Zone, Taylori Subzone (beds 501–30)
521	<i>Tragophylloceras</i> sp. indet.
520.5	} <i>T. numismale</i>
520.35	
520.2	
517.73	} <i>Tragophylloceras</i> sp. indet.
515.5	
506	
505.2	<i>T. numismale</i>

Bed 569 could be the horizon from which the holotype of *Ammonites ambiguus* Simpson (= *T. loscombi*) was obtained, and it may also have been the horizon of the holotype of *A. robinsoni* Simpson. The holotype of *A. nanus* Simpson and the paratype of *A. hunttoni* Simpson figured by Buckman (1921, pl. 219) (both are synonyms of *T. numismale*) came from beds 517 or 520.

Pabay, Inner Hebrides. *Tragophylloceras numismale* was obtained by Spath (1922, p. 550) in association with *Platypleuroceras caprarium* (Quenstedt) and *Radstockiceras* ('*Metoxy-noticerus*') in beds just below the lowest *Platypleuroceras brevispina* (J. de C. Sowerby) at Pabay. The horizon can be fixed accurately as the upper part of the Polymorphus Subzone, Jamesoni Zone.

Tragophylloceras numismale (Quenstedt)

Plate 48, fig. 5

- ? *Ammonites hunttoni* Simpson 1843, p. 41.
- Ammonites heterophyllus numismalis* Quenstedt 1845, p. 100, pl. 6, figs. 4a, b, 5a, b, non figs. 3a, b, 5c.
- Ammonites nanus* Simpson 1855, p. 38.
- ? *Ammonites hunttoni* Simpson 1855, p. 83.
- ? *Ammonites heterophyllus numismalis* Quenstedt 1856, p. 119, pl. 14, fig. 3.
- Ammonites heterophyllus numismalis* Quenstedt 1885, p. 291, pl. 37, figs. 8–11, 21.
- Phylloceras numismale* (Quenstedt); Pompeckj 1893, p. 14, pl. 3, figs. 4–7.
- Phylloceras elteni* Pompeckj 1893, p. 18, pl. 3, fig. 3.
- Phylloceras paucicostatum* Pompeckj 1893, p. 20, pl. 3, fig. 2.
- Tragophylloceras typicum* Buckman 1912, p. viii (holotype, Quenstedt 1885, pl. 37, fig. 11).
- Tragophylloceras hunttoni* (Simpson); Buckman 1921, pl. 219.
- Tragophylloceras numismale* (Quenstedt); Buckman 1921, pl. 233.
- Tragophylloceras nanus* (Simpson); Buckman 1926, pl. 679.
- Tragophylloceras loscombi* (J. Sowerby); Maubeuge 1951, p. 1, pl. 1, fig. 1.

Type specimen. The specimen from Ofterdingen figured by Quenstedt (1845, pl. 6, figs. 5a, 5b) was selected lectotype by Buckman (1912, p. viii).

Description and remarks. The available material of *T. numismale* consists of the Swabian examples figured by Quenstedt and Pompeckj, stated to come from the Jamesoni Zone, and the small collections from various British localities. In Britain it occurs most

commonly in Yorkshire; specimens obtained from Robin Hood's Bay consist almost entirely of small pyritized inner whorls, and Mr. L. Bairstow's careful collecting has shown that these come from beds containing species of *Phricodoceras* and referable to the Taylori Subzone of the Jamesoni Zone (see stratigraphical section above). Similar small inner whorls were obtained from material excavated from the railway tunnel one mile south-east of Old Dalby, Leicestershire (Woodward 1893, pp. 170-1), in beds presumed to belong to the Jamesoni Zone. The species may occur rarely in beds of Jamesoni Zone age in Gloucestershire, and a few medium to large specimens are known from the Radstock area, Somerset. No specimens are known from Dorset. The age of the species is again known accurately from its occurrence in beds at Pabay, Inner Hebrides (Spath 1922, p. 550), that are referable to the Polymorphus Subzone, Jamesoni Zone. Thus the stratigraphical range of *T. numismale* known so far embraces the Taylori and Polymorphus Subzones.

The complicated ontogeny of *T. numismale*, in which several of the growth stages have different features, and the considerable amount of variation within each growth stage, has led to the proposal of the six specific names listed in the synonymy. The first whorl after the protoconch is smooth, and constrictions commence on the second whorl at about 1.5 mm. diameter. Deeply incised constrictions occur on the second and most of the third whorls, numbering six to seven per whorl, up to a diameter of 5 to 6 mm. The holotype of *Ammonites namus* Simpson 1855, figured by Buckman (1926, pl. 679), is an example of small inner whorls at this stage of growth. From a diameter of 6 mm. onwards the whorl section becomes rapidly more compressed, and the constrictions remain as prominent, slightly curved bands, numbering six to eight per whorl, though not so deeply incised as at the smaller sizes. The strength of the constrictions varies, but in only a few individuals are they difficult to detect, and in most examples irregular low ribs appear between the constrictions. Several Swabian specimens in this stage of growth have been figured (Quenstedt 1845, pl. 6, fig. 4; 1885, pl. 37, fig. 21; Pompeckj 1893, pl. 3, figs. 4-7), and almost all the material from the Yorkshire coast and Old Dalby, Leicestershire, consists of inner whorls of this size. One of these is the paratype of *Ammonites hunttoni* Simpson 1843, from Robin Hood's Bay, figured by Buckman (1921, pl. 219). This specimen is probably not the holotype of Simpson's species (see Howarth 1962a, p. 98), and as it cannot now be determined whether Simpson's description refers to the same species, *Ammonites hunttoni* is best regarded as a *nomen dubium*. Acceptance of *A. hunttoni* on the basis of the paratype of 10.5 mm. diameter not known to belong definitely to the species Simpson described, would relegate Quenstedt's much better defined species to its synonymy. The characteristic constrictions of this stage, which

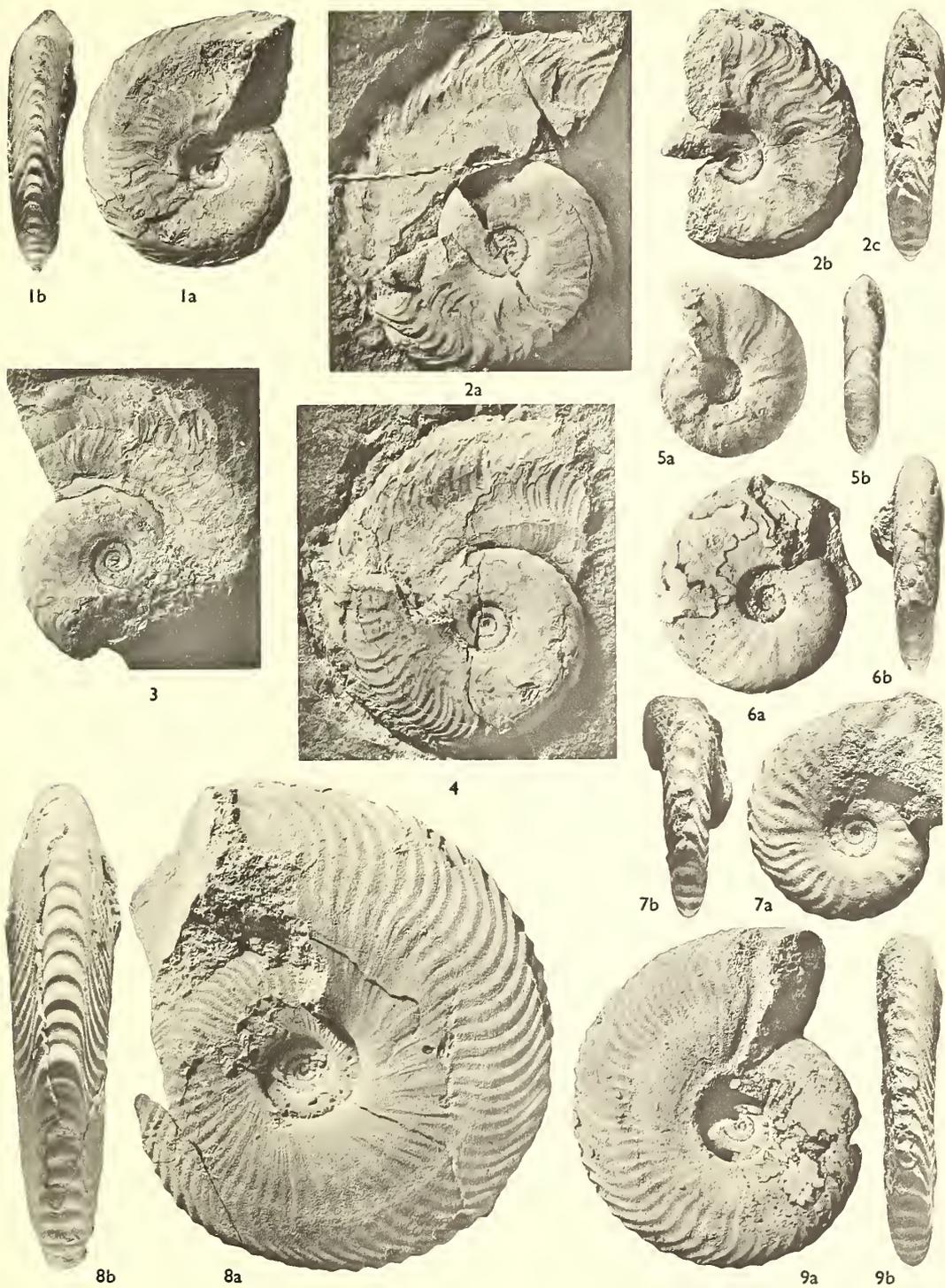
EXPLANATION OF PLATE 48

All figures natural size, except fig. 5, $\times 1.6$. Specimens coated with ammonium chloride.

Figs. 1a, b; 2a, b, c; 3; 4. *Galaticeras jacksoni* sp. nov. Bed 83, Flatstones, Obtusum Subzone, Stonebarrow, Charmouth, Dorset. 1a, b, Holotype, BM C50904. 2a, b, c, Paratype, BM C50907. 3, Paratype, BM C71099. 4, Paratype, NMW 60.510 G1887.

Figs. 5a, b. *Tragophylloceras numismale* (Quenstedt). Jamesoni Zone, Robin Hood's Bay, Yorkshire. BM C67766, $\times 1.6$, maximum diameter 17.5 mm.

Figs. 6a, b; 7a, b; 8a, b; 9a, b. *Tragophylloceras undulatum* (Smith). 6a, b, Microconch, BM C49721, Kilmersdon Road, Radstock, Somerset. 7a, b, GSM 24441, Radstock. 8a, b, Macroconch, BM C50451, Radstock. 9a, b, Microconch, GSM 24430, Radstock.



occur on the inner, and not on the outer surface of the shell, continue up to 15–23 mm. diameter, when they die out. A well-preserved Yorkshire example with constrictions up to 17.5 mm. diameter is figured in Plate 48, fig. 5.

The specimens from Old Dalby, Leicestershire, were described in some detail by Trueman (1916). The range of variation between examples with constrictions up to 23 mm. diameter, through others with less marked constrictions, to rare examples with no constrictions and rather more involute whorls, led Trueman to believe that both *T. numismale* and *T. loscombi* were present together with a whole series of intermediate forms, and that the evolution of the latter species from the former could be traced through the intermediates according to recapitulation theory. There is no reason to believe, however, that anything younger than Jamesoni Zone was present in the tunnel heaps at Old Dalby, and the whole fauna probably came from one restricted part of the Jamesoni Zone. The variation found and described by Trueman is that of immature forms of *T. numismale*, and it is no greater than the variation commonly found in the young whorls of other ammonite species that can be proved to be strictly contemporaneous.

At sizes larger than 25 mm. diameter there is considerable variation in the presence or absence of ornament. The lectotype (Quenstedt 1845, pl. 6, figs. 5*a*, *b*) and another Swabian example (Quenstedt 1885, pl. 37, fig. 8) are figured as entirely smooth. In others, ribs form chevrons of varying strength on the venter—Quenstedt 1885, pl. 37, fig. 10, and the Radstock specimen figured by Buckman (1921, pl. 233) have rudimentary chevrons; Quenstedt 1885, pl. 37, fig. 11, which is the holotype of *Tragophylloceras typicum* Buckman (1912, p. viii), Quenstedt 1856, pl. 14, fig. 3, and the holotype of *Phylloceras elteni* Pompeckj (1893, pl. 3, fig. 3), have larger chevrons on the venter. Still other specimens have chevrons on the venter combined with very irregular, low ribs—such are the holotype of *P. paucicostatum* Pompeckj (1893, pl. 3, fig. 2) and the only large specimen (BM C18115, 80 mm. diameter) found so far at Robin Hood's Bay, Yorkshire. Specimens at this stage are readily distinguishable from similar-sized specimens of *T. loscombi* by their thicker whorls and larger umbilici, and the variation in the presence and strength of their ornament is not markedly greater than the variation of the ornament in *T. loscombi*.

Larger examples are rare; they are smooth and have the typical trapezoidal whorl section seen in the specimen figured by Quenstedt (1885, pl. 37, fig. 9). The largest known specimens are two body chambers found by Spath in the Polymorphus Subzone of Pabay. Both appear to be smooth except for growth-lines, and the whorl sections are trapezoidal. The larger body chamber is incomplete at its maximum size of 200 mm. diameter, but it has a small part of an apparently plain mouth border near the umbilicus at a size which would indicate about 220 mm. diameter. The smaller specimen is nearly, if not quite complete at 200 mm. diameter; the mouth border, if present, is plain; and it has typical inner whorls. No evidence of the existence of smaller adults has been found.

Tragophylloceras undulatum (Smith)

Plate 48, figs. 6–9; Plate 49, fig. 1; text-fig. 1*d*, *e*

Ammonites undulatus Smith 1817, p. 114.

Ammonites heterophyllus numismalis Quenstedt 1845, p. 100, pl. 6, fig. 5*c*.

Ammonites ibex-heterophyllus Quenstedt 1856, p. 119, pl. 14, fig. 2.

Ammonites wechsleri Oppel 1862, p. 135, pl. 43, fig. 1a, b.

Phylloceras loscombi (Sowerby); Wright 1883, p. 419, pl. 39, figs. 1-3.

Ammonites heterophyllus intracrustatus Quenstedt 1885, p. 293, pl. 37, figs. 12, 13.

Ammonites ibex-heterophyllus Quenstedt 1885, p. 293, pl. 37, figs. 14, 18.

Phylloceras wechsleri (Oppel); Pompeckj 1893, p. 19.

Tragophylloceras radstockense Spath 1923, p. 293.

Tragophylloceras undulatum (Smith); Cox 1930, p. 303, pl. 12, fig. 5a, b.

Type specimen. The caption 'Fig. 3, Marlstone Plate' in Smith's (1817, p. 114) original description refers to a projected plate which was never prepared or published. BM C33499 was designated lectotype and figured for the first time by Cox (1930, p. 303, pl. 12, fig. 5); this specimen bears Smith's number 'C 3', which denotes the third species of the genus *Ammonites* described by Smith in his Marlstone section. There is a second specimen in Smith's collection (BM C721) bearing his number 'E 6', which differs in no way from the lectotype. 'E 6' does not coincide with any of his descriptions, so the number of specimens from which Smith described *A. undulatus* remains unknown.

The locality of the lectotype was given as 'Coal Canal', and the possible localities can be narrowed down greatly by considering where the Somerset Coal Canal, the construction of which William Smith supervised during 1794-9, crossed the outcrop of the upper part of the Lower Lias. This canal ran in two branches from Midford, 3 miles south-south-east of Bath. The northern branch ran west up the valley of the Cam brook to end at a point just short of Paulton, while the southern branch, which was partly constructed but never completed, was to have run south-west up the valley of the Wellow Brook to Radstock. After a century of use the northern branch was drained and replaced by a railway, which has recently been removed. The northern branch of the canal crossed the top of the Lower Lias one mile south-west of Dunkerton, where quarries and cuttings exposing the Jamesoni Limestone have been described by Tutcher and Trueman (1925, pp. 622-4, text-figs. 8, 9). Excavations on the uncompleted southern branch of the canal crossed this horizon between Wellow and Stoney Littleton, and the Jamesoni Limestone occurs in a quarry near the latter locality (Tutcher and Trueman 1925, p. 614). Smith's type specimen could only have been obtained from one of these two localities, which are 2 miles apart.

Description and remarks. In Britain *T. undulatum* is best known from the Radstock area of Somerset. In addition to Smith's originals there are forty-five specimens of this species in the British Museum, Geological Survey and Bristol University collections, and associated with them are several examples of *T. ibex* and a few of *T. numismale*. The horizons of these three species are discussed in the stratigraphical section above, and it can be deduced that *T. undulatum* occurs in the Masseanum and Valdani Subzones of the Ibex Zone, and possibly occurs also in the Jamesoni Zone below.

Some of the Radstock specimens show clear adult features: a prominent constriction at the mouth border, diminution of the whorl height on the last quarter whorl, modification of the ribs at the end of the body chamber, and crowding and some modification of the last two or three suture-lines. The type specimen (Cox 1930, pl. 12, fig. 5) is one such adult, and another specimen with more marked adult features is figured in Plate 48, fig. 9. These two have adult mouth borders at 49 mm. diameter and final suture-lines at 33-34 mm. Ten other specimens have adult mouth borders at sizes between 42 and 49 mm. diameter, and there is one smaller specimen with an incomplete body chamber that has adult suture-lines at 25 mm. diameter (Pl. 48, fig. 6; text-fig. 1e), which indicates a mouth border at about 38 mm. There are a few considerably larger specimens which are not adult and have maximum sizes between 60 and 80 mm. diameter and are septate up to 53 mm. (Pl. 48, fig. 8). There is a possibility that adults of two distinct sizes are represented here, the smaller series being complete at diameters between 38 and 50 mm. and having a constricted mouth border, the larger series being complete at sizes greater than 65 mm. and of which the mouth border characters are not yet known.

The Radstock population shows a certain amount of variation in ornament. From the normal type as exhibited by the type specimen and the example of Plate 48, fig. 9, there is a continuous series leading to a rather more coarsely ribbed form as in the specimens figured in Plate 48, fig. 7, and Plate 49, fig. 1. Two examples of unspecified locality, but almost certainly from Radstock, were figured by Wright (1883, pl. 39, figs. 1–3). Neither has been found, but assuming the drawings to be accurate, the original of Wright's figs. 1 and 2 is one of the more coarsely ribbed Radstock examples; it has a constricted mouth border and appears to be adult, but its maximum size is not known. [As drawn, the specimen is 83 mm. diameter, but the drawing has some features which suggest that it might be magnified. The size is not stated in the plate explanation; on the same plate, fig. 5, also of unstated size, is magnified $\times 2$, while fig. 4, said to be magnified, is in fact natural size. Wright was careless in this respect throughout his monograph.] Spath (1923, p. 293) renamed Wright's figs. 1 and 2 *T. radstockense*. In view of the complete series of transitions between the normal type and this slightly more coarse-ribbed form, and the fact that none of the coarse-ribbed forms approach the style of ribbing in *T. ibex*, *T. radstockense* is considered to be a synonym of *T. undulatum*. The specimen of Wright's fig. 3 is a more finely ribbed example and is close to the normal *T. undulatum*.

In Dorset a few crushed specimens are known from beds 118d and 119 of Lang (1928, pp. 191–2), which are referable to the Valdani Subzone. The best preserved example is from bed 119 and matches the type specimen of *T. undulatum* exactly; it shows distinct traces of a constriction at its mouth border at 47 mm. diameter. Another fragment from the same bed has a similar constriction at roughly the same size. A few specimens have been found in excavations near Kilsby, Northamptonshire, at an horizon low in the Valdani Subzone and a few feet below the lowest *T. ibex*.

T. undulatum is widely known in Germany from the descriptions and figures of Quenstedt and Opperl. One of Quenstedt's earliest figures (1845, pl. 6, fig. 5c) agrees with *T. undulatum* in ornament, and his later figures of this species (1856, pl. 14, fig. 2; 1885, pl. 37, figs. 14, 18) carried the name *Ammonites ibex-heterophyllus*, denoting a transitional form. Two specimens figured as *A. heterophyllus intracrystatus* (Quenstedt 1885, pl. 37, figs. 12, 13) also agree closely with *T. undulatum*. Meanwhile Opperl (1862, p. 293, pl. 43, fig. 1) had proposed the name *A. wechsleri* for a large and typical example of *T. undulatum* from the Ibex Zone of the Swabian Alb in Württemberg. Opperl's figure is probably idealized, but the drawing matches the larger Radstock specimens exactly (Pl. 48, fig. 8) and the relegation of *A. wechsleri* to the synonymy of *T. undulatum* cannot be doubted. A specimen figured more recently by Gerth (1956, pl. 1, fig. 7) might also be a *T. undulatum*.

Tragophylloceras ibex (Quenstedt)

Plate 49, figs. 2, 3

Ammonites ibex Quenstedt 1843, p. 179.

Ammonites boblayei d'Orbigny 1844, p. 251, pl. 69.

Ammonites boblayei d'Orbigny; Buckman 1845, p. 89, pl. 12, fig. 1a, b.

Ammonites ibex Quenstedt 1845, p. 101, pl. 6, fig. 6a–d.

Ammonites ibex Quenstedt; Opperl 1853, p. 87, pl. 2, figs. 7, ?8.

Ammonites ibex Quenstedt 1856, p. 119, pl. 14, figs. ?4, 5.

Amaltheus ibex (Quenstedt); Wright 1882, p. 395, pl. 39, figs. 4, 5.

Ammonites ibex Quenstedt 1885, p. 293, pl. 37, figs. 15–17, 19, 20.

Phylloceras ibex (Quenstedt); Pompeckj 1893, pp. 21–24.

Tragophylloceras ibex (Quenstedt); Dean, Donovan and Howarth 1961, pl. 69, fig. 4.

Type specimens. The two syntypes from Reutlingen, Swabia, were figured by Quenstedt (1845, pl. 6, figs. 6a, b, and 6c, d).

Description and remarks. Further Swabian specimens from Hinterweiler were figured by Oppel (1853, pl. 2, figs. 7, 78) and Quenstedt (1856, pl. 14, figs. 74, 5; 1885, pl. 37, figs. 15–17, 19, 20), and this fauna was described in more detail by Pompeckj (1893, pp. 21–24). *T. ibex* is a highly distinctive species and can be accurately interpreted even though no Swabian specimen has been figured photographically. *Ammonites boblayei* d'Orbigny (1844, p. 251, pl. 69) is clearly synonymous with Quenstedt's species. Four British specimens from Gloucestershire have been figured by Buckman (1845, pl. 12, fig. 1a, b) and Wright (1882, pl. 39, figs. 4, 5), and a Northamptonshire specimen was figured by Dean, Donovan and Howarth (1961, pl. 69, fig. 4).

The stratigraphical range of *T. ibex* is confined to the zone of which it is the index species. In Swabia, where its zonal value was first recognized, it is particularly common in the Valdani Subzone. In Britain it occurs widely in the Ibex Zone from Somerset to Warwickshire, often in association with *Acanthopleuroceras valdani* (d'Orbigny), and in Dorset the only definitely identifiable specimens occur in bed 119, which also belongs to the Valdani Subzone. No specimens have yet been found in the Lower Lias of the Yorkshire coast. *T. ibex* has not been found in the Luridum Subzone, the uppermost subzone of the Ibex Zone, where it appears to be replaced by *T. loscombi*, nor in the Masseanum Subzone at the base of the Ibex Zone. According to the accurately dated records available at present, *T. ibex* is confined, therefore, to the Valdani Subzone.

The ontogeny of *T. ibex* is seen in a series of specimens, from the area around Cheltenham, in which the inner whorls can be exposed back to the protoconch. The first two whorls after the protoconch up to a diameter of 2 mm. are smooth. The third whorl and early part of the fourth whorl from 2 to 6 mm. diameter contain constrictions of varying

EXPLANATION OF PLATE 49

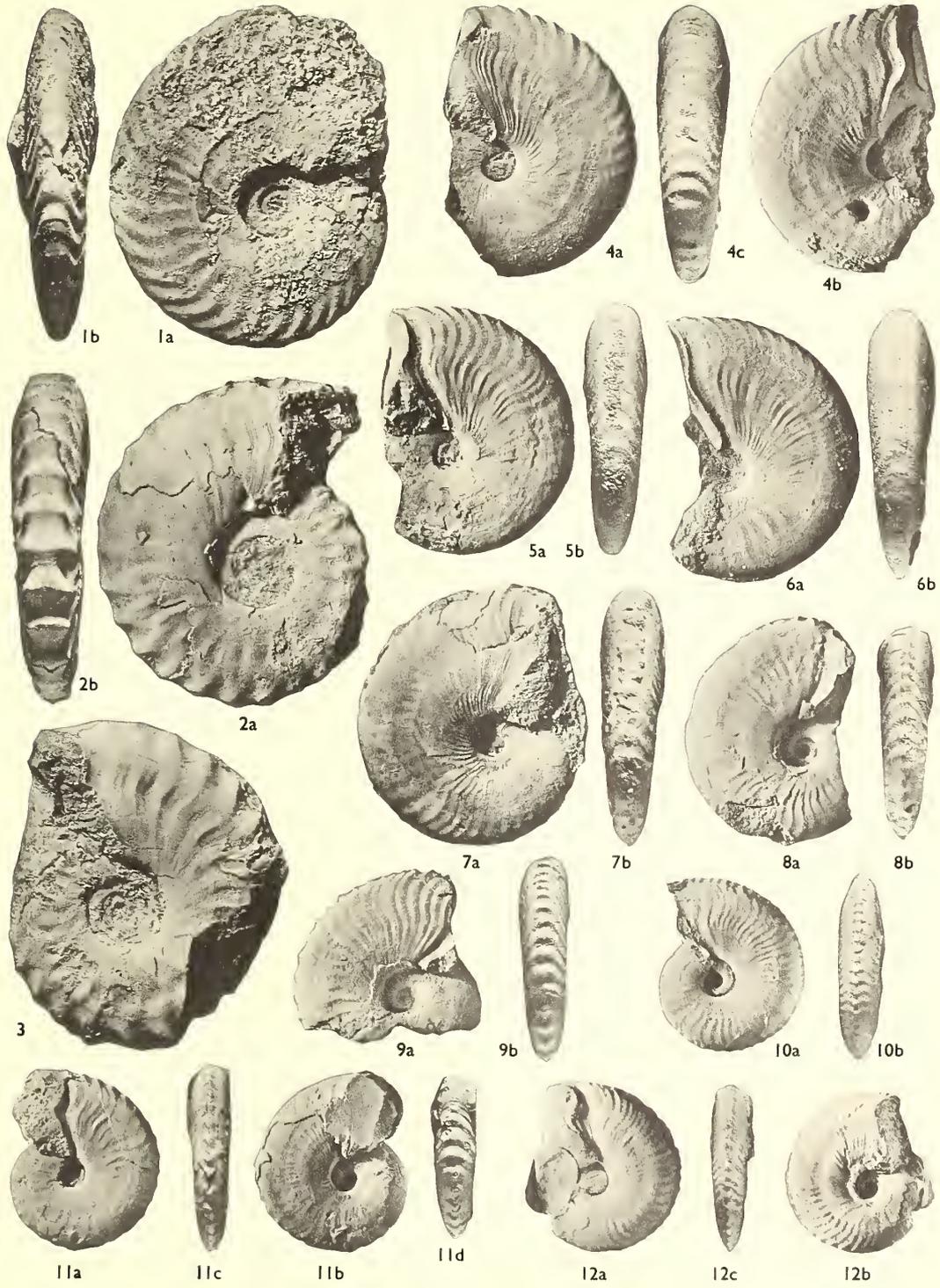
All figures natural size. Specimens coated with ammonium chloride.

Figs. 1a, b. *Tragophylloceras undulatum* (Smith). GSM 24439, Radstock, Somerset.

Figs. 2a, b, 3. *Tragophylloceras ibex* (Quenstedt); microconchs. 2a, b, GSM 24443, Radstock, Somerset; complete specimen with constriction at aperture mostly concealed by shell. 3, Bristol University, 13148-1, North Wick, Dundry, Bristol; shows part of constricted aperture.

Figs. 4a, b, c; 5a, b; 6a, b; 7a, b. *Tragophylloceras loscombi* (J. Sowerby); microconchs. Eype Nodule Bed, Margaritatus Zone, Dorset. 4a, b, c, BM C36719, Eype Mouth, Dorset; opposite sides show constriction at aperture on internal mould, but unconstricted and striate external surface of shell. 5a, b, BM C49765, Doghouse Hill, Seatown, Dorset. 6a, b, BM C70873, Ridge Cliff, 400 yards east of Seatown, Dorset. 7a, b, SM J44818, Eype Mouth, Dorset; constriction at aperture concealed by shell.

Figs. 8a, b; 9a, b; 10a, b; 11a, b, c, d; 12a, b, c. *Tragophylloceras carinatum* sp. nov. 8a, b; 9a, b, Paratypes, BM C71121 and C71122, Luridum Subzone, brickpit at Blockley Station, Gloucestershire. 10a, b, Paratype, BM C28222, Ibex Zone, Battledown brickpit, Cheltenham. 11a, b, c, d, Holotype, BM C56679, Stonebarrow, Charmouth, Dorset; 11a shows constriction and rudimentary lappet; 11d shows completely preserved rostrum. 12a, b, c, Paratype, BM C28226, Ibex Zone, Battledown brickpit, Cheltenham; opposite sides show constricted internal mould and unconstricted external surface of shell.



strength. In the majority of examples the constrictions are only moderately marked, but a few show three or four deep constrictions at 3.0 to 3.5 mm. diameter; in a few others, however, the constrictions are so weak as to be barely detectable. As in all constrictions in *Tragophylloceras*, these occur on the inner surface of the shell and not on the outer surface. From a diameter of 6 mm. the shell is smooth until fine ribs appear at about 10 mm.; these increase rapidly in strength and the characteristic ribbing of *T. ibex* is attained at diameters varying between 13 and 20 mm. The ribs on the venter forming the forwardly pointing chevrons are not connected with the ribs on the side of the whorl, but each commences between two of the latter ribs near the edge of the venter. This alternating character of ribs and chevrons makes *T. ibex* readily separable from more coarsely ribbed examples of *T. undulatum*.

In most examples the bold ribs persist to approximately the beginning of the adult body-chamber at diameters varying between 80 and 100 mm. The ribs on the side of the whorl then quickly disappear and are replaced by falciform striae; the chevrons persist for up to one-eighth of a whorl longer and then disappear to leave the venter rounded-tabulate. The adult body-chamber is smooth for nearly half a whorl, then broad folds appear on the side of the whorl just before the adult mouth border which occurs at 130 to 140 mm. diameter. Only a few complete adults of this sort are known and it is probable that the size range of adults is much greater.

A few much smaller adults are known. The smaller of the two specimens figured by Wright (1882, pl. 39, fig. 5—twice natural size) is from Cheltenham, and has a widening umbilicus and sharpening of the chevrons on the venter as if close to the adult state at its maximum diameter of 42 mm. Three similar specimens are known from Northamptonshire which appear to be nearly adult at 40–45 mm. diameter, but there are two specimens from the Valdani Limestone at Radstock which show clear adult features. Both are 49 mm. in diameter at a constricted mouth border which has a small rostrum and a slight lateral lappet. The ribs remain bold up to the mouth border but they become somewhat sharper. The umbilicus widens towards the end of the body-chamber and the final suture-lines are approximated. The best preserved specimen is figured in Plate 49, fig. 2. A third complete adult with a constricted mouth border at 48 mm. diameter and crowded final suture-lines is known from North Wick, Dundry (Plate 49, fig. 3). Another specimen showing similar adult features and a mouth border at 48 mm. diameter is from an unknown locality. Septate whorls of these specimens cannot be distinguished from similar-sized specimens of the much larger adults.

Tragophylloceras loscombi (J. Sowerby)

Plate 49, figs. 4–7; text-fig. 1f, g

- Ammonites loscombi* J. Sowerby 1817, p. 185, pl. 183.
Ammonites ambiguus Simpson 1843, p. 8.
 ? *Ammonites robinsoni* Simpson 1843, p. 42.
Ammonites loscombi Sowerby; d'Orbigny 1844, p. 262, pl. 75, figs. 1–3.
Phylloceras loscombi (Sowerby); Wright 1883, p. 419, pl. 40, figs. 4, 5.
Rhacoceras ambiguum (Simpson); Buckman 1910, pl. 16.
Tragophylloceras loscombi (Sowerby); Spath 1914, pp. 336–62, pls. 48, 49.
 ? *Tragophylloceras robinsoni* (Simpson); Buckman 1921, pl. 220.
Tragophylloceras loscombi (J. Sowerby); Spath 1936, pp. 439–41, pl. 33, figs. 2–5.
Tragophylloceras loscombi (J. Sowerby); Howarth 1957, p. 194, pl. 17, fig. 7.

The stratigraphical range of *T. loscombi* is best known from its development in Dorset, where it occurs in considerable numbers at many horizons from the Belemnite Stone of the Luridum Subzone, Ibex Zone, up to the Margaritatus Zone. The horizon of the holotype (Sowerby 1817, pl. 183; Spath 1914, pl. 49, fig. 1) is not known accurately, but by comparing matrixes Spath (1914, p. 337) surmised that it came from either the Upper or Lower Limestone (bed 129 or 123a) of the Green Ammonite Beds (Davoei Zone) near Charmouth. Comparison with the extensive Dorset coast collection made by Lang suggests, however, that the nearest matrix match is with the Belemnite Stone. In inland areas of Britain the species occurs in most exposures of the Davoei Zone and Stokesi Subzone, Margaritatus Zone, but precise stratigraphical details are lacking in most cases. In Yorkshire the species was described by Simpson (1843, p. 8; holotype figured by Buckman 1910, pl. 16) as *Ammonites ambiguus*, and Spath (1914, p. 347) first pointed out that this was a synonym of *T. loscombi*. It is apparently rather rare at Robin Hood's Bay, for Mr. L. Bairstow has found only one specimen *in situ*, in bed 569 at the base of the Luridum Subzone, a specimen which matches the Dorset fauna exactly. *A. robinsoni* Simpson (1843, p. 42) might also be a synonym of *T. loscombi*; a paratype from Robin Hood's Bay figured by Buckman (1921, p. 220; see Howarth 1962a, p. 98) may or may not be the same as the lost holotype. It agrees well with the inner whorls of *T. loscombi* at the same size, and it has the characteristic suture-line of this species.

The development of *T. loscombi* from the protoconch to the adult was described in great detail by Spath (1914). Constrictions are present only at very small growth stages and never occur beyond 3.5 mm. diameter. This is the most important feature for separating small inner whorls from those of *T. uunismale* (Quenstedt), where marked constrictions occur up to about 23 mm. diameter. At larger sizes *T. uunismale* has considerably more evolute and thicker whorls. A large Dorset specimen was figured by Wright (1883, pl. 40, figs. 4, 5), and further medium-sized and small specimens from the same area were figured by Spath (1936, pl. 33, figs. 2-5) and Howarth (1957, pl. 17, fig. 7). In relative whorl dimensions, variation in *T. loscombi* is small, but considerable variations occur in ornament, the radial ribbing varying from striae to bold folds on the side of the whorl which form ribs and crenulations on the venter.

The only feature of significance which was not dealt with in these previous descriptions concerns the characters and size variations of adult specimens. Body-chambers at or near the adult stage in the Davoei and Margaritatus Zones in Dorset and Gloucestershire vary in size between about 90 and 150 mm. diameter at the mouth border. This adult mouth border has the same slightly sinuous curve as the growth lines, and there are no traces of lappets or of a constriction immediately before the aperture. The adult body-chamber occupies two-thirds of a whorl and in some cases the final approximated suture-lines can be seen.

A series of much smaller adult specimens occurs at two horizons in Dorset. Nine examples are known from the Eype Nodule Bed (Stokesi Subzone) near Seatown and Eype Mouth, and one example is known from the Lower Limestone (bed 123a, Davoei Zone) of Black Ven, Charmouth. The Eype Nodule Bed examples (one was figured by Spath 1936, pl. 33, fig. 5) vary from 30 to 41 mm. diameter at the mouth border and the Lower Limestone example is 37 mm. diameter. All are characterized by a marked constriction immediately preceding the mouth border, a small lappet in the mouth border in the middle of the side of the whorl, a small rostrum on the venter, and the appearance of

prominent crenulations on the venter of the final quarter whorl (Pl. 49, figs. 4–7). The constriction at the mouth border occurs only on the internal surface of the shell, the outer surface is not constricted, and consequently the shell thickness is greatly increased at the constriction (Pl. 49, fig. 4*a, b*). The body-chamber occupies two-thirds of a whorl and in each case where the final suture-lines are visible they are markedly approximated. The suture-lines (text-fig. 1*f, g*) agree exactly with those of the large form at a similar size (cf. Spath 1914, p. 341, fig. 1*m*). A considerable number of inner whorls of the large form have been examined at the same size as the small forms, but no traces of any of the adult characters of the small forms have been detected on these inner whorls. It is concluded that the small forms are truly adult, and they are classified here as a small form of *T. loscombi* because they show no morphological differences from the large forms, other than those directly connected with the attainment of the adult stage (i.e. crowded suture-lines, constrictions, lappets, and venter crenulations).

Tragophylloceras carinatum sp. nov.

Plate 49, figs. 8–12; text-figs. 1*h–j*.

Material. Eight specimens: BM C56679 from Stonebarrow, Charmouth, Dorset; BM C28216, 28222, 28225 and 28226 from Battledown Brickworks, Cheltenham; BM C71121–2 from Blockley Station brickpit, Gloucestershire; and GSM 102184 from Wyboston borehole, Cambridgeshire.

Holotype. BM C56679 (Pl. 49, fig. 11*a–d*); its dimensions are: at 26.0 mm.: 12.8, 6.0, 4.5; at 20.0 mm.: 10.2, 4.5, 3.2. *Paratypes.* The other seven specimens listed above.

Diagnosis. A small species of *Tragophylloceras* in which a ventral keel is developed on the adult body-chamber. Fine sigmoidal ribs on the sides of the whorl end in small tubercles on the middle of the venter, and the partial amalgamation of these tubercles forms the crenulated keel. The adult mouth border is slightly flared and is preceded by a constriction, and there is a rudimentary lateral lappet and a small rostrum. Maximum size varies between about 23 and 32 mm. diameter.

Description and remarks. Only eight specimens of this species have been found so far. Six are complete adults with mouth borders at diameters of 32 mm. (C71121–2), c. 30 mm. (C28216), 26.5 mm. (C56679, the holotype), 26.5 mm. (C28222), and 23.5 mm. (C28226). The remaining two specimens are incomplete; C28225 has half a whorl of nearly adult body-chamber ending at 23 mm. diameter, and GSM 102184 has a complete body-chamber with mouth border at 24.0 mm. diameter, but it is not quite adult. The ventral keel in this species is unique in the genus *Tragophylloceras*, but the species is included in this genus because the characters of the whorls before the body-chamber and the suture-lines are clearly those of *Tragophylloceras*. The venter becomes sharpened on the last half whorl before the body-chamber, then distinct tubercles appear at the ends of the ribs at about the beginning of the adult body-chamber, and these partly join to form a well-marked crenulated keel on the final half whorl. A constriction occurs immediately before the mouth border, on the inside surface of the shell and not on the outer surface, so that the shell thickness is greatly increased at the constriction. The rudimentary lateral lappet is only a slight prolongation in the mouth border, while the rostrum on the venter is better developed. Only one specimen could be developed back to the inner whorls and this has four well-marked constrictions in the larger half of the second whorl ending at 2.5 mm. diameter. The fine sigmoidal ribs appear at about

10 mm. diameter. The only significant variation in the six specimens is in the size of the crenulations on the keel. In the holotype and C71122 (Pl. 49, figs. 9, 11) they are relatively large and widely spaced, but in the Cheltenham specimens and C71121 (Pl. 49, figs. 8, 10, 12) they are smaller. All six specimens show considerable variation in this respect and it does not appear to be of significance. The suture-lines (text-fig. 1*h-j*) are characteristic of *Tragophylloceras* and compare well with those of *T. loscombi* at a similar size (Spath 1914, p. 341, fig. 1*l, m*). A particularly fine example of approximated suture-lines is figured in text-fig. 1*j*.

The four specimens from Cheltenham were collected by L. Richardson and were recorded by him as from the Ibex Zone. The Wyboston specimen is also from the Ibex Zone, either the Valdani or Luridum Subzone. The specimens from Blockley station are from the Luridum Subzone. The zonal position of the Dorset holotype is not known, but it is preserved in a grey limestone matrix suggestive of the Belemnite Stone (Luridum Subzone) or possibly higher beds of the Davoei Zone, and it is most unlikely to have come from a lower horizon. If *T. carinatum* is the small form of a species which also has a large form, then the large form has not yet been found. There is nothing to suggest that it could be the small form of *T. undulatum*, for none have been found amongst the extensive Radstock collections, and *T. undulatum* has no trace of a keel at any growth stage.

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CRETACEOUS AND TERTIARY COCCOLITHS FROM ATLANTIC SEAMOUNTS

by MAURICE BLACK

ABSTRACT. Fragments of white chalky limestone dredged from Galicia Bank off the west coast of Spain contain coccoliths of two different ages. At a station on the northern slope, all the fragments have coccoliths of Middle Eocene age; the same species are also present on Muir Seamount, north-east of Bermuda, but are unknown in any rock exposed on land. In a sample from the underwater escarpment on the east side of Galicia Bank, only Cretaceous species can be recognized. Material dredged from the top of the bank has an intimate mixture of well-preserved Maestrichtian and Middle Eocene species in the same rock. This composite assemblage is believed to have been brought together by mud-feeding organisms which burrowed through a thin layer of Eocene sediment into an unconsolidated Cretaceous ooze below. Three new genera, *Colvillea*, *Ericsonia*, and *Favocentrum*, and eleven new species, are described.

THE purpose of this communication is to describe a few previously unnamed coccoliths which have been used in dating a collection of soft chalky limestones dredged from the Iberian Seamounts in 1958 by R.R.S. *Discovery II* (Black, Hill, Laughton, and Matthews 1964). A list of dredging stations with their latitudes and longitudes will be found on p. 315.

The rocks in question are firm but uncemented limestones, rather like ordinary chalk in appearance and texture, and no harder than much of the Yorkshire Chalk. Most specimens are white, sometimes with a grey infiltration of manganese dioxide or a yellow stain of ferric hydroxide. The sample from Station 4272 on Galicia Bank is strongly iron-stained, and the preservation of the coccoliths is poor. Samples from Station 4279 on Vigo Seamount are even more heavily impregnated with ferric hydroxide, and although coccoliths could be seen in polarized light, none could be identified specifically.

Cretaceous species were present at Stations 3804, 3809, and 4272. Counting of individual coccoliths showed that at Station 3804 about half belonged to various Upper Cretaceous species; at Station 3809 the proportion was one-fifth, and at Station 4272 all the identifiable coccoliths belonged to a single Maestrichtian species. In addition to *Zygrhablithus cretaceus* (Archangelsky), *Colvillea barnesae* (Black), and *Microrhabdulus decoratus* Deflandre, which are well-known Upper Cretaceous forms, there were several previously undescribed species which in East Anglia and Denmark are confined to the Maestrichtian stage. These are described below as species of *Favocentrum* and *Coccolithites*.

At Stations 3804 and 3809 the samples also contained substantial proportions of the Eocene species to be mentioned below, and smaller numbers of *Gephyrocapsa oceanica* Kamptner, *Coccolithus pelagicus* (Wallich), and *C. luxleyi* (Lohmann), which are common in the modern plankton off the Iberian coast. The presence of a few modern coccoliths is not surprising, since porous rocks lying exposed on the sea-floor very readily become contaminated in this way. The Tertiary coccoliths, on the other hand, are much too numerous to have been introduced by casual contamination, and suggest a thorough mixing of two deposits of different ages. Station 3804, where the mixing is

most thorough, is on the shallowest part of Galicia Bank, and redeposition of eroded Cretaceous coccoliths is improbable in such an exposed situation. A more likely explanation is that the mixing was brought about by mud-feeding organisms burrowing beneath the sea-floor. The unlithified Cretaceous deposits of Galicia Bank are probably overlain directly by similar material of Eocene age, and disturbance during the deposition of the first few centimetres of this Tertiary cover would result in mixed assemblages such as those of Stations 3804 and 3808. Such mixing of sediments by burrowing animals is now known to be very widespread on the ocean floor; indeed Arrhenius (1952, p. 86) has remarked that the absence of its effects indicates abnormal conditions, such as a very high rate of deposition. The effects are most conspicuous when there is an abrupt change in the properties of the sediment: in its colour, its petrological composition, or its fossil-content. The first produces a distinctive colour-mottling (Ericson *et al.* 1961, pl. 2, fig. 2), and an example of the vertical redistribution of volcanic glass in deep-sea sediments has been described by Bramlette and Bradley (1940, p. 22). Ericson found that 'normal mud feeders rarely penetrate much more than 10 cm. below the sediment-water interface and that really significant mixing of sediment by burrowers is confined to the uppermost 5 cm.' It is not surprising therefore that only two of the samples examined have yielded this anomalous mixture of Cretaceous and Tertiary species.

All the samples examined from Station 3808 contained a remarkable assemblage of coccoliths dominated by *Coccolithus marismontium* and its associates, *C. lusitanicus*, *C. muiri*, and *Ericsonia alternans*, to be described on a later page. None of these has yet been found at any locality on shore, and the age of the assemblage must be determined by the other fossils associated with it. These include a few examples of *C. eopelagicus* Bramlette and Riedel, *Braarudosphaera discula* B. and R., and *Discoaster aster* B. and R. The presence of these three species together in the same rock suggests a Middle Eocene age. Dr. B. M. Funnell has examined the foraminifera, and finds that they also indicate a horizon within the Middle Eocene.

The same assemblage has been seen in core A150-1, from Muir Seamount. *C. marismontium* and its associates are abundant in a coccolith ooze 125-6 cm. below the top, at which level the core also contains Middle Eocene foraminifera. A form which appears to be identical with *C. marismontium* has recently turned up in a deep-sea core (DWBG 23B) from the Pacific Ocean, where it is again associated with Middle Eocene foraminifera.

On this evidence, there can be little doubt that the *C. marismontium* assemblage of Galicia Bank and Muir Seamount is of Middle Eocene age, and it is remarkable that these species have not yet been found in rocks exposed on land. It is just possible that these are strictly pelagic forms which avoided the shallow seas in which the Eocene rocks of western Europe were deposited, but this does not seem likely in view of the cosmopolitan distribution of other Tertiary assemblages. Since they are all rather small forms, difficult to identify under the light-microscope, an alternative explanation may be that they are short-ranged species, confined to a relatively thin stratigraphical unit that has not yet been examined under the electron microscope.

SYSTEMATIC DESCRIPTIONS

In the following descriptions, specimens of coccoliths are identified by their serial numbers in the reference collection of electron micrographs at the Sedgwick Museum,

Cambridge. Photographs by P. J. W. Hyde of chromium-shaded carbon replicas taken with an Associated Electrical Industries EM 6 electron microscope provided by a grant from the Department of Scientific and Industrial Research.

Coccolithus lusitanicus sp. nov.

Plate 50, figs. 1, 2

Diagnosis. Placoliths of approximately circular outline consisting of two shields surrounding a relatively flat central area 50 to 60 per cent. of the diameter of the complete coccolith; central area usually, but not always, with a circular central perforation.

Holotype. 11605, from Galicia Bank, Discovery 3809.1.

Dimensions of holotype. $7.3 \times 7.0 \mu$; central area $4.3 \times 3.8 \mu$. Thirty-nine rays.

Range of dimensions. Of the numerous specimens examined, twenty-one were measured in detail, giving the following ranges: overall diameter 6.5 – 8.5μ , exceptionally up to ten; central area 3.8 – 5.5μ ; perforation commonly 0.8 – 1.0μ , exceptionally up to 1.5 and down to 0.1 , or apparently absent. Rays 39 to 51.

Distribution. Abundant in soft chalky limestone dredged at Discovery Stations 3804, 3808, and 3809 on Galicia Bank; less abundant, but not rare, in coccolith ooze from core A150–1, Muir Seamount. At present unknown from any locality on land.

Horizon. Middle Eocene.

Description. The rays are straight with gently rounded ends, overlapping, and flat-surfaced. The central area is approximately circular, and has a saw-toothed margin at the circumference. Its structure is not always easy to make out; in clean, well-preserved specimens it is seen to consist of closely fitted radial elements, about twenty in number near the centre, but increasing by insertion until near the circumference they are approximately equal in number to the rays in the distal part of the shield. In most specimens, the radial elements of the central area are smooth-sided, but in a few they are finely crenulate (Pl. 50, fig. 2). More than half the specimens examined have a clearly defined central perforation, usually slightly less than 1μ in diameter, but there is considerable variation in size. In many of the others, the place where a perforation might be expected is obscured by fine debris, but there remains a small number of coccoliths in which the centre appears to be perfectly clean and shows no trace of a hole. In the main, it is the larger coccoliths that tend to be imperforate; they may have been borne on some special part of the living cell, in the same way that modified coccoliths are localised by some modern species in the apical or equatorial regions.

In its general appearance, *C. lusitanicus* resembles the form figured by Hay and Towe

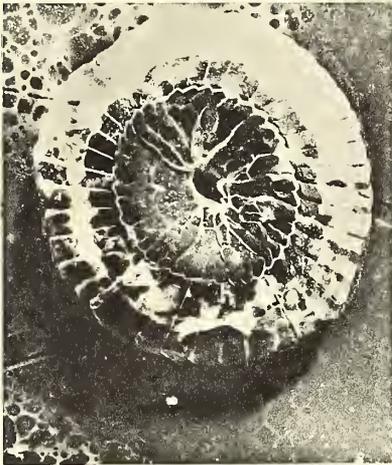
EXPLANATION OF PLATE 50

All figures $\times 6,000$.

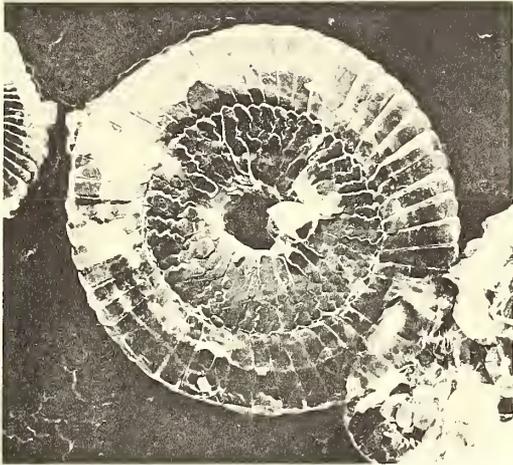
Figs. 1–2. *Coccolithus lusitanicus* sp. nov. 1, External view of holotype, No. 11605 from Galicia Bank, Discovery Station 3809, Sample 1. 2, External view of No. 11066 from Muir Seamount.

Figs. 3–4. *Coccolithus muiri* sp. nov. 3, External view of unusually broad specimen; No. 11656 from Muir Seamount. 4, External view of holotype No. 11666 from Muir Seamount.

Figs. 5–6. *Coccolithites turbatus* sp. nov. 5, No. 13677 from the Lower Maestrichtian Chalk of Sidstrand, Norfolk. 6, Holotype, No. 10957 from Galicia Bank, Discovery Station 3804, Sample 1.



1



2



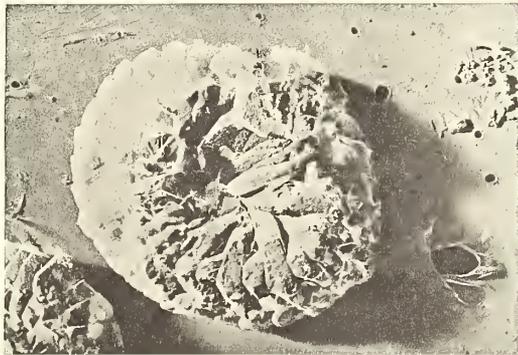
3



4



5



6

(1962, p. 500 and pl. vi, fig. 5) as the basal shield of *Cyathosphaera diaphragma* Hay and Towe, but the dimensions given by Hay are smaller ($2.7\text{--}4.5\ \mu$) and entirely outside the range for *Coccolithus lusitanicus* ($6.5\text{--}8.5\ \mu$). Furthermore, in the best preserved specimens of our species the central area is smooth and shows no sign of having lost an additional disc by fracture.

Coccolithus marismontium sp. nov.

Plate 51, figs 1-4; Plate 52, fig. 3

Diagnosis. Elliptical to nearly circular placoliths with the smaller shield about three-quarters the diameter of the larger, each consisting of narrow slightly flexuous rays, between 38 and 65 in number, not appreciably overlapping.

Holotype. 11048, from the Muir Seamount.

Dimensions of holotype. Larger shield $6.9 \times 6.0\ \mu$; smaller shield $5.2 \times 5.1\ \mu$; pore $2.0 \times 1.5\ \mu$. Fifty rays in each shield.

Range of dimensions. Larger shield $5.0\text{--}8.0\ \mu$; smaller shield $4.0\text{--}6.0\ \mu$; pore $1.2\text{--}2.5\ \mu$. Rays 38-65, approximately equal numbers in the two shields.

Distribution. Abundant in soft chalky limestone dredged at Discovery Stations 3804, 3808, and 3809 on Galicia Bank; abundant in core A150-1, Muir Seamount; common in core DWBG 23B, Pacific Ocean. At present unknown from any locality on land.

Horizon. Middle Eocene.

Description. This is a variable but easily recognized species. The rays lie side by side without appreciable overlap, and their exposed surfaces tend to be slightly swollen; each ray terminates in a blunt point. On the internal surface, the rays are sharply bent towards the pore, forming a central depression whose diameter is equal to about two-sevenths of the width of the coccolith. There is a similar but wider depression in the larger shield, within which lies a ring of broad, polygonal plates surrounding the central pore; these plates are loosely attached, and in many specimens the ring is incompletely preserved or entirely missing. The pore is usually about $2.0\ \mu$ in greater diameter and broadly elliptical in shape.

Coccolithus muiri sp. nov.

Plate 50, figs. 3, 4

Diagnosis. Placoliths of elliptical shape and somewhat irregular outline, with thirty to forty rays in each shield, and with a more or less depressed central area of variously shaped granules, with or without a slot-shaped pore along the major diameter.

Holotype. 11666, from Muir Seamount.

Dimensions of holotype. $8.5 \times 7.1\ \mu$; central area $5.0 \times 3.4\ \mu$. Thirty-five rays.

Range of dimensions. Overall length $6.5\text{--}10.5\ \mu$; central area $4.0\text{--}6.0\ \mu$. Rays 30-40.

Distribution. Abundant in core A150-1 from Muir Seamount; frequent in soft chalky limestones dredged at Discovery Stations 3804, 3808, and 3809 on Galicia Bank (Black, Hill, Laughton, and Matthews 1964, pl. 44c). At present unknown elsewhere.

Horizon. Middle Eocene.

Description. The rays are straight-sided and flat, overlap each other, and have gently rounded terminations, which are sometimes slightly oblique. In these respects they are much like the rays of certain other species of *Coccolithus*, such as *C. pelagicus* (Wallich) and *C. sarsiae* Black (1962, pl. ix, figs. 2–6). *C. pelagicus*, however, has much larger coccoliths with more numerous rays (Black 1963, pl. 1, fig. 7), whilst *C. sarsiae* is a smaller form with more crowded rays than *C. muiri*. In *C. lusitanicus*, which also has rays of this type, they are more numerous, the central area is differently constructed, and the pore when visible is nearly circular.

Coccolithites turbatus sp. nov.

Plate 50, figs. 5, 6

Diagnosis. Broadly elliptical to nearly circular coccoliths consisting of two layers of roughly radiating elements, closely packed together, but not forming distinct shields.

Holotype. 10957 from Station 3804, Galicia Bank.

Dimensions of holotype. $7.2 \times 5.7 \mu$, with about thirty-two rays at the periphery.

Range of dimensions. Major diameter 5.8 – 8.8μ . Rays about thirty-two, difficult to count in most specimens.

Distribution. On Galicia Bank it is common in chalky limestones at Station 3804, where it is associated with various Upper Cretaceous and Lower Tertiary species, and at Station 4272, where it is the only species that can be identified. Rare in the chalk of Sidestrand, Norfolk (Lower Maestrichtian).

Horizon. Upper Cretaceous, at present only known in the Maestrichtian.

Description. Eight or more radial elements arise from the centre, and by insertion of additional rays increase to about thirty-two at the periphery.

Kamptner's name *Coccolithites* is used for this species since it cannot be assigned to any known genus, and its structure is too obscure to justify the creation of a new generic name.

Genus COLVILLEA gen. nov.

Diagnosis. Coccoliths consisting of two elliptical shields in contact with each other; external shield larger than the internal, both curved, with the concave surface on the internal side.

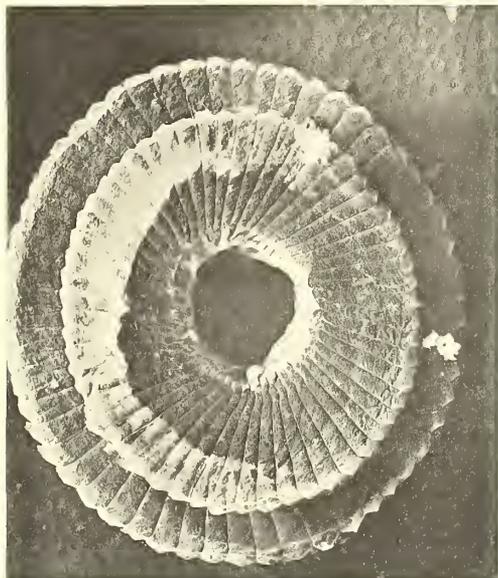
Type species. *Tremalithus barnesae* Black.

Discussion. As Bramlette and Sullivan (1961, p. 138) have pointed out, the use of Kamptner's paragenus *Tremalithus* for species founded upon isolated placoliths like those of *Coccolithus* is unnecessary, and such species are now usually included in *Coccolithus*. *T. barnesae*, in which the two shields are in contact and are not pierced by

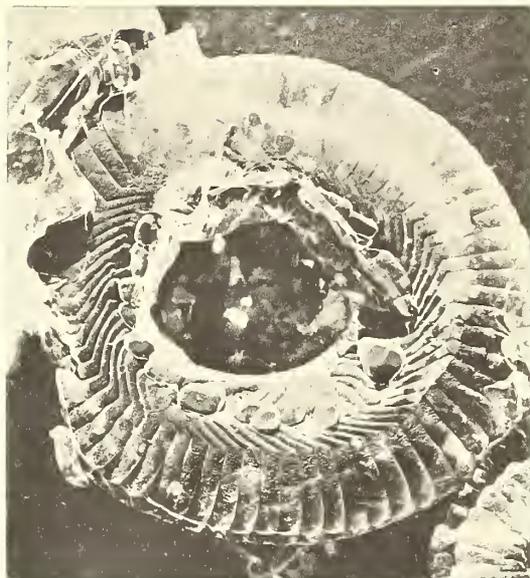
EXPLANATION OF PLATE 51

All figures $\times 8,000$.

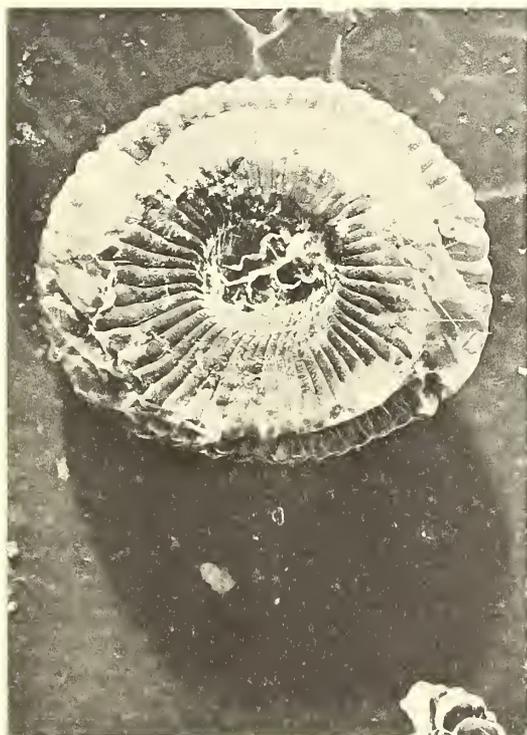
Figs. 1–4. *Coccolithus marismontium* sp. nov. 1, Internal view of exceptionally clean specimen No. 14278 from the central Pacific. 2, External view, showing a common state of preservation; No. 11058 from Muir Seamount. 3, Internal view of holotype No. 11048 from Muir Seamount. 4, External view of specimen with the central ring preserved; No. 10925 from Galicia Bank, Discovery Station 3808, Sample 5.



1



2



3



4

a pore, cannot be transferred to *Coccolithus*, nor can it remain in *Tremalithus* as thus interpreted, since complete spheres are now known. It would also be excluded by Kamptner's redefinition of *Tremalithus* as a genus to include species bearing placoliths modified by suppression of the inner shield (Kamptner 1958, p. 82). A new generic name is therefore required to accommodate this and several related species which are abundant in the Cretaceous.

Colvillea barnesae (Black) comb. nov.

1959 *Tremalithus barnesae* Black, in Black and Barnes 1959, p. 325; pl. ix, figs. 1, 2.

Revised description. Coccoliths imperforate with two broadly elliptical or nearly circular shields, one slightly smaller than the other, and each consisting of 28 rays (exceptionally 27 or 29). Rays of the smaller shield gently curved, filling the centre, in contact for their whole length but not overlapping, slightly swollen and bluntly pointed at their distal ends. Rays of the larger shield not reaching the centre, but radiating obliquely from an oval ring of quadrate granules, smooth at the external surface, and obliquely truncated at their distal ends.

Distribution and horizon. *C. barnesae* is common in the chalks of Europe, Australia, and North America. It ranges from the Cenomanian to the Maestrichtian, but is not known outside these limits. In the Iberian Seamounts, this species was recorded in the soft chalky limestones dredged at Discovery Stations 3804 and 3809 on Galicia Bank.

Genus ERICSONIA gen. nov.

Diagnosis. Circular or elliptical coccoliths with a well-defined central opening surrounded by three or more apparently concentric rings of granules which are differently orientated in adjacent rings.

Type species. *Ericsonia occidentalis* sp. nov.

Discussion. The interior structure of these coccoliths is at present imperfectly known. They give the impression of having a wide, perforated disc made of rays extending from the central opening to the periphery. The other rings are narrower; they surround the central opening and appear to overlie the principal disc. They consist of vertical or inclined granules which in some species give a herring-bone pattern due to the opposite inclination of the granules in two adjacent rings.

Three species are known in sediments of Lower Tertiary age from seamounts in the Atlantic Ocean. The genus also appears to be represented in the Danian by one or two undescribed species.

Ericsonia occidentalis sp. nov.

Plate 52, figs. 1, 2

Diagnosis. Nearly circular *Ericsonia* with three concentric rings, the second and third rings from the outside consisting of narrow crystals inclined in opposite directions, producing a chevron pattern.

Holotype. 11667, from Muir Seamount.

Dimensions of holotype. $8.4 \times 7.8 \mu$; second ring $6.0 \times 5.9 \mu$; third ring $4.3 \times 3.9 \mu$; pore $2.5 \times 2.0 \mu$. Forty rays in the outer ring.

Range of dimensions. In the few specimens available, the major diameter ranges from 6·7 to 8·4 μ , and the number of rays at the outer margin from twenty-eight to forty. Departures from a circular shape are slight, and the minor diameter is always more than nine tenths of the major.

Distribution. Known only from Muir Seamount.

Horizon. Middle Eocene.

Comparison. *E. occidentalis* is easily distinguished from the other species described below by having three rings instead of four, and by the striking herring-bone pattern of the second and third rings.

Ericsonia alternans sp. nov.

Plate 52, fig. 4

Diagnosis. Nearly circular *Ericsonia* with four concentric rings and a nearly circular central opening.

Holotype. 10954, from Galicia Bank (Discovery 3804.1).

Dimensions of holotype. 7·0 \times 7·0 μ ; second ring 6·3 \times 6·0 μ ; third ring 5·2 \times 4·8 μ ; inner ring 3·1 \times 2·7 μ ; pore 1·1 \times 1·0 μ . About forty-five rays.

Range of dimensions. Diameter 6·0 to 8·8 μ . Rays in the outermost ring thirty-two to forty-five. All the specimens examined appeared circular to the eye, but measurements usually show a slight departure from the strictly equidimensional form; in extreme examples the minor diameter is only nine-tenths of the major.

Distribution. Muir Seamount and Galicia Bank (Discovery Stations 3804, 3808, and 3809).

Horizon. Middle Eocene.

Description. There is some variation in the appearance of the component rings, which in part at least seems to depend upon the state of preservation of individual specimens. The granules in the second ring from the outside tend to be narrow and are inclined at an angle which may be as much as 45° to the radial direction. The granules of the third and fourth rings are for the most part keystone-shaped or quadrate, and the sutures separating them are directed radially.

Ericsonia ovalis sp. nov.

Plate 52, figs. 5, 6

Diagnosis. Elliptical *Ericsonia* with four concentric rings, and an elongate central opening.

EXPLANATION OF PLATE 52

Figs. 1–2. *Ericsonia occidentalis* sp. nov. 1, Holotype No. 11667 from Muir Seamount, \times 6,000. 2, Details of second and third rings; No. 10005 from Muir Seamount, \times 10,000.

Fig. 3. *Coccolithus marismontium* sp. nov., internal view showing a common state of preservation on the Iberian Seamounts, with slightly damaged internal disc; No. 10966 from Galicia Bank, Discovery Station 3804, Sample 1, \times 6,000.

Fig. 4. *Ericsonia alternans* sp. nov., holotype; No. 10954 from Galicia Bank, Discovery Station 3804, Sample 1, \times 6,000.

Figs. 5–6. *Ericsonia ovalis* sp. nov., \times 6,000. 5, No. 11650 from Muir Seamount. 6, Holotype No. 11659 from Muir Seamount.



1



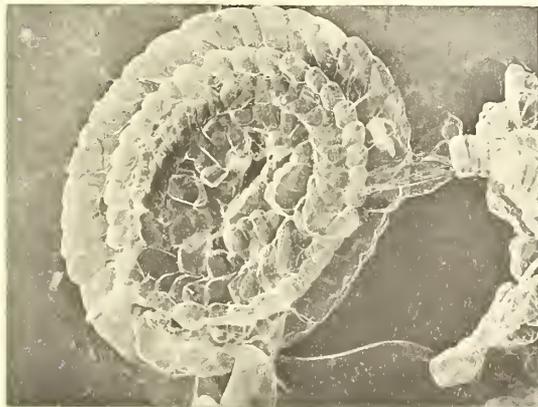
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Holotype. 11659, from Muir Seamount.

Dimensions of holotype. $7.4 \times 6.0 \mu$; second ring $5.4 \times 4.7 \mu$; third ring $4.2 \times 3.7 \mu$; inner ring $3.6 \times 2.5 \mu$; pore $2.0 \times 0.3 \mu$. Thirty-three rays in the outer ring.

Range of dimensions. The major diameter ranges from 7.0 to 8.8 μ , the minor from 6.0 to 8.0, and the number of rays from thirty-one to forty.

Distribution. This is the commonest species of *Ericsonia* at Muir Seamount. One specimen only was found in the material from Galicia Bank (11613 in Discovery Sample 3809.1).

Horizon. Middle Eocene.

Description. Coccoliths of this species are noticeably elliptical in shape, with the minor diameter between four-fifths and nine-tenths of the major. The second ring from the outside is made up of equidimensional granules, which in most specimens are not inclined to the radial direction. The most nearly circular specimens are similar in shape to the most elliptical of *E. alternans*, but are readily distinguished by the different structure of the second ring, and by the shape of the central opening, which in many specimens of *E. ovalis* takes the form of a narrow slit.

Genus FAVOCENTRUM gen. nov.

Diagnosis. Coccoliths with two shields of radial elements surrounding an oval central area of equidimensional granules arranged in a honeycomb pattern.

Type species. *Favocentrum laughtoni* sp. nov.

Discussion. The two shields are constructed of radially disposed calcite crystals as in some elliptical species of *Coccolithus*, but there is no pore and the central structure is quite unlike anything seen in *Coccolithus sensu stricto*. The granules that make up the central area are fitted together in a way that suggests a hexagonal packing of short prisms; when they can be examined more clearly in broken specimens, they are seen to be of no great length, and are often nearly as wide as long. In their general plan of construction, coccoliths of this genus are reminiscent of some that have been included in *Cribrosphaera*, but they differ in always being imperforate.

A characteristic flattening of the rays parallel to the presumed internal surface of the coccolith is noticeable in well-preserved specimens.

Species of this genus are distributed throughout the Maestrichtian chalks of Denmark and East Anglia, and up to the present have not been found in either older or younger beds. They have also been found associated with late Cretaceous coccoliths in the chalky limestones dredged by *Discovery II* from Galicia Bank.

Favocentrum laughtoni sp. nov.

Plate 53, figs. 1, 2

Diagnosis. *Favocentrum* in which the length of the central area is not less than seven-tenths of the total length of the coccolith, and in which the central area has an outer ring of granules larger than those within.

Holotype. 11461 from the Upper Maestrichtian Chalk of Stevns Klint, Denmark.

Dimensions of holotype. $8.5 \times 6.7 \mu$; central area $6.3 \times 4.5 \mu$. Twenty-three rays.

Range of dimensions. Length 8.0–9.2 μ ; central area 6.0–6.4 μ . Rays 21–26.

Distribution. In the Upper Maestrichtian of Stevns Klint, Denmark; on Galicia Bank at Discovery Station 3804 (Black, Hill, Laughton, and Matthews 1964, pl. 43c). A single specimen was found at Sidestrand, Norfolk, in chalk near the base of the Maestrichtian. Specimens of *Favocentrum* resembling *F. laughtoni* are not uncommon in the Grey Beds at Trimmingham, Norfolk, but their preservation is not good enough for measurements to be reliable.

Horizon. Upper Cretaceous (Maestrichtian).

Discussion. Only one shield, presumably the outer, is visible in the specimens so far examined. The polygonal granules of the central area are usually 0.5 μ or a little less in diameter, except in the outermost ring, where they are noticeably larger, and measure up to 0.7 μ .

Favocentrum hilli sp. nov.

Plate 53, figs. 3, 4

Diagnosis. *Favocentrum* in which the two shields are approximately equal in size, and the length of the central area is about half the total length of the coccolith.

Holotype. 10968, from Discovery Station 3804, Galicia Bank.

Dimensions of holotype. Larger shield 8.0 \times 6.8 μ ; smaller shield 7.7 \times 6.5 μ ; central area 3.3 \times 2.5 μ . Thirty rays.

Range of dimensions. Length of larger shield 7.0–8.5 μ ; smaller shield 6.8–8.1 μ ; central area 2.8–4.3 μ . Rays in the smaller shield 26–32; the larger shield probably has a similar number, but it is difficult to confirm this by counting.

Distribution. In Lower Maestrichtian Chalk at Sidestrand, Norfolk; On Galicia Bank at Discovery Station 3804 (Black, Hill, Laughton, and Matthews 1964, pl. 43d).

Horizon. Upper Cretaceous (Maestrichtian).

Comparison. Coccoliths of this species tend to be slightly smaller than those of *F. laughtoni*. They differ also in showing a second shield, just visible outside the margin of the conspicuous smaller shield, and in the smaller size of the central area in proportion to the coccolith. The polygonal grains in the central area are 0.5–0.6 μ in diameter, and are of approximately uniform size in any individual coccolith.

Favocentrum matthewsi sp. nov.

Plate 53, figs. 5, 6

Diagnosis. *Favocentrum* with the two shields distinctly different in size, and a central area not more than three-fifths of the total length of the coccolith.

EXPLANATION OF PLATE 53

All figures \times 6,000.

Figs. 1–2. *Favocentrum laughtoni* sp. nov. 1, No. 13705 from the Lower Maestrichtian Chalk of Sidestrand, Norfolk. 2, Holotype, No. 11461 from the Upper Maestrichtian Chalk of Stevns Klint, Denmark.

Figs. 3–4. *Favocentrum hilli* sp. nov. 3, Holotype, No. 10968 from Galicia Bank, Discovery Station 3804, Sample 1. 4, No. 13716 from the Lower Maestrichtian Chalk of Sidestrand, Norfolk.

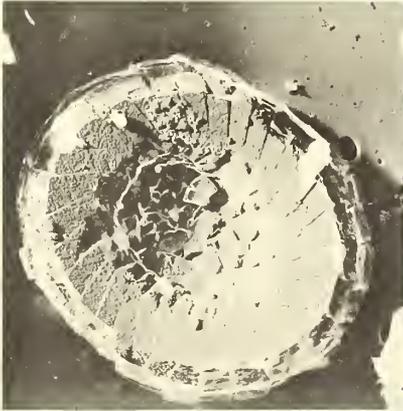
Figs. 5–6. *Favocentrum matthewsi* sp. nov. 5, No. 13812 from the Lower Maestrichtian Chalk of Sidestrand, Norfolk. 6, Holotype, No. 11447 from the Upper Maestrichtian Chalk of Stevns Klint, Denmark.



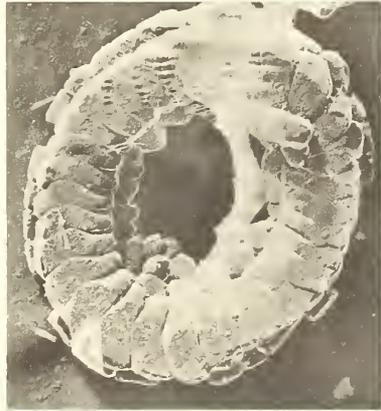
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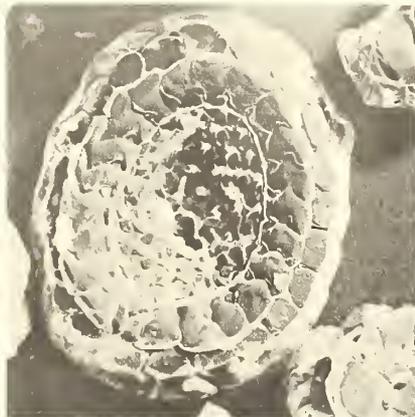
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Holotype. 11447, from the Upper Maestrichtian of Stevns Klint, Denmark.

Dimensions of holotype. Larger shield $8.4 \times 6.8 \mu$; smaller shield $6.6 \times 5.4 \mu$; central area $4.5 \times 3.2 \mu$. Twenty-two rays in each shield.

Range of dimensions. Larger shield $7.2-9.2 \mu$; smaller shield $5.0-7.0 \mu$; central area $3.9-5.1 \mu$. Rays 21-26, with equal numbers in each shield.

Distribution. In the Upper Maestrichtian of Stevns Klint, Denmark; in chalk near the base of the Maestrichtian at Sidestrand, Norfolk; on Galicia Bank at Discovery Station 3804 (Black, Hill, Laughton, and Matthews 1964, pl. 43*b*).

Horizon. Upper Cretaceous (Maestrichtian).

Discussion. This species is readily distinguished from the two described above by the noticeable difference in size between its shields, and by the smaller size of the granules in the central area, which are no more than 0.33μ in diameter.

There are slight differences between specimens collected from separate localities, and when more material becomes available it may prove desirable to recognize some of these variants as distinct species. For the present it may be said that the single specimens from Galicia Bank and from Sidestrand are more closely similar to each other than to specimens from the type locality at Stevns Klint.

LIST OF DREDGING STATIONS AND LOCALITIES ON SHORE

The positions of stations dredged by *Discovery II* which are mentioned in this paper are as follows:

- Station 3804, on the shallowest part of Galicia Bank, $42^{\circ} 36' N.$, $11^{\circ} 35' W.$, at 380 fathoms.
- Station 3808, on the northern slope of Galicia Bank, $42^{\circ} 55' N.$, $11^{\circ} 47' W.$, at 600 fathoms.
- Station 3809, on the northern slope of Galicia Bank, $42^{\circ} 56' N.$, $11^{\circ} 47' W.$, at 650 fathoms.
- Station 4272, on the eastern escarpment of Galicia Bank, dredging up-slope from 680 to 530 fathoms; $42^{\circ} 49' N.$, $11^{\circ} 37' W.$
- Station 4279, on the top of Vigo Seamount, $41^{\circ} 15' N.$, $10^{\circ} 40' W.$, at 1,100 fathoms.

The localities of other samples mentioned below which contain coccoliths similar to those of the Iberian Seamounts are:

- Muir Seamount. Deep-sea core A150-1 in the collection at Lamont Geological Observatory, New York. Position $33^{\circ} 42' N.$, $62^{\circ} 30' W.$, about 170 sea miles NE. of North Rock Light, Bermuda; depth 1,555 metres. I am indebted to Dr. D. B. Ericson for a sample of coccolith-ooze taken 125-6 cm. below the top of this core.
- Deep-sea core DWBG 23B in the collection at Scripps Institute of Oceanography, La Jolla. Position $16^{\circ} 42' S.$, $145^{\circ} 48' W.$, between Tuamotu Archipelago and Tahiti; approximate depth 2,200 metres. I am indebted to Dr. M. N. Bramlette and Dr. B. M. Funnell for the opportunity of examining a sample of siliceous coccolith-ooze taken 10-12 cm. below the top of this core.
- Lower Maestrichtian Chalk from the cliff-section at Sidestrand, Norfolk. Horizon: lower part of the *Belemnella lanceolata* Zone, probably not far above the Campanian-Maestrichtian boundary (Zone I of Troelsen).
- Lower Maestrichtian Chalk from the Grey beds exposed in the foreshore near low water mark at Trimmingham, Norfolk. Sample taken from the interior of an *Echinocorys*, No. 185 in the duplicate collection at the Sedgwick Museum, Cambridge. Horizon: near the top of the Lower Maestrichtian (Zone III of Troelsen).
- Upper Maestrichtian Chalk from Stevns Klint, S. of Copenhagen, Denmark. Horizon: Zone IV of Troelsen.

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Sedgwick Museum, Cambridge

REVISION OF THE OSTRACODA FROM THE BARGATE BEDS IN SURREY

by P. KAYE

ABSTRACT. Nineteen species of ostracoda are described from the Bargate beds exposed south-west of Guildford. The type material from an earlier paper is revised and refigured. Two of the species are found to require renaming and five new species are described. Four forms are left under open nomenclature.

BRITISH Aptian ostracoda have been somewhat neglected in the past, reference to forms found in the Bargate beds near Guildford by Chapman (1894) being the major contribution. Chapman's type specimens which have been preserved at the Sedgwick Museum, Cambridge, are here revised and refigured. These specimens were collected by Chapman from two localities, the most prolific horizon being in Littleton Lane Quarry, 1 mile south-west of Guildford. He obtained additional specimens from a lane leading to Great Halfpenny Farm on the west side of St. Martha's Hill, Chilworth. Unfortunately, due to absence of exposures, I have not been able to re-sample Chapman's localities but a comparative fauna has been found in a sample taken from the mortuary pit at Compton during a Palaeontological Association field trip led by Dr. F. A. Middlemiss (27 April 1963). The coarse grain of the bulk of the Bargate beds is not conducive to ostracod preservation but a clay-rich lens preserved between two large calcareous concretions at Compton has yielded a well preserved assemblage.

The Bargate beds are noted for their derived fossils, particularly of Oxfordian and Kimmeridgian age, and it seemed possible that part of the ostracod fauna could be derived. This hypothesis was rejected on a basis of identical preservation of specimens of undescribed species and those of well-known Aptian age. The pyritic nature of the derived fossils as against the heavily calcified ostracod valves and indigenous brachiopods augmented this conclusion. Slight abrasion of the whole ostracod fauna had, however, occurred but this seemed consistent with the coarse nature of the deposit. The undescribed forms were each compared with earlier faunas and were found to be distinct from any species either described or detected. The author is grateful for the help of Mr. D. Barker of the Dept. of Geology, Leicester, for comparing the specimens with his Portlandian and Purbeckian material. In the preparation of this paper the author is most grateful to the Curator of the Sedgwick Museum, Cambridge, for the loan of Chapman's type specimens and to Professor P. Allen for encouragement and provision of facilities at Reading. I am also indebted to Mr. J. Watkins who undertook the photography of the specimens and produced the plates.

Chapman's type specimens are in the Sedgwick Museum at Cambridge (S.M.) whilst the author's types and comparative material are in the collection at the British Museum of Natural History (B.M.N.H.).

SYSTEMATIC DESCRIPTIONS

Order PODOCOPIDA

Suborder PLATYCOPINA

Family CYTHERELLIDAE Sars 1866

Genus CYTHERELLOIDEA Alexander 1929

Cytherelloidea sp.

Plate 54, fig. 1

Material. Carapace B.M.N.H. Io1500 from the Bargate beds at Compton.

Remarks. Only a single specimen of this species has been found. This rather eroded carapace is, however, described because of its marked difference from other Cretaceous species and our lack of knowledge of the genus in the Aptian. The valves are rather similar to *Cytherelloidea williamsoniana* (Jones) in shape and degree of compression but the dorsal rib is absent. Only the long straight ventral rib which is connected posteriorly to the lower of two nodes is present. The lateral surface is faintly pitted. There is a low anterior marginal rib which is continued along the whole length of the ventral margin as a shelf.

Suborder PODOCOPINA

Superfamily BAIRDIACEA

Family BAIRDIIDAE Sars 1887

Genus BAIRDIA M^cCoy 1844*Bairdia* sp.

Plate 54, fig. 3

Material. Carapace B.M.N.H. Io1506 from the Bargate beds at Compton.

Remarks. As species of this genus are rare in the British Lower Cretaceous this single specimen is thought worthy of description. The carapace is rather elongate with a comparatively low degree of arching of the dorsal margin. It is probably related to forms occurring in the Tealby series of Lincolnshire. The genus has not so far been found at any level in the Speeton Clay but occurs in the Upper Albian at a variety of localities.

Superfamily CYTHERACEA

Family CYTHERURIDAE Müller 1894

Genus CYTHERURA Sars 1866

Cytherura reticulosa (Chapman 1894)

Plate 55, figs. 7, 9

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

Material. (i) Holotype, a left valve, Sedgwick Museum B 28837, from the Bargate Beds at Littleton. (ii) Eight specimens from the authors collection B.M.N.H. Io1549, 50, from the Tealby limestone at Nettleton, Lincolnshire.

Measurements.

L.V., B 28837, length 0.41 mm., height 0.22 mm.

R.V., Io1549 ,, 0.40 mm. ,, 0.25 mm.

Remarks. This characteristically ornamented species was found only as a single specimen by Chapman but is abundant in the Tealby Clays and Limestone series in Lincolnshire. The dominant features of the ornament are the series of longitudinal ribs crossing the medio-lateral surface. The ventral rib is more prominent and forms a strong spine posteriorly. Marginal areas are broad and crossed by a series of wavy radial pore canals. Hinge strong, crenulate, merodont. Right valves are shorter and rather more strongly arched dorsally due to the presence of a strong shelf above the median hinge element.

Genus *CYTHEROPTERON* Sars 1866

Cytheropteron (*C.*) *vesiculosum* (Chapman 1894)

Plate 55, figs. 1-3

1894 *Cythere vesiculosa* Chapman, p. 106, pl. 33, fig. 1a-c.

Material. (i) Holotype, a right valve, S.M. B 28815, from the Bargate beds at Littleton. (ii) A left valve B.M.N.H. Io1532, from the Bargate beds at Compton.

Measurements.

Holotype, R.V., B 28815, length 0.42 mm., height 0.22 mm.

L.V., Io1532 ,, 0.48 mm. ,, 0.25 mm.

Description. Valves small, with prominent ventral alae. Dorsal and ventral margins straight and parallel; anterior margin subrectangular, posterior margin pointed at two-thirds height. Lateral surface covered with a series of nodulose swellings. A well-developed eye tubercle occurs antero-dorsally. The duplicature is broad and crossed by a few straight, simple radial pore canals. Hinge crenulate, merodont, consisting in the left valve of two strongly divided elongate sockets separated by a denticulate median bar. The terminal hinge elements in the holotype are unfortunately broken.

Remarks. The species is not a characteristic *Cytheropteron* but shows affinities in its shape, alae, marginal features, and hinge structure.

Cytheropteron (*Eocytheropteron*) *comptonense* nom. nov.

Plate 54, figs. 15, 16

non 1854 *Cythere laticristata* Bosquet, p. 118, pl. 7, fig. 11a-d.

1894 *Cytheropteron laticristatum* (Bosquet); Chapman, p. 692.

Material. (i) Holotype, a left valve, S.M. B 28836 from the Bargate beds at Littleton. (ii) A right valve and a broken carapace, B.M.N.H. Io1524, 25, from the Bargate beds at Compton.

Diagnosis. A species of *Cytheropteron* with prominent symmetrical ventral alate expansion and smooth lateral surface.

Measurements.

Holotype, L.V., B 28836, length 0.54 mm., height 0.34 mm.

R.V., Io1524 ,, 0.55 mm. ,, 0.35 mm.

Description. Valves small, strongly inflated ventrally. Dorsal margin arched with the greatest height at one-third length. Ventral margin obscured by the ventral alate expansion. Lateral surface smooth. The hinge is unfortunately broken in all of the available

specimens but appears in the right valves to be a continuous row of crenulations highest at the ends.

Remarks. Chapman's original interpretation of this specimen is now found to be erroneous and a new name is required. The size and prominence of the ventral alae and lack of surface ornament make it distinct from other related species of the same sub-genus.

? *Cytheropteron costuliferum* Chapman 1894

1894 *Cytheropteron costuliferum* Chapman, p. 692, pl. 33, fig. 7a-c.

Material. A single closed carapace S.M. B 28838 from the Bargate beds at Littleton.

Remarks. As only this single carapace has been found, generic allocation is not possible. The strong ventral expansion of the valves makes them triangular in end view and the longitudinal striations along the lateral surface make the specimen quite unlike any other figured Cretaceous form.

Genus EUCYTHERURA Müller 1894

Eucytherura chapmani nom. nov.

Plate 55, fig. 4

non 1890 *Cythereis ornatissima reticulata* Jones and Hinde, p. 24, pl. 1, figs. 67, 68, 77; pl. 4, figs. 9-12.

1894 *Cythereis ornatissima reticulata* Jones and Hinde; Chapman, p. 689.

Material. Holotype, a right valve, S.M. B 28818, from the Bargate beds at Littleton.

EXPLANATION OF PLATE 54

All figures $\times 50$.

Fig. 1. *Cytherelloidea* sp., Aptian, Compton; carapace from right; B.M.N.H. Io1500.

Figs. 2, 4, 5. *Veenia robusta* sp. nov., Aptian, Compton. 2, Carapace (paratype), dorsal view; B.M.N.H. Io1502. 4, Right valve (paratype), lateral view; B.M.N.H. Io1503. 5, Left valve (holotype), lateral view; B.M.N.H. Io1501.

Fig. 3. *Bairdia* sp., Aptian, Compton; carapace from right; B.M.N.H. Io1506.

Figs. 6, 8, 9. *Cythereis cristata* nom. nov., Aptian. 6, Female left valve (holotype), lateral view; B 28816, Littleton. 8, Female left valve (holotype), internal view; B 28816, Littleton. 9, Male carapace from left; B.M.N.H. Io1507, Compton.

Figs. 7, 10. *Macrodentina* sp., Aptian, Compton. 7, Adult carapace from right; B.M.N.H. Io1509. 10, Juvenile right valve, lateral view; B.M.N.H. Io1510.

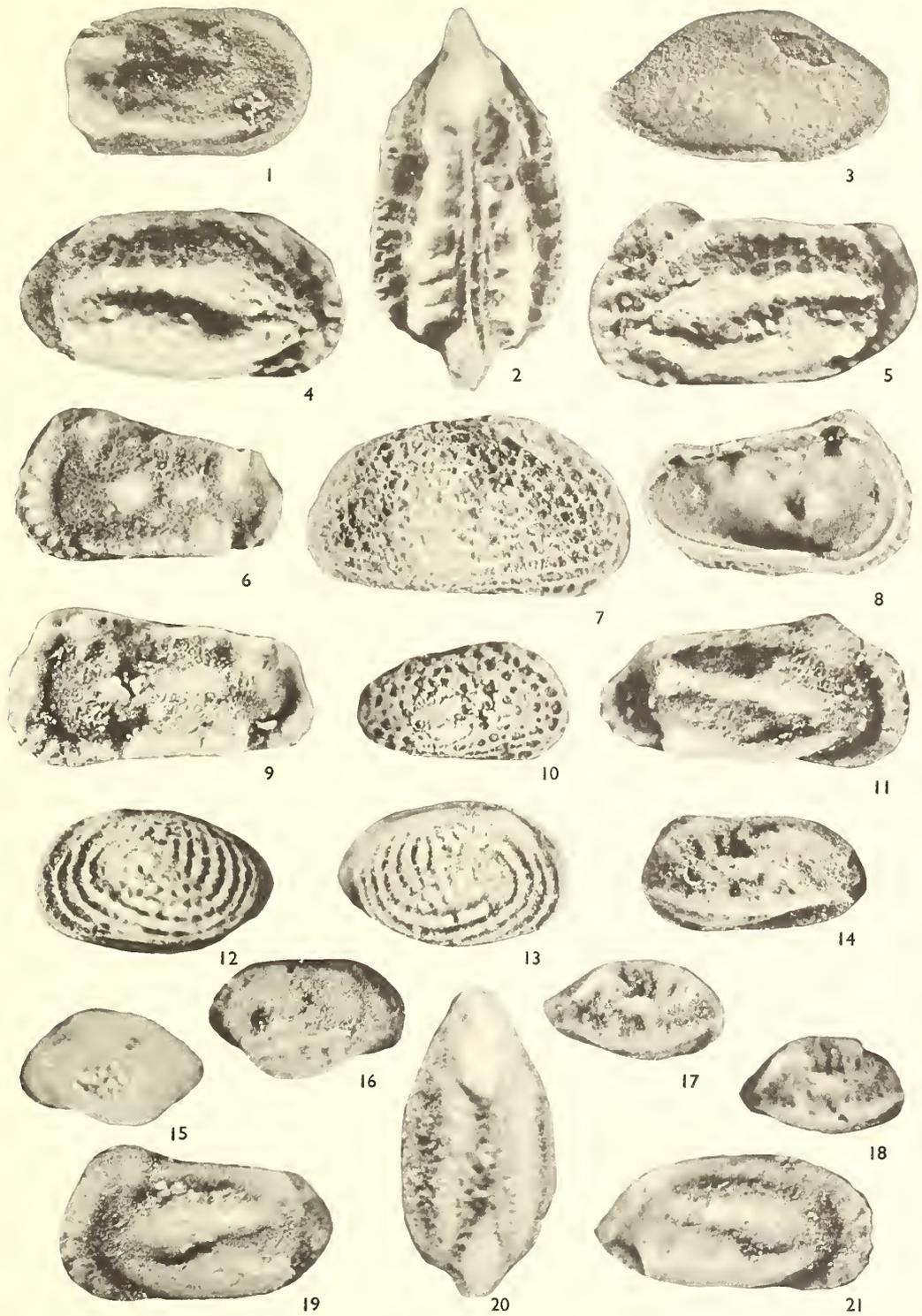
Fig. 11. *Cythereis angulata* sp. nov., Aptian, Compton; right valve (holotype), lateral view; B.M.N.H. Io1512.

Figs. 12, 13. *Neocythere* (*N.*) *vanveeni* Mertens, Aptian, Compton. 12, Adult carapace from left; B.M.N.H. Io1517. 13, Adult carapace from right; B.M.N.H. Io1518.

Figs. 14, 17, 18. *Pseudobythocythere vellicata* (Chapman), Aptian. 14, Male left valve, lateral view; B.M.N.H. Io1521, Compton. 17, Female right valve, lateral view; B.M.N.H. Io1522, Compton. 18, Female right valve (Chapman *C. bicarinata*), lateral view; B 28824, Littleton.

Figs. 15, 16. *Cytheropteron* (*Eocytheropteron*) *comptonense* nom. nov., Aptian. 15, Left valve (holotype), lateral view; B 28836, Littleton. 16, Right valve, lateral view; B.M.N.H. Io1524, Compton.

Figs. 19-21. *Protocythere inornata* sp. nov., Aptian, Compton. 19, Female left valve (holotype), lateral view; B.M.N.H. Io1526. 20, Male carapace, dorsal view; B.M.N.H. Io1527. 21, Female right valve, lateral view; B.M.N.H. Io1528.



Diagnosis. A small species of *Eucytherura* with a strong inflated ventral longitudinal rib, well-developed eye tubercle and marked anterior marginal rib.

Measurements.

Holotype, R.V., B 28818, length 0.40 mm., height 0.20 mm.

Description. Valves small, laterally compressed subrectangular in shape. Anterior margin rather truncate; dorsal and ventral margins straight and subparallel. A low anterior marginal rib connects dorsally with a prominent eye tubercle. An inflated ventral rib of constant height runs parallel to the margin. Postero-dorsally there is a longitudinally elongated nodular process. Three tubercles occur on the lower half of the anterior margin. Lateral surface finely pitted. The duplicature is broad and crossed by few, simple radial pore canals. The hinge is broken but appears to be smooth, merodont.

Remarks. The species differs considerably from *Cythereis reticulata* and Chapman's confusion is surprising. He does, however, state that the size is only half that of normal specimens. In shape *E. chapmani* is rather similar to the Albian form *E. rectangulata* Kaye and the Barremian form *E. neocomiana* Kaye. It differs in the possession of a strong inflated ventral rib and the lack of surface reticulation. It is nearest to *E. neocomiana* in shape and in the nature of the eye tubercle. *E. rectangulata* from the Albian possesses oblique ribs antero-laterally and is more closely related to *E. nettletonensis* described below.

Eucytherura nettletonensis sp. nov.

Plate 55, figs. 5, 6, 8

Material. (i) Holotype, a left valve B.M.N.H. Io1533 from the Tealby Limestone series at Nettleton, Lincolnshire (Horizon 2' above the second limestone band). (ii) Fifteen paratypes from the same sample B.M.N.H. Io1534-48.

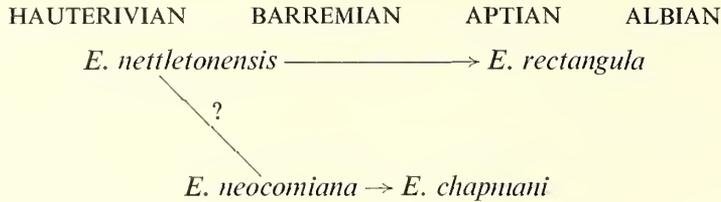
Diagnosis. A quadrangular species of *Eucytherura* with a short median longitudinal rib present antero-laterally and a marked eye tubercle. The prominent ventral longitudinal rib diverges from the margin anteriorly.

Measurements. Holotype, L.V., Io1533 length 0.35 mm., height, 0.21 mm.

Description. Valves small, compressed dorsally and laterally. Dorsal and ventral margins straight and parallel; anterior margin subquadrate, posterior margin rounded at two-thirds height. Antero-dorsally a large smooth eye tubercle is connected to the anterior margin by a short, swollen rib. A prominent ventral longitudinal rib follows the margin posteriorly but diverges anteriorly to meet the anterior margin at one-quarter height; below it antero-ventrally there is a narrow flat shelf. A short median longitudinal rib runs across the antero-lateral surface from the margin to terminate at one-quarter length. Postero-dorsally an irregular tubercle is connected by a short rib to the posterior margin. The lateral surface is strongly reticulate. The duplicature is broad and is crossed by few thick radial pore canals. A vestibule occurs anteriorly. The hinge is merodont with smooth terminal elements.

Remarks. This species though of Hauterivian age is described here because of its relationship to the other British Cretaceous species of the genus. *E. nettletonensis* is most closely

related to *E. rectangula* and is distinguished from the *E. chapmani*-*E. neocomiana* group by the lack of an anterior marginal rib and the presence of a median longitudinal rib. It differs from *E. rectangula* in the greater elongation, the smooth eye tubercle and the increased prominence of the ventral rib. A possible evolutionary sequence is:



Genus DOLOCYHERE Mertens 1956

Dolocythere rara Mertens 1956

Plate 55, figs. 12, 14, 15

non 1888 *Cytheridea retorrída* Jones and Sherborn, p. 260, pl. 1, fig. 8a-c.

1894 *Cytheridea retorrída* Jones and Sherborn; Chapman, p. 689.

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

Material. (i) A right valve S.M. B 28820 (Chapman *C. retorrída*) from Littleton. (ii) Four specimens from the author's collection B.M.N.H. Io1551-3, locality Compton.

Measurements.

R.V., B 28820,	length 0.53 mm.,	height 0.24 mm.	
L.V., Io1551	„ 0.50 mm.	„ 0.25 mm.	
R.V., Io1552	„ 0.50 mm.	„ 0.25 mm.	

Remarks. The specimen recorded by Chapman as *C. retorrída* is now seen to differ significantly from that species and belongs to *D. rara* Mertens.

EXPLANATION OF PLATE 55

All figures × 100.

Figs. 1-3. *Cytheropteron* (*C.*) *vesiculosum* (Chapman), Aptian. 1, Left valve, lateral view; B.M.N.H. Io1532, Compton. 2, Right valve (holotype), dorsal view; B 28815, Littleton. 3, Right valve (holotype), lateral view; B 28815, Littleton.

Fig. 4. *Eucytherura chapmani* nom. nov., Aptian, Littleton; right valve (holotype), lateral view; B 28818.

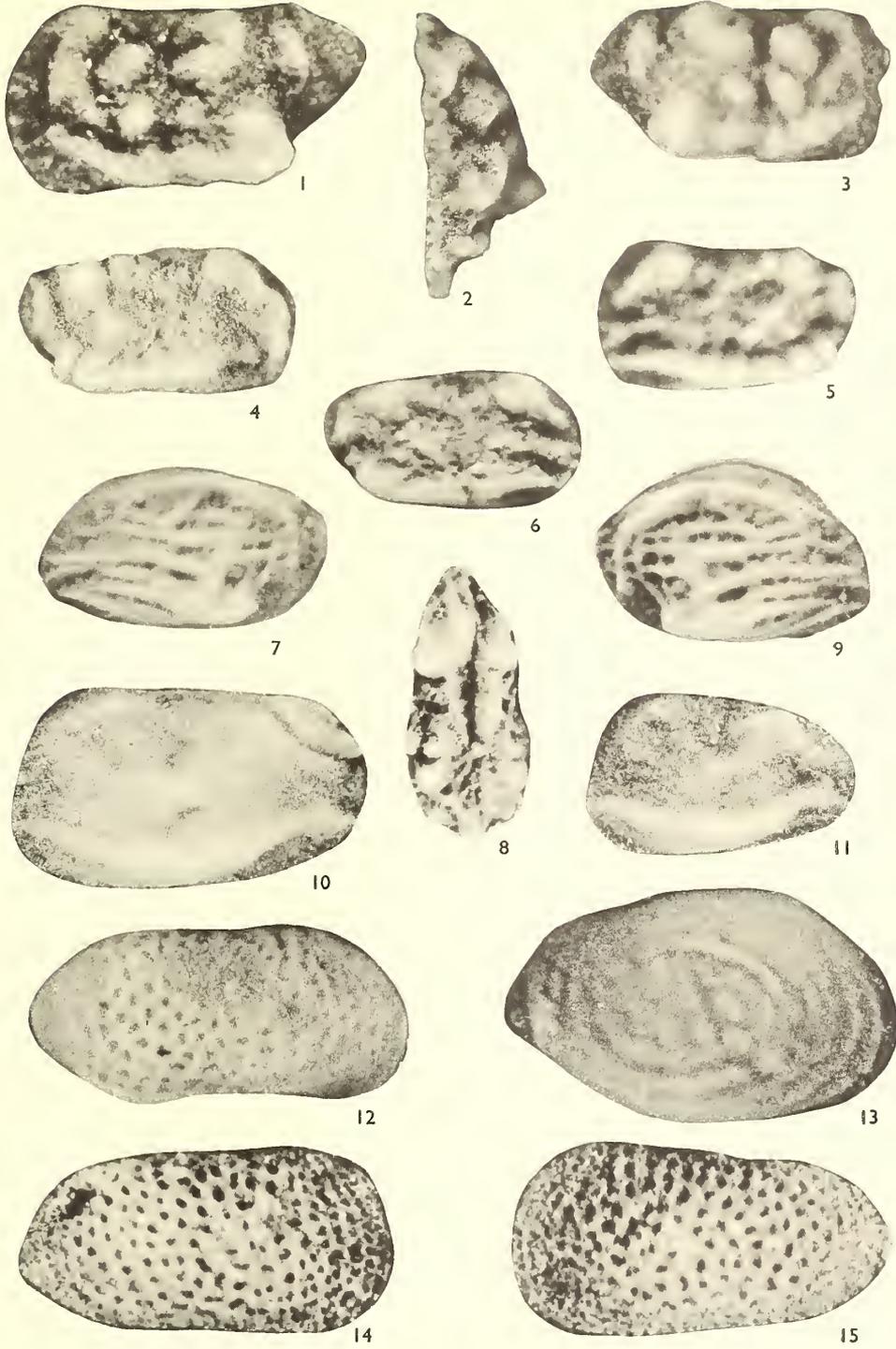
Figs. 5, 6, 8. *Eucytherura nettletonensis* sp. nov., Hauterivian, Nettleton. 5, Left valve (holotype), lateral view; B.M.N.H. Io1533. 6, Right valve (paratype), lateral view; B.M.N.H. Io1534. 8, Carapace (paratype), dorsal view; B.M.N.H. Io1535.

Figs. 7, 9. *Cytherura reticulosa* (Chapman). 7, Left valve (holotype), lateral view; B 28827, Aptian, Littleton. 9, Right valve, lateral view; B.M.N.H. Io1549, Hauterivian, Nettleton.

Figs. 10, 11. *Pseudocythera vellicata* (Chapman), Aptian, Littleton. 10, Juvenile left valve, lateral view; B 28828 (Chapman *C. vellicata*). 11, Juvenile left valve, lateral view; B 28829 (Chapman *C. fenestrata*).

Figs. 12, 14, 15. *Dolocythere rara* Mertens, Aptian. 12, Right valve, lateral view; B 28820, Littleton. 14, Right valve, lateral view; B.M.N.H. Io1551, Compton. 15, Left valve, lateral view; B.M.N.H. Io1552, Compton.

Fig. 13. *Neocythere* (*N.*) *vanveeni* Mertens, Aptian, Littleton; juvenile right valve, lateral view; B 28834.



Genus PSEUDOBYTHOCYTHERE Mertens 1950

Pseudobythocythere vellicata (Chapman 1894)

Plate 54, figs. 14, 17, 18; Plate 55, figs. 10, 11

- non 1849 *Cythereis lonsdaleiana* Jones, p. 20, pl. 5, fig. 12a-c.
 non 1888 *Cytheridea bicarinata* Jones and Sherborn, p. 272, pl. 4, figs. 9, 10.
 1894 *Cythereis lonsdaleiana* Jones; Chapman, p. 689.
 1894 *Cytheridea bicarinata* Jones and Sherborn; Chapman, p. 690.
 1894 *Cytheridea vellicata* Chapman, p. 690, pl. 33, fig. 3a-c.
 1894 *Cytheridea fenestrata* Chapman, p. 690, pl. 33, fig. 4.

Material. (i) An adult right valve (mounted as *C. bicarinata*) B 28824 from Littleton. (ii) A juvenile left valve (mounted as *C. lonsdaleiana*) B 28819 from Littleton. (iii) An adult left valve (figured as *C. vellicata*) B 28828 from Littleton. (iv) A juvenile left valve (figured as *C. fenestrata*) B 28829 from Littleton. (v) Three juvenile left valves (mounted and figured as *C. bicarinata* var. *nodulosa*) B 28825-7 from Littleton. (vi) Five specimens from the author's collection B.M.N.H. Io1521-3, locality Compton.

Measurements.

R.V., B 28824,	length 0.49 mm.,	height 0.29 mm.
L.V., B 28828	,, 0.48 mm.	,, 0.28 mm.
L.V., B 28819	,, 0.40 mm.	,, 0.22 mm.
Male, L.V. Io1521	,, 0.60 mm.	,, 0.30 mm.
Female, R.V. Io1522	,, 0.50 mm.	,, 0.27 mm.

Description. Valves elongate with straight subparallel dorsal and ventral margins in the left valves and arched dorsal margin in the right valves. A high, keel-like rib runs in a convex arc above the ventral margin, it reaches the margin anteriorly and is connected posteriorly to the median rib. This latter rib parallels the ventral rib but becomes indistinct anteriorly. Posteriorly it crosses a large postero-dorsal swelling before being deflected downwards to join the posterior end of the ventral rib. The postero-dorsal swelling becomes increasingly prominent in younger instars whilst the median rib becomes less distinct. A low eye tubercle occurs antero-dorsally which is joined to the median rib by a low cross rib. Other cross ribs connect the median portions of the ventral and median ribs. A flattened shelf-like region occurs along the dorsal margin. Hinge crenulate merodont with a long straight median element.

Remarks. Chapman was in great confusion about this form figuring left valves, right valves, dimorphs, and instars as different species. He figured a right valve as *C. bicarinata* but a corresponding left valve was labelled *C. vellicata*. This confusion was perhaps brought about by the strong arching of the dorsal margin in the right valves as compared with the straight margin in the left valves. The increase in prominence of the postero-dorsal tubercle and decrease in prominence of the median rib during ontogeny led Chapman to figure juveniles as three further distinct types. As *C. bicarinata* Jones and Sherborn and *C. lonsdaleiana* Jones were misidentified by Chapman, *C. vellicata* is here proposed as the valid name for the species.

Chapman's material and the Compton material both come from the Upper Aptian Bargate beds and the author has obtained other specimens from a similar horizon in the Isle of Wight. Closely comparative forms such as *P. ornata* Kaye occur in the Hauterivian Tealby Limestone Series of Lincolnshire and the Lower Barremian portion of the

Speeton Clay. *P. ornata* differs principally from *P. vellicata* in the bifurcation of the median longitudinal rib anteriorly.

Family PROGONOCYTHERIDAE Sylvester-Bradley 1948

Genus NEOCYTHERE Mertens 1956

Neocythere (N.) vanveeni Mertens 1956

Plate 54, figs. 12, 13; Plate 55, fig. 13

- non 1849 *Cythere punctatula* var. *virginea* Jones, p. 12, pl. 1, fig. 2n.
 non 1884 *Cythere subconcentrica* Jones, p. 768, pl. 34, figs. 28, 29.
 non 1884 *Cythere drupacea* Jones, p. 772, pl. 34, fig. 30.
 non 1890 *Cytheropteron concentricum* (Reuss) Jones and Hinde, p. 31, pl. 1, figs. 5–10; pl. 4, fig. 19.
 1894 *Cytheropteron concentricum* (Reuss); Chapman, p. 691.
 1894 *Cytheropteron concentricum* var. *virginea* Jones; Chapman, p. 691.
 1894 *Cytheropteron subconcentricum* (Jones); Chapman, p. 691.
 1894 *Cytheropteron drupaceum* (Jones); Chapman, p. 691.
 1956 *Neocythere vanveeni* Mertens, p. 205, pl. 12, figs. 72–78; pl. 14, figs. 100–2.
 1963 *Neocythere (N.) vanveeni* Mertens; Kaye, p. 276, pl. 41, figs. 23, 25.

Material. (i) S.M. B 28832, B 28840 (Chapman—*C. concentricum*) one from Littleton, one from Chilworth. (ii) S.M. B 28834 (Chapman—*C. subconcentrica*) from Littleton. (iii) S.M. B 28835 (Chapman—*C. drupaceum*) from Littleton. (iv) S.M. B 28833 (Chapman—*C. concentricum* var. *virginea*) from Littleton. (v) Five specimens from the author's collection B.M.N.H. Io1517–19, locality Compton.

Remarks. Most of Chapman's specimens of this species are juveniles and have been specifically differentiated largely on a basis of size. The degree of abrasion of the specimen also seems to have affected his terminology. The largest specimen, figured as *C. subconcentricum*, is refigured here (Pl. 55, fig. 13).

Neocythere (Centrocythere) denticulata Mertens 1956

1956 *Centrocythere denticulata* Mertens, p. 204, pl. 11, figs. 66–71; pl. 14, figs. 97, 99.

Material. Two specimens from the author's collection B.M.N.H. Io1520, locality Compton.

Genus ACROCYTHERE Neale 1960

Acrocythere hauteriviana (Bartenstein 1956)

Remarks. The specimen described by Chapman as *Cytheridea craticula* Jones and Sherborn (B 28830) is found to be a worn specimen of *Acrocythere hauteriviana*. No other material has been found from Compton or as yet from the Isle of Wight but it is found in the basal Aptian at Speeton.

Genus MACRODENTINA Martin 1940

? *Macrodentina* sp.

Plate 54, figs. 7, 10

Material. (i) A fragmentary valve B 28823 attributed by Chapman to *Cytheridea rotundata*, locality Littleton. (ii) Three specimens from the author's collection B.M.N.H. Io1509–11, locality Compton.

Remarks. Several poorly preserved specimens from Compton seem to belong within this genus. The characteristic ventral lineation and strong surface reticulation seem to fit well. Chapman's specimen attributed to *C. rotundata* though fragmentary also belongs within this category. It differs considerably from *C. rotundata* which itself has been noted (Kaye 1964) to be conspecific with *Schuleridea jonesiana* Bosquet. The specimen described by Jones (1849) as '*Cythere*' *bairdiana* and subsequently refigured (Kaye 1964, pl. 1, fig. 9) from the sponge gravels at Farringdon is also conspecific with this form and appears to be a juvenile. Its occurrence in the same zone of the Aptian at two different localities may contradict my earlier suggestion of derivation and it could possibly be indigenous. I have not been able to match the species with any published or unpublished British Upper Jurassic form. The juveniles which have the ventral lineation poorly developed are seen to have a strongly crenulate merodont hinge. The only adult specimen is, however, a closed carapace.

Family CYTHERIDEIDAE Sars 1925
Genus CLITHROCYTHERIDEA Stephenson 1936

? *Clithrocytheridea* sp. (juv.)

Remarks. The specimen described by Chapman as *Cytheridea subperforata* Jones appears to be an early instar of a species of *Clithrocytheridea*. Two specimens are preserved, a left valve B 28822 and a right valve B 28840. The valves have the long margins converging strongly posteriorly. The lateral surfaces are finely pitted. The duplicature is very narrow; the hinge, however, has a median bar in the left valve and complementary furrow in the right. Low terminal elements are developed in the right valve.

The shape, small size, narrow duplicature, and poorly developed hinge seem to suggest that these specimens are only juveniles and until adult material is found the species cannot be described. The left valve comes from Littleton, the right valve was found at St. Martha's Hill.

The specimen figured as *Cytheridea bipapillata* by Chapman probably should also belong here. This species B 28831 is so broken as to be valueless. Only a portion of the margin preserved is the anterior where the narrow duplicature and short radial pore canals point to it being a pre-adult form. The strongly punctate surface is the only definite recognizable feature. Unfortunately no comparative material of these forms has been found from Compton.

Family PROTOCYTHERIDAE Mandelstam 1960
Genus PROTOCYTHERE Triebel 1938

Protocythere inornata sp. nov.

Plate 55, figs. 19-21

Material. (i) Holotype a female left valve B.M.N.H. Io1526 from the Bargate beds at Compton.
(ii) Four paratypes B.M.N.H. Io1527-31 from the same sample.

Diagnosis. An inflated species of *Protocythere* with rather subdued ornament compared to other members of the genus. The median longitudinal rib runs somewhat obliquely across the lateral surface.

Measurements.

Holotype, female L.V., B.M.N.H. Io1526,	length 0.79 mm.,	height 0.46 mm.
Paratype, female R.V., B.M.N.H. Io1528	„ 0.79 mm.	„ 0.42 mm.
Male carapace, B.M.N.H. Io1527	„ 0.85 mm.	„ 0.45 mm.

Description. Valves elongate strongly built. Dorsal and ventral margins straight and subparallel. Prominent anterior and more subdued posterior hinge ears present in the left valves. Lateral surface somewhat inflated and bearing three poorly developed longitudinal ribs. The dorsal rib is least distinct and is separate both anteriorly and posteriorly. The median rib runs somewhat obliquely across the lateral surface being nearer the dorsal margin posteriorly; anteriorly it is joined to a low smooth muscle node. The ventral rib is most prominent becoming more inflated posteriorly; it is separated from the margin anteriorly by a flattened shelf but runs to meet it posteriorly. An inflated rib follows the anterior margin, being joined dorsally to a low eye tubercle set some distance from the margin. The anterior margin and lower half of the posterior margin bear a series of tubercles. The intercostal and marginal areas are smooth. The hinge is strongly crenulate merodont, having in the right valve two high strongly divided terminal teeth decreasing in size towards the median element, which is a locellate, almost interoculate, furrow. The anterior hinge ear in the left valve makes a prominent prolongation anterior to the terminal socket.

Remarks. This species is most similar to *P. hechti* Triebel but differs in the greater lateral inflation, subdued ribbing and the oblique path of the median rib. A strongly related but as yet undescribed form, which however, lacks the anterior marginal rib and tuberculation, occurs in the Tealby Limestone Series of Lincolnshire.

Genus VEENIA Butler and Jones 1957

Veenia robusta sp. nov.

Plate 54, figs. 2, 4, 5

Material. (i) Holotype a female left valve B.M.N.H. Io1501 from the Bargate beds at Compton. (ii) Four paratypes from the same sample B.M.N.H. Io1502-5.

Diagnosis. A large robust species of *Veenia* with large reticulations over the whole of the lateral surface. The anterior marginal area is crossed by a series of short irregular ridges.

Measurements.

Female L.V., holotype B.M.N.H. Io1501,	length 0.97 mm.,	height 0.52 mm.
Female R.V., B.M.N.H. Io1503	„ 0.95 mm.	„ 0.50 mm.
Male carapace, B.M.N.H. Io1502	„ 1.12 mm.	„ 0.55 mm.

Description. Valves large, strongly built. Dorsal and ventral margins straight and subparallel. Marked anterior and posterior hinge ears occur in the left valves. Lateral surface crossed by three subparallel longitudinal ribs. The dorsal rib obscures the central part of the hinge margin and is separate both anteriorly and posteriorly. The median rib is shorter and is joined anteriorly to a large elongate muscle node. There is, however,

no increased height over this node. The ventral rib is slightly convex and does not obscure the margin. A low eye tubercle occurs antero-dorsally. The anterior marginal area is crossed by a series of low radially arranged ribs. The whole of the lateral surface is covered by a series of large reticulations. These reticulations, which often bear a series of pits within them, cross the costae without interruption. They are also prominent on the dorsal and ventral surfaces. The hinge is amphidont consisting in the left valve of terminal crenulate sockets separated by a long straight denticulate bar enlarged anteriorly to form a large smooth boss. The hinge ears form prominent internal swellings whilst a narrow shelf separates the median element and the margin.

Remarks. This large species has been found only at Compton and is not represented either in Chapman's assemblage or in the Isle of Wight material. The pattern of continuous reticulations is not matched in any other described species of *Veenia* or of related genera.

Family TRACHYLEBERIDIDAE Sylvester-Bradley 1948
Genus CYTHEREIS Jones 1849

Cythereis angulata sp. nov.

Plate 54, fig. 11

Material. (i) Holotype, a female right valve B.M.N.H. Io1512 from the Bargate beds at Compton.
(ii) Paratypes, three carapaces and fragments from the same sample B.M.N.H. Io1513-16.

Diagnosis. A species of *Cythereis* with somewhat angular appearance. The ventral longitudinal rib obscures the margin posteriorly but anteriorly curves upwards towards the muscle node.

Measurements.

Holotype, female R.V., B.M.N.H. Io1512,	length 0.87 mm.,	height 0.42 mm.
Paratype, female carapace, B.M.N.H. Io1513	„ 0.87 mm.	„ 0.50 mm.
Paratype, male carapace, B.M.N.H. Io1514	„ 0.98 mm.	„ 0.48 mm.

Description. Valves elongate compressed. Dorsal and ventral margins straight, converging posteriorly. Anterior cardinal angle well marked in both valves, forming the position of greatest height at one-quarter length. A large flattened eye tubercle occurs antero-dorsally. Dorsal rib rather indistinct, following the margin; it is joined anteriorly to the eye tubercle. Median rib short, rather oblique, joined cross rib to the posterior end of the dorsal rib. Ventral rib very prominent following the margin posteriorly but curving upwards below the muscle node anteriorly; antero-ventrally of it there is a low shelf-like area. Marginal areas depressed both with prominent tuberculate ribs following the margin. Intercostal areas finely pitted. Hinge strong amphidont consisting in the right valve of two high terminal faintly divided teeth separated by a long locellate furrow deepened anteriorly to form an oval socket.

Remarks. This species is differentiated from related forms by its angular appearance, marked anterior cardinal angle and upward swing of the ventral rib. It differs from *C. cristata* in the prominence of the median rib.

Cythereis cristata sp. nov.

Plate 54, figs. 6, 8, 9

non 1846 *Cytherina ornatissima* Reuss, p. 104, pl. 24, figs. 12, 18.1894 *Cythereis ornatissima* (Reuss); Chapman, p. 688.

Material. (i) Holotype, a left valve S.M. B 28816, from the Bargate beds at Littleton, Surrey. (ii) A right valve and three carapaces B.M.N.H. Io1507, 8, from the Bargate beds at Compton.

Diagnosis. A subquadrate species of *Cythereis* with a finely punctate surface and high smooth muscle node.

Measurements. Holotype L.V., B 28816, length 0.80 mm., height 0.22 mm.

Description. Valves subquadrate, strongly compressed both dorsally and laterally. Dorsal and ventral margins straight and subparallel. A prominent inflated rib follows the anterior margin; dorsally it merges with a low eye tubercle. It bears a double row of small tubercles on its upper surface for the lower half of its path. A high smooth muscle node is separated from a weak short median longitudinal rib; a marked ventral longitudinal rib and a short irregular dorsal longitudinal rib are found. The lateral surfaces are strongly punctate. The hinge is strong amphidont having weakly divided terminal elements.

Remarks. Chapman interpreted this species as a worn *C. ornatissima* (Reuss) but there is neither any sign of abrasion in his specimen nor close relationship to any of the later Cretaceous species of the genus. The subquadrate shape, lack of inflation and punctate rather than reticulate ornament are its most distinct features.

CONCLUSIONS

Revision of the twenty species of ostracoda recorded by Chapman from the Bargate beds has led them to be considered under thirteen species. Only four of these species are validly attributed to Chapman's authorship whilst of the remaining eight, three are distinct and have had to be renamed: viz. *Cytheropteron* (*Eo.*) *comptonense*, *Eucytherura chapmani*, and *Cythereis cristata*. Two are left under open nomenclature and three are attributed to species described elsewhere. The material obtained from Compton has produced specimens comparable to most of Chapman's types but certain additional species have been found. Of the six species not recorded by Chapman, three are new: viz. *Protocythere inornata*, *Veenia robusta*, and *Cythereis angulata*; two are left under open nomenclature and one is referred to a species described elsewhere. Other fragmentary and abraded specimens included some attributable to the genera *Paracypris*, *Pontocyprella*, and *Monoceratina*; these specimens, however, were rare and very poorly preserved and are therefore not included in the systematics. Similarities were noted in the fauna to that of the (Hauterivian) Tealby Series of Lincolnshire with the predominance of Cytheridae and Protocytheridae. A new species of *Eucytherura* from the Tealby Limestone series is included for comparison.

Two of the species recorded from outside this area, *Neocythere* (*N.*) *vanveeni* and *N. (C.) denticulata* are characteristic of the Albian in this country whilst *Acrocythere*

hauteriviana ranges up from the Hauterivian. *Dolocythere rara* occurs in the Aptian and Lower Albian of Germany and in the Lower Albian at Speeton.

The fauna as a whole is of shallower water forms comparable with the Tealby fauna which also seems to have lived close inshore. The deeper water forms characteristic of the Speeton Clay and many of the forms shortly to be described from the Atherfield Clay and other horizons in the Isle of Wight are rare or absent. The genera *Cytherura*, *Eucytherura*, *Cytheropteron*, *Veenia*, and *Cythereis* are rare or absent in the Speeton Clay proper but are abundant in the Tealby series. Conversely these genera are most prominent at Compton whilst *Schuleridea*, *Dolocytheridea*, *Apatocythere*, and *Orthonotacythere* found abundantly at Speeton and in the Atherfield Clay of the type locality, are absent. A summary of Chapman's species with the present revised names is as follows:

Chapman	Present identification
<i>Cythere vesiculosa</i> sp. nov.	<i>Cytheropteron vesiculosum</i> (Chapman)
<i>Cythereis ornatissima</i> Reuss	<i>Cythereis cristata</i> nom. nov.
<i>Cythereis ornatissima</i> var. <i>reticulata</i> (Jones and Hinde)	<i>Eucytherura chapmani</i> nom. nov.
<i>Cythereis lonsdaleiana</i> Jones	<i>Pseudobythocythere vellicata</i> (Chapman)
<i>Cytheridea retorrída</i> Jones and Sherborn	<i>Dolocythere rara</i> Mertens 1956
<i>Cytheridea subperforata</i> Jones	? <i>Clithrocytheridea</i> sp. (juv.)
<i>Cytheridea rotundata</i> Chapman and Sherborn	? <i>Macrodentina</i> sp.
<i>Cytheridea bicarinata</i> Jones and Sherborn	<i>Pseudobythocythere vellicata</i> (Chapman)
<i>Cytheridea bicarinata</i> var. <i>nodulosa</i>	<i>Pseudobythocythere vellicata</i> (Chapman)
<i>Cytheridea vellicata</i> sp. nov.	<i>Pseudobythocythere vellicata</i> (Chapman)
<i>Cytheridea fenestrata</i> sp. nov.	<i>Pseudobythocythere vellicata</i> (Chapman)
<i>Cytheridea craticula</i> Jones and Sherborn	<i>Acrocythere hauteriviana</i> (Bartenstein 1956)
<i>Cytheridea bipapillata</i> sp. nov.	? <i>Clithrocytheridea</i> sp. (juv.)
<i>Cytheropteron concentricum</i> Reuss	<i>Neocythere</i> (<i>N.</i>) <i>vanveeni</i> Mertens
<i>Cytheropteron concentricum</i> var. <i>virginea</i> Jones	? <i>Neocythere</i> (<i>N.</i>) <i>vanveeni</i> Mertens
<i>Cythere subconcentrica</i> Jones	<i>Neocythere</i> (<i>N.</i>) <i>vanveeni</i> Mertens
<i>Cytheropteron drupaceum</i> (Jones)	? <i>Neocythere</i> (<i>N.</i>) <i>vanveeni</i> Mertens
<i>Cytheropteron laticristatum</i> (Bosquet)	<i>Cytheropteron</i> (<i>E.</i>) <i>comptonense</i> nom. nov.
<i>Cytheropteron reticulosum</i> sp. nov.	<i>Cytherura reticulosa</i> (Chapman)
<i>Cytheropteron costuliferum</i> sp. nov.	<i>Cytheropteron costuliferum</i> Chapman

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THE ECHINOID GENUS *SALENIA* IN THE EASTERN PACIFIC

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ABSTRACT. The three occurrences of the stirodont echinoid *Salenia* Gray 1835 which Durham and Allison reported from the eastern Pacific in 1960 are described. A single, fragmentary specimen from the Aptian-Albian Alisitos formation of Baja California, Mexico, is tentatively referred to *S. mexicana* Schlüter of the Mexican and Texas middle Cretaceous. Numerous specimens from the lower Oligocene Keasey formation of northwestern Oregon are described as *S. schencki* sp. nov. *S. scrippsae* sp. nov. is based on living specimens dredged from depths between about 200 and 350 metres on an unnamed guyot (Station 73, S10 58-42; lat. 25° 44' S., long. 85° 25' W.) near the south-west end of Nasca Ridge, off the coast of Chile.

THE echinoid genus *Salenia* is abundantly represented in the European Cretaceous, but has been less commonly recorded in other areas and in later epochs. Until recently, it had not been reported from the eastern Pacific. Since the publication of volume 2 of Mortensen's (1935) *Monograph of the Echinoidea* with its summary of the Family Saleniidae, there have been at least forty-one reports of the genus *Salenia*, of which only one has been from the Recent fauna. The single Recent record and two of the above-mentioned fossil records were those noted by Durham and Allison (1960a, p. 1854; 1960b, p. 83) as the first records of *Salenia* in the eastern Pacific. These three eastern Pacific occurrences, based on material contained in the collections of the University of California Museum of Paleontology (abbreviated hereafter as UCMP), form the basis of this study.

In January 1958 during Expedition DOWNWIND, the University of California—Scripps Institution of Oceanography IGY cruise to the south-east Pacific, the R.V. *Horizon* dredged twenty-two specimens of a new species of *Salenia* from an unnamed guyot (text-fig. 1). This flat-topped seamount appears to have a diameter of about 13 kilometres (8 miles) and a minimum depth of 210 metres (115 fathoms). It is located on the south-west end of Nasca Ridge, about 1,280 kilometres (800 miles) off the coast of Chile and 480 kilometres (300 miles) approximately N. 80° W. of San Felix Island (Fisher 1958, fig. 8, station HD-73). A triglid fish with an interesting trans-Pacific distribution (Isla Juan Fernández to Australia) from the same sample has been reported by Hubbs (1959, pp. 313-15). This sample provides the first record of *Salenia* in the Recent fauna of the eastern Pacific, and adds one more species to the five living species previously recognized. Three of the five previously described species of the genus are recorded from the western Pacific and Indian Oceans (Mortensen 1935, pp. 374, 376, 379):

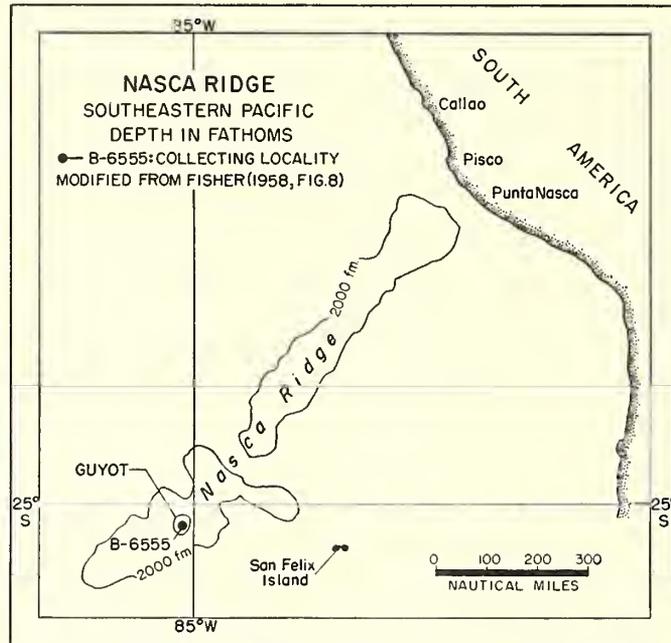
Salenia cincta Agassiz and Clark (1907, p. 116). Goto Islands, Kagoshima Gulf, and Sagami Bay in Japanese Seas; off Tawitawi in the Sulu Archipelago; and off the Kei Islands in the Banda Sea. Distributed bathymetrically between 170 and 520 metres.

Salenia sculpta Koehler (1927, p. 71, pl. 11, figs. 10-13; pl. 12, figs. 1-2, 10; pl. 25, fig. 5). Collected by the *Investigator* from a single locality off the Andaman Islands, Bay of Bengal, at 110-135 metres depth.

Salenia unicolor Mortensen (1934, p. 166). Sagami Sea, Celebes sea, and the Moluccan Straits, from 290 to 470 metres depth.

Of the two remaining species, one, *S. phoinissa* Agassiz and Clark (1908, p. 54), is based on a single specimen collected by the *Valdivia* on Agulhas Bank off the southern tip of South Africa at a depth of 102 metres (Mortensen 1935, p. 378), and the other, *S. goesiana* Lovén (1874, p. 27, pl. 19) [spelling altered from *goësiana* to agree with Article 32(c)(1) of the International Code of Zoological Nomenclature, 1961], is known only from the West Indies at depths between 90 and 540 metres (Mortensen 1935, p. 373).

Geographically the occurrence of *Salenia* off Chile fills a gap in the Recent distribution



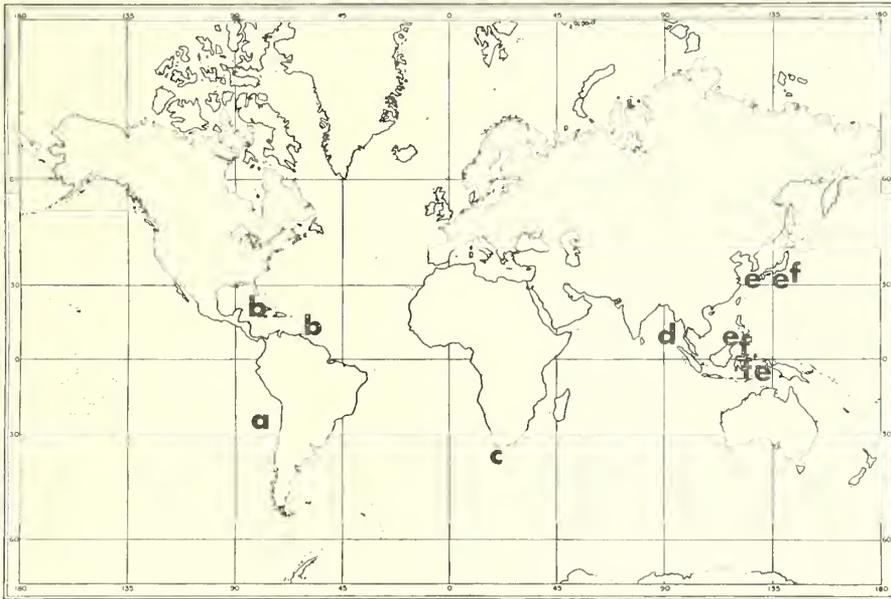
TEXT-FIG. 1. Map showing location of UCMP locality B-6555 on Nasca Ridge, south-eastern Pacific. Nasca Ridge delimited by 2,000-fathom contour. Map modified from Fisher (1958, fig. 8).

of the genus (text-fig. 2) and, perhaps coincidentally, has one or more characters in common with each of the other known living species, yet it is sufficiently distinctive to be easily recognized as a separate species.

During the summer of 1949, J. Wyatt Durham and H. E. Vokes visited outcrops of the lower Oligocene Keasey formation exposed along the west bank of the Nehalem River near Mist, Oregon. Their primary intention was to collect additional specimens of some stem-bearing crinoids that had recently been discovered in this area. In addition to the discovery of several specimens of the pentacrinoid *Isocrinus* von Meyer, which were later incorporated in Moore and Vokes's (1953) study of the Keasey crinoids, a diverse and abundant fauna and fragmentary plant remains were collected. This collection (UCMP locality A-5018) and additional collections from these exposures made by Durham and a field class in the Fall of 1952 (UCMP locality A-8721) contain numerous remains of echinoderms, among which are four species of asterozoans, one ophiuran, fragments tentatively referred to the spatangoid echinoid *Brisaster maximus*

Clark (1937), and several hundred specimens of a new species of *Salenia*. All the specimens of the *Salenia* are crushed, but remarkably complete. In many instances the primary and secondary spines are attached or in close proximity to their respective tubercles. Complete lanterns, including braces, are apparent in several specimens.

Excellent and unusual preservation is characteristic not only of the *Salenia* specimens, but of the entire fauna and flora from this Keasey locality. These strata have yielded



TEXT-FIG. 2. Distribution of the extant species of *Salenia*. a, *Salenia scrippsae* sp. nov.; b, *S. goeessiana* Lovén; c, *S. phoinissa* Agassiz and Clark; d, *S. sculpta* Koehler; e, *S. ciucta* Agassiz and Clark; f, *S. unicolor* Mortensen.

a number of elements not usually found as fossils, and are lacking in many of the common components usually found in Tertiary faunas of similar age. The changed aspect of the fauna is such as to indicate that it must have been deposited under a different environment than most of the known contemporary faunas of the region.

Moore and Vokes (1953, p. 140) concluded from the physical character of the deposits that 'the comparatively great thickness of the Keasey deposits, coupled with the strongly tuffaceous nature of the middle and upper members, indicates that if the site of sedimentation was in moderately deep, or deep water, the area was not far removed from land on which a number of explosive volcanic vents were recurrently active. . . . Lack of bedding and general uniformity through considerable thicknesses of the deposit are not features to be expected in the littoral zone and suggest offshore conditions where the bottom was not agitated by waves or affected by current. Analysis of all known physical characters associated with the crinoid-bearing part of the Keasey formation therefore indicates nearness (at most a few tens of miles) to land and a sea bottom ranging from intermediate depth to greater than 500 fathoms.'

Moore and Vokes (1953, p. 141) further concluded that the molluscan faunas of these deposits were also indicative of 'intermediate' to 'deep' water in which 'intermediate' depth was defined as ranging from 100 to 500 fathoms (183 to 914 metres) and 'deep' water as depths greater than 500 fathoms.

Although the material from this locality in the UCMP collections is not a complete representation of the fauna, the elements available give much information on certain aspects of the environment of deposition. Below is a list of the thirty-six taxa which have been identified from the Keasey locality. Those marked by an '*' were recorded by Moore and Vokes (1953, p. 119), but are not represented in the UCMP collections. Those taxa preceded by a '†' have not previously been reported from this Keasey locality.

Foraminifera		
†	<i>Operculina</i> sp. (of Durham 1937, p. 367)	rare
†	<i>Plectofrondicularia packardi</i> Cushman and Schenck	abundant
Coelenterata		
†	<i>Caryophyllia</i> sp. indet.	one specimen
	<i>Flabellum hertleini</i> Durham (1942, p. 92)	
	Thirty-two specimens in a block with less than 80 square inches of surface	eighty-six specimens
†	Gorgonid coral	one specimen
Pelecypoda		
	<i>Acila (Truncacila) nehalemensis</i> Hanna	several
	<i>Delectopecten</i> sp. nov.	several
*	<i>Emmcula</i> sp. nov.	
*	<i>Minormalletia</i> sp. nov.	
*	<i>Nuculana washingtonensis</i> (Weaver) subsp. nov.	
*	<i>Propeanmissium</i> sp. nov.	
	<i>Solenya (Acharax) willapaensis</i> Weaver	few
*	<i>Tellina</i> sp. nov.	
	<i>Yoldia (Portlandella) chehalisensis</i> (Arnold)	
Gastropoda		
*	' <i>Cancellaria</i> ' sp.	
†	<i>Epitonium keaseyensis</i>	one specimen
*	<i>Exilia lincolnensis</i> Weaver	
*	<i>Fulgurofusus</i> sp. nov.	
*	<i>Polinices</i> sp. nov.	
*	<i>Scaphander stewarti</i> Durham	
Arthropoda		
†	Fragmentary crustacean remains	few
Crinoidea		
	<i>Isocrinus nehalemensis</i> Moore and Vokes	several
	<i>I. oregonensis</i> Moore and Vokes	common
Asteroidea		
†	Brisingid (?) sp. nov. (new genus?)	one specimen
†	<i>Astropecten</i> (?) sp. nov.	three specimens
†	Two undetermined asteroids	
Ophiuroidea		
	Undetermined ophiuran	one specimen

Echinoidea

- | | |
|--------------------------------------|-----------------|
| † <i>Brisaster maximus</i> Clark (?) | one specimen |
| † <i>Salenia schencki</i> sp. nov. | several hundred |

Vertebrata

- | | |
|---------------|--------|
| † Fish scales | common |
|---------------|--------|

Plantae

- | | |
|--|--------------|
| † Coralline algae | one fragment |
| † ' <i>Zostera</i> ' sp. (with attached diatoms) | few |
| * <i>Quercus consinilis</i> Newberry | |
| * <i>Myrica</i> sp. | |
| † <i>Thuja</i> sp. | few |
| † <i>Ocotea eocernua</i> Chaney and Sanborn | one specimen |

The above list of taxa is apparently an anomalous association, containing some forms which grow only in shallow water whereas the modern relatives of others live only in 'deep' water. Living members of the genus *Acila* live in depths varying from about 10 to 803 fathoms (Schenck 1936, pp. 33–35). In certain pockets *Acila* (*Truncacila*) *nehalemensis* is rather abundant at this locality. The living mud pecten genus *Delectopecten* is found in depths of 10–1,100 fathoms (Woodring 1938, pp. 37, 38, pl. 3), and is restricted to depths below 100 fathoms in temperate and warmer climates. *Solemya johnsoni* Dall, the closest living relative of *S. willapaensis* on the Pacific Coast, lives in depths of 200–1,100 fathoms (Woodring 1938, pl. 3). Some of the specimens of *S. willapaensis* found at this locality retain impressions of the edge of the mantle extending beyond the margin of the shell. The asteroid listed as *Brisingid* (?) sp. nov. appears to be a member of the Suborder *Brisingina* Fisher (1928, p. 4), a group of archaic 'deep sea' starfish. The starfish *Astropecten* (?) sp. nov. appears to belong to a genus which ranges from shallow water to depths of at least 450 fathoms, but with most of its species in shallow water (Durham and Roberts 1948, p. 434). All living members of the genus *Salenia* are found in depths ranging from about 50–250 fathoms (Mortensen 1935, pp. 373–80). The specimens of *Salenia* here recorded occur in great numbers in a relatively thin bed, all with their spines attached or in close proximity. The starfish are found in association with them, suggesting that the starfish may have preyed on the echinoids. The coral *Flabellum hertleini* is closely related to the living *F. pavoninum* Lesson which is found in depths of 78–519 fathoms (Faustino 1927, p. 46; Vaughan 1907, p. 55), its optimum being between 178 and 220 fathoms. This coral also occurs abundantly in local pockets. Considering the great abundance of the echinoid and this coral, it would appear that the most likely depth habitat was around 200 fathoms (365 metres).

The coral *Caryophyllia* sp. indet. belongs to a genus with a depth range of 0–1,500 fathoms (Vaughan and Wells 1943, p. 203). The foraminifer *Operculina* belongs to the group of so-called larger foraminifera which characteristically live in waters of less than 100 fathoms depth, but which are carried into deeper water, as is evident by their occurrence in the Marshall Islands (Cushman, Todd, and Post 1954, table 3) where they occur at depths of several hundred fathoms. The foraminifer *Plectofrondicularia packardi* is a member of a genus recorded from 129 to 766 fathoms (Kleinpell 1938, fig. 5); inasmuch as it occurs in much greater numbers than the *Operculina*, it is probably much more significant. The single fragment of coralline alga belongs to a group which is largely confined to continental shelf environments (Lemoine 1940, p. 86; Johnson 1957,

p. 211), but the fragment could have been transported into deeper water. Similarly the fragments of the eelgrass '*Zostera*' could have been transported from depths of less than about 8 fathoms, where it lives (Sverdrup *et al.* 1942, p. 302), to a deeper site. The preceding data are summarized in the following table:

<i>Species</i>	<i>Depth range of relatives</i>
<i>Acila nehalemensis</i>	10-803 fathoms
<i>Delectopecten</i> sp. nov.	10-1,100 "
<i>Solenya willapaensis</i>	200-1,100 "
Brisingid (?) sp. nov.	'deep sea' "
<i>Astropecten</i> (?) sp. nov.	0-450 "
<i>Salenia schencki</i> sp. nov.	50-250 "
<i>Flabellum hertleini</i>	78-519 "
<i>Caryophyllia</i> sp. indet.	0-1,500 "
<i>Operculina</i> sp.	0-100 "
<i>Plectofrondicularia packardi</i>	129-766 "
Coralline algae	0-100 "
' <i>Zostera</i> ' sp.	0-8 "

Inasmuch as other analyses (Durham 1942, p. 87; 1950, p. 1254) have suggested that the surface temperatures prevailing during the Oligocene at this latitude were above 20° C., and from the known fact that many deep water organisms live at somewhat greater depths in the tropics than in cooler areas, it would appear that the minimum depths recorded above for the various 'deep water' organisms would be less than the depths at which this assemblage lived.

The undisturbed condition of the echinoids, the entire star-fish (plates not dissociated), and the complete crinoid skeletons indicate that the site was deep enough to be below the zone of effective wave and current action, a factor which would also indicate a depth of over 100 fathoms. Similarly, the well-preserved state of the organisms listed above would indicate either rapid, live burial, and/or a scarcity of the scavengers and detritus feeders which usually work over dead organisms on the sea floor.

Although the available organic evidence from these strata indicates greater depths of deposition than are common for contemporary deposits, it would appear that the depth at this locality was closer to 200 fathoms (365 metres) than to the 500 fathoms (914 metres) or greater depths as proposed by Moore and Vokes. However, the presence of shallow water, littoral, and land organisms in the deposits, such as the eel grass ('*Zostera*') fragments, the foraminifer *Operculina*, the coralline algae, and the angiosperm and gymnosperm fragments, does support Moore and Vokes's conclusion that the Keasey locality was, at the most, only a few tens of miles from shore.

Although the Keasey specimens agree in most details with Mortensen's (1935, p. 367) definition of the genus *Salenia*, they differ by having crenulations on the primary ambulacral tubercles. The presence of crenulate ambulacral tubercles recalls the genus *Salenocidaris* Agassiz 1869 or *Salenidia* Pomel 1883. In *Salenocidaris*, however, the ambulacra are composed of single plates, except for a few near the peristomial edge which are bigeminate. The ambulacra of *Salenidia* are composed of single plates throughout. The ambulacra of the Keasey specimens are distinctly bigeminate throughout. The crenulations on the primary ambulacral tubercles may be of sufficient taxonomic importance to place the Keasey specimens in a separate genus, but because of the meagre

Tertiary record of *Salenia*, especially in North America, such a change is not considered to be justified at present.

The single Cretaceous record of *Salenia* in the eastern Pacific Basin is based on a fragmentary specimen collected by M. V. Kirk and J. R. McIntyre in February 1950 from exposures of the Alisitos formation at Punta San Isidro on the Pacific coast of Baja California, Mexico. Kirk and McIntyre (1951, p. 1505) correlated the Alisitos formation with the Cenomanian deposits of the State of Jalisco, Mexico. This correlation was based primarily on the comparison of the rudistid fauna of the Alisitos formation with that described by Palmer (1928). Kirk and McIntyre noted also that the coral, echinoid, and rudistid elements of the Alisitos formation were comparable to those found in middle Cretaceous deposits in southern Mexico and Texas. Allison (1955, p. 404), on the basis of the gastropod fauna and the occurrence of *Orbitolina texana* (Roemer), assigned an Aptian-Albian age to the Alisitos formation. This age assignment is repeated by Durham and Allison (1960*b*, table 1).

The *Salenia* from the Alisitos formation, tentatively referred to *S. mexicana* Schlüter of the Mexican and Texas middle Cretaceous, is much larger than previously reported specimens of the species and differs somewhat in the shape of the primary interambulacral tubercles. This specimen may represent another species distinct from *S. mexicana*, but the available material is not adequate for a detailed comparison.

Tertiary records of *Salenia* are meagre, especially in the Western Hemisphere. According to Cooke (1959) only one valid species, *S. tumidula* Clark (1891, p. 75), from the Paleocene Vincentown formation of New Jersey, has hitherto been described from Cenozoic deposits in North America. *Salenia bellula*, which was also described by Clark (1891, p. 75) from the same formation, is considered a synonym of *S. tumidula* by Cooke (1959, p. 13). Unidentifiable, isolated plates of *Salenia*, possibly representing *S. tumidula*, have also been reported by Cooke (1941, p. 7) from the Paleocene Salt Mountain limestone of Alabama.

On a world-wide basis, eleven Tertiary species have been referred to the genus *Salenia*. These include the following species in addition to those recorded by Lambert and Thiéry (1911, p. 212; 1925, p. 567):

Paleocene

Salenia sp. of Cooke (1941, p. 7), Alabama.

Eocene

S. persica Clegg (1933, p. 8, pl. 1, fig. 3*a-d*), Iran.

Oligocene

'*Salenia uoenuprovincialis* Nisiyama MS' reported by Morishita (1960, p. 54) from the Oligocene of Japan (a *nomen nudum*).

Pliocene

Salenia (?) *hakkaidoensis* Loriol (1902, p. 29, pl. 3, fig. 1), Tokunaga (1903, p. 4, pl. 2, fig. 1), Morishita (1960, p. 54). This species has been referred to *Pleurosalenia* Pomel (a synonym of *Salenidia* Pomel) by all the above-mentioned authors. However, the specimen (the type?) illustrated by Tokunaga (1903, pl. 2, fig. 1) exhibits bigeminate ambulacral plates with non-crenulate ambulacral tubercles which are features suggestive of *Salenia*.

The earliest recorded occurrence of *Salenia* is that of *S. taurica* Veber (1934) from the Kimmeridgian of the Crimea. The genus is otherwise unknown from the Jurassic. The

greatest specific diversification was achieved in the Cretaceous. Mortensen (1935, p. 368) noted that about seventy-five nominal species had been described from Cretaceous deposits, and since that time at least fourteen nominal species have been added. The following nominal species of Mesozoic age in addition to those recorded by Lambert and Thiéry (1911, p. 212; 1925, p. 567) have been referred to *Salenia*. Some, as indicated, have been referred subsequently to other genera. With few exceptions no attempt has been made to evaluate the specific validity or stratigraphic allocation of these species.

- Salenia acupicta* Desor 1856, in Desor (1855–8), referred to *Hyposalenia* Desor.
S. alcaldei Sanchez-Roig (1949, p. 44, pl. 2, figs. 14–17), Maestrichtian, Cuba.
S. areolata Agassiz (1838), referred to *Hyposalenia*.
S. bella Szörényi (1955, p. 163, pl. 1, figs. 7–9), Cenomanian, Hungary.
S. bella parva Szörényi (1955, p. 164, pl. 1, figs. 21–23), Cenomanian, Hungary.
S. blanfordi Duncan and Sladen (1882), referred to *Salenidia* Pomel.
S. bonissenti Cotteau (1858–80), referred to *Salenidia*.
S. bunburyi Forbes, in Morris (1854), referred to *Hyposalenia*.
S. clathrata Agassiz, in Morris (1843), referred to *Hyposalenia*.
S. cottreani Lambert 1931, in Lambert (1931–2, p. 63, pl. 3, figs. 2–4, text-fig. 3), Neocomian, Algeria.
S. dombeensis triangularis Gregory (1916, p. 586, figure p. 587), Cenomanian, Angola; Darteville (1953, p. 16, fig. 2), Albian, Angola.
S. gibba Agassiz (1838), type species of *Salenidia*.
S. hawkinsi Checchia-Rispoli (1948, p. 169, text-figs. 1–2; plate figs. 1–4), Cenomanian, Somaliland.
S. heberti Cotteau (1861–7), referred to *Salenidia*.
S. heliophora Agassiz and Desor (1846), referred to *Hyposalenia*.
S. heliophora Sorignet (1850), referred to *S. grannlosa* Forbes.
S. hemisphaerica Agassiz (1836), referred to *Hemicidaris* Agassiz.
S. hoffmani Agassiz (1836), referred to *Hemicidaris*.
S. hondoensis Cooke (1953, p. 6, pl. 1, figs. 3–4). Possibly a synonym of *S. whitneyi* Cannon, in Ikins (1940).
S. kansasense Twenhofel (1924, p. 52, pl. 7, fig. 7), Comanchean, Kansas. Cooke (1946, p. 204) questionably refers this species to *S. mexicana* Schlüter.
S. keatingi Fourtau (1919, p. 38, pl. 1, fig. 3), ?Cenomanian (Bagh beds), India.
S. lamberti Checchia-Rispoli (1932, p. 6, pl. 2), Maestrichtian, Tripoli.
S. leanderensis Ikins (1940, p. 16, pl. 1, fig. 4a–c), Albian, Texas. Cooke (1946, p. 204) questionably refers this species to *S. volana* Whitney. From Ikins's description of the ambulacra (composed throughout of single plates, each bearing a crenulate tubercle), this species is probably referable to *Salenidia*.
S. jencorhodian Bronn (1848, p. 1107). New name for *Echinus areolatus* var. König (1825).
S. humulata Morris (1854), referred to *Goniophorus* L. Agassiz.
S. mathuri Chiplonker (1937, p. 61, pl. 6, fig. 3a–d), Cenomanian, India.
S. ornata Agassiz, in Morris (1843), referred to *Hyposalenia*.
S. peltata Agassiz (1836), type species of *Goniopygus* L. Agassiz.
S. pentagonifera Gras (1848), referred to *Hyposalenia heliophora* (Agassiz and Desor).
S. personata Agassiz and Desor (1846), referred to *S. petalifera* (Desmarest).
S. portlockii Forbes, in Morris (1854), referred to *S. geometrica* Agassiz.
S. pseudowhitneyi Ikins (1940, p. 17, pl. 1, fig. 5a–c), Campanian, Texas.
S. punctata Forbes, in Morris (1854), referred to *Hyposalenia wrightii* Desor.
S. saxigera Lamarck (1840), misspelling of *S. scutigera*?
S. scotti Ikins (1940, p. 18, pl. 2, fig. 1a–c), Albian, Texas. Cooke (1946) questionably refers this species to *S. mexicana*.
S. scripta Agassiz (1838, p. 8, pl. 1, figs. 9–16), locality unknown.
S. scutigera Cotteau (1861–7), referred to *S. geometrica* Agassiz.

- S. scutigera* Forbes, in Morris (1854), referred to *S. granulosa* Forbes.
S. scutigera hungarica Szörényi (1955, p. 165, pl. 1, figs. 15–17), Senonian, Hungary.
S. similis lastroensis Maury (1936, p. 269), middle Albian, Brazil. Possibly a synonym of *S. mexicana* Schlüter (Cooke 1946, p. 204).
S. somaliensis Hawkins, in Cox (1935, p. 48, pl. 6, fig. 9a–b, text-figs. 1–2), upper Senonian (?), British Somaliland.
S. stellulata Agassiz (1838), referred to *Hyposalenia*.
S. stenzeli Ikins (1940, p. 19, pl. 2, fig. 2a–c), Albian, Texas. Cooke (1946, p. 204) questionably refers this species to *S. volana* Whitney.
S. studeri Agassiz (1840), referred to *Hyposalenia*.
S. taurica Veber (1934, pp. 59, 86, pl. 9, fig. 6a–d; text-fig. 5), Kimmeridgian, Crimea.
S. tertiaria Tate (1877), referred to *Salenidia*.
S. triboleti Desor 1856, in Desor (1855–8, p. 151), referred to *S. prestensis* Desor.
S. trigeri Desor 1858, in Desor (1855–8, p. 448), Cenomanian, France.
S. trigonopyga Lambert (1933, p. 13, pl. 1, figs. 25–27), upper Turonian, Madagascar.
S. umbrella Agassiz, in Morris (1843), referred to *Hyposalenia*.
S. whitneyi Cannon, in Ikins (1940, p. 20, pl. 2, fig. 3a–c), Campanian, Texas.

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SYSTEMATIC DESCRIPTIONS

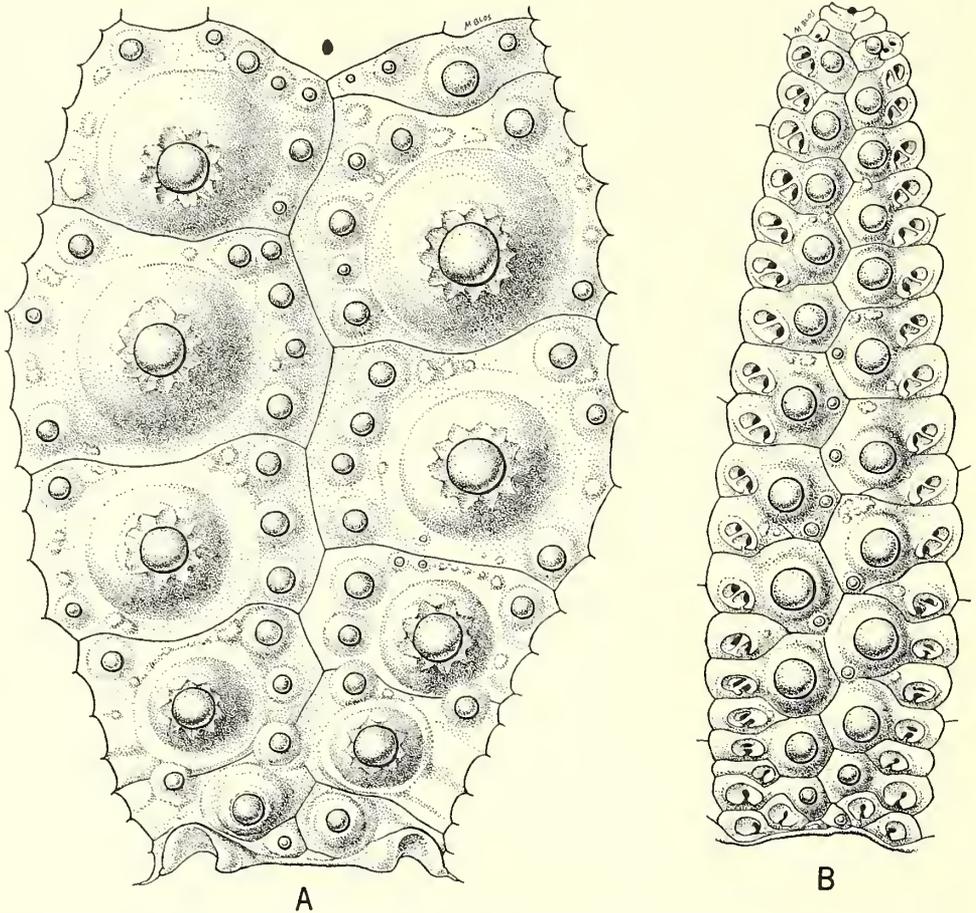
- Class ECHINOIDEA Leske
 Subclass EUECHINOIDEA Bronn
 Superorder ECHINACEA Claus
 Order HEMICIDAROIDA Beurlen
 Family SALENIIDAE Agassiz
 Subfamily SALENINAE Mortensen
 Genus SALENIA Gray 1835

Salenia scrippsae sp. nov. [by Zullo and Allison]

Text-figs. 3A, B; 4C, D; 6D–G; Plate 56, figs. 1–3

Description. Small (6 to 9 mm. in diameter, 3 to 5 mm. in height), white; test hemispherical with flattened oral surface; apical system slightly raised, covering most of aboral surface; ambulacra narrow, straight; ambulacral plates bigeminate except for few single plates interposed between bigeminate plates near apical system; pore-zones widening slightly at peristomial edge; primary tubercles of ambulacra non-crenulate, imperforate, coloured orange-red with tinges of green above ambitus, coloured white below ambitus, increasing gradually in size from apical system to ambitus, decreasing in size from ambitus to peristomial edge; few (5–7) secondary tubercles present between primary ambulacral tubercles near ambitus; interambulacra consisting of five to six plates per column; primary interambulacral tubercles crenulate, imperforate, coloured white,

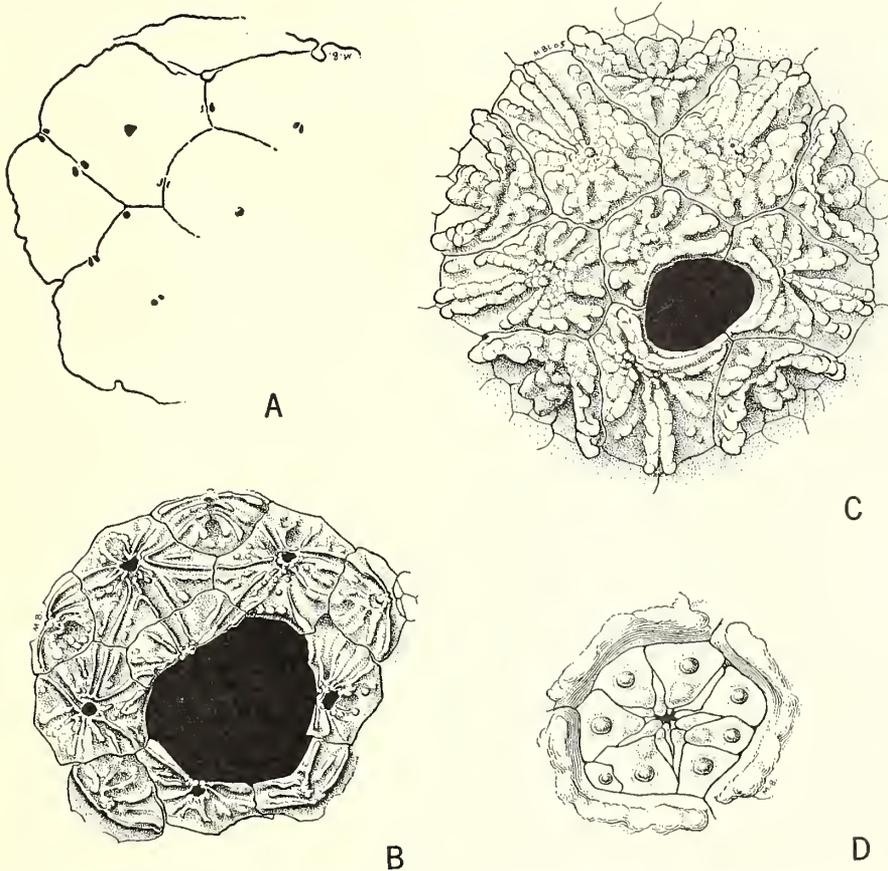
large and equal in size except near apical system and peristomial edge; areoles large, shallow, confluent throughout interambulacral column; secondary tubercles variable in number, not forming complete scrobicular circle; median area of interambulacra without tubercles, slightly sunken.



TEXT-FIG. 3. *Salenia scrippsae*, paratype UCMP no. 30758, $\times 24$. A, interambulacrum I. B, ambulacrum V.

Apical system with single, large angular suranal plate of regular pentagonal shape, except where notched on right posterior side by periproct; periproct to the right posterior between ocular I and the suranal plate; oculars exsert; genitals, including madreporite, of equal size; madreporite indistinguishable from exterior; madreporic pores visible on interior in small pit located in adapical part of plate; exterior surface of apical system highly ornamented by well-developed ridges and knobs; median ridges of genital plates and central knobs of oculars usually coloured yellow-green; other knobs and protuberances of apical system variously coloured white, yellow-green, or red; periproct bordered by elevated rim interrupted at the intersections of bordering apical plates

sutures of apical plates defined by shallow grooves in ornamented surface; proximal edges of oculars delimited by white or light green-tinted elevated ridge; genital pores located on distal margin of plates; both genital and ocular pores not observable from above, being covered by prolongations of the median ridge of the genital plates and the



TEXT-FIG. 4. A, Apical system of *Salenia* sp. aff. *S. mexicana*, hypotype, UCMP 30741, $\times 6$. B, Apical system of *S. schencki*, paratype, UCMP 30752, $\times 6$. C, Apical system of *S. scrippsae*, paratype, UCMP 30758 (periproctal plates not shown), $\times 12$. D, Detail of periproctal plates of *S. scrippsae*, paratype, UCMP 30757, $\times 20$.

central knob of the ocular plates respectively; periproct covered by imbricating whorls of small plates; each plate (numbering up to eight) of the outer whorl bearing a small spine and tubercle.

Peristome violet-tinged, with numerous, small, imbricating plates surrounding larger buccal plates; gill notches shallow.

Primary interambulacral spines above ambitus long (up to 24 mm. on holotype), slender, straight or slightly curved at distal end, longitudinally ribbed with a slight indication of verticillation, but not thorny, banded green and white, usually with bands or zones of pink or orange-red on either side of white bands; collar of spine short, finely

longitudinally striate; shaft of spine covered with cortex layer; milled ring finely striate; acetabular edge crenulate; transverse section of spine with small, central core with irregular holes throughout, thick median layer of radiating septa, and thin outer cortex; largest primaries at ambitus; interambulacral primary spines of oral surface coloured white, short, spear-shaped, flattened, longitudinally striate, occasionally with serrate edges; primary ambulacral spines short, broad, flat, longitudinally striate, coloured orange-red to dark brown-red, with yellow-green bases; secondary spines of interambulacra similar to ambulacral primaries in shape, but white in colour; secondary spines of ambulacra located between primary ambulacrals, short, stout, tinted yellow-green; spines of periproct light yellow-green and white in colour, short, stout, somewhat triangular.

Ophiocephalous pedicellariae (paratype UCMP 30763) present on and about apical system and also on peristomial plates; triphyllous pedicellariae (paratype UCMP 30763) present in ambulacral areas near ambitus; tridentate and claviform pedicellariae not observed.

Sphaeridia hyaline, ovoid, situated between tube feet and primary ambulacral spines at ambitus; a single sphaeridium situated in midline between ambulacral plates at peristomial edge.

Tube feet with well-developed sucking disk; lantern of stirodont type, with keeled teeth and open foramen magnum.

Name. This species is named in honour of the Scripps Institution of Oceanography, University of California.

Holotype. UCMP 30756. *Paratypes.* UCMP 30757-63.

Occurrence. Recent, 200-350 metres depth on an unnamed guyot, situated near the south-west end of Nasca Ridge, longitude 85° 25' W., latitude 25° 44' S., about 800 miles (1,280 kilometres) off the coast of Chile and 300 miles (480 kilometres) N. 85° W. of San Felix Island in the south-eastern Pacific. Dredged by the R.V. *Horizon* on 26 January 1958, during Expedition DOWNWIND, University of California-Scripps Institution of Oceanography IGY cruise to the south-east Pacific. UCMP locality B-6555 (listed as station HD-73 in Fisher 1958, table 8).

Discussion. *Salenia scrippsae* is readily distinguished from the other known living species of *Salenia* by its unique pattern of colouration, which consists of rows of orange- or brownish-red primary ambulacral spines and tubercles radiating from a greenish-white apical system flecked with spots of brownish-red. The tricolour banding of the primary interambulacral spines is also distinctive, differing from the solid greenish-white spines of *S. unicolor* and the white, or greenish-white, and red-banded spines of the other species (text-fig. 6E; Plate 56, fig. 1).

The ambulacral plates of *Salenia scrippsae* are not all bigeminate, as a few single plates alternate with the bigeminate plates near the apical system (text-fig. 3B). In this character *S. scrippsae* somewhat resembles species of the genus *Salenocidaris*. The ambulacra of

EXPLANATION OF PLATE 56

Fossil and extant representatives of the echinoid *Salenia* from the eastern Pacific.

Figs. 1, 3, 4. *Salenia scrippsae* sp. nov. 1, 3, Paratype UCMP 30956, oral and aboral views, $\times 4.7$.

4, Holotype, UCMP 30756, lateral view, $\times 2.3$.

Fig. 2. *Salenia* sp. aff. *S. mexicanus* Schlüter. Hypotype, UCMP 30741, lateral view, $\times 2$.

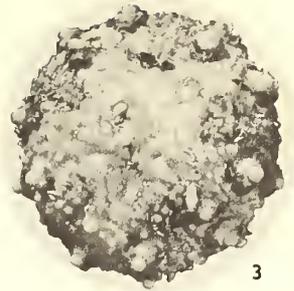
Fig. 5. *Salenia schencki* sp. nov. Block, UCMP 30755, showing distribution and abundance, $\times 0.6$.



1



2



3



5



4

Salenocidaris consists of single plates except for one to three near the distal end which are bigeminate (Mortensen 1935, p. 348). This condition, however, is evidently not confined to *S. scrippsae* in the genus *Salenia*, but also has been noted in some fossil species (Mortensen 1935, p. 348).

The ornamentation of the apical system of *S. scrippsae* is more complex than that of any of the previously described extant species (text figure 4C). The well-developed, angular, elevated ledge bounding the proximal side of the ocular plates is not dark in colour as it is in other species.

The primary interambulacral spines of *S. scrippsae* (text fig. 6E, F) are similar to those of *S. goesiana* in lacking distinct verticillation, but differ in bearing distinct longitudinal ribs, whereas the spines of *S. goesiana* are smooth.

Salenia scrippsae also differs from other extant species of *Salenia* in the possession of a single sphaeridium at the peristomial edge in the ambulacral midline. Mortensen (1935, p. 332) states that 'sphaeridia are found, usually two in number, at the peristomial edge of each ambulacrum, in the genus *Salenocidaris*', but notes that sphaeridia occur only in the region of the ambitus in species of the genus *Salenia*.

Salenia schencki sp. nov. [by Kaar]

Text—figs. 4B, 5, 6A–C; Plate 56, fig. 5

Description. Test large for genus (up to 15 mm. in diameter), circular in outline at ambitus, flattened orally and aborally; apical system somewhat elevated.

Ambulacra straight, narrow; ambulacral plates bigeminate; primary ambulacral tubercles crenulate; eight minute crenulations on each tubercle; each pore of pore-pair surrounded by ridge externally; pore openings flush with plate surface internally; marginal pore perpendicular to plate surface, inside pore oblique to plate surface, approaching marginal pore externally.

Interambulacra more than twice as wide as ambulacra; interambulacral plates with one large, crenulate primary tubercle on each plate; boss convex; eight to ten crenulations on each primary interambulacral tubercle; about five secondary interambulacral tubercles along marginal and intermarginal sutures of each plate.

Apical system without spines; periproct elliptical in outline, elevated, displaced to the right posterior, encroaching on suranal plate, ocular I, and genitals 1, 2, 4, 5; periproctal plates unknown; genital pore displaced distally from centre of genital plate; genital plates ornamented by serrated ridges with chevron pattern radiating from genital pores; periproct encroaching on all genitals except genital 3; ocular I insert, remaining oculars exsert.

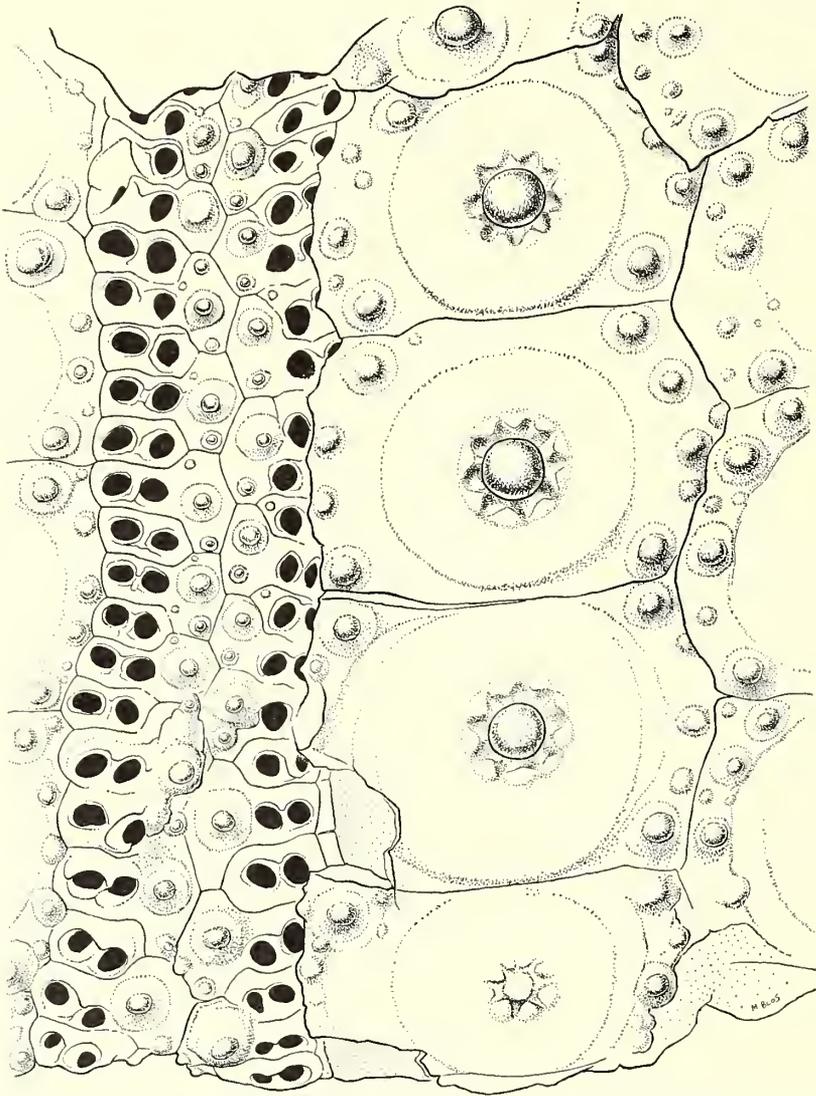
Primary interambulacral spines long, slender, nearly smooth, slightly curved toward distal end, occasionally with longitudinal ridges near distal end; tip of primary ambulacral spine occasionally flattened; marginal and secondary spines short, paddle-shaped; pedicellariae unknown.

Peristome concave; gill notches shallow; character of buccal and peristomial plates unknown; lantern stirodont.

Name. *Salenia schencki* is named after the late Dr. Hubert G. Schenck.

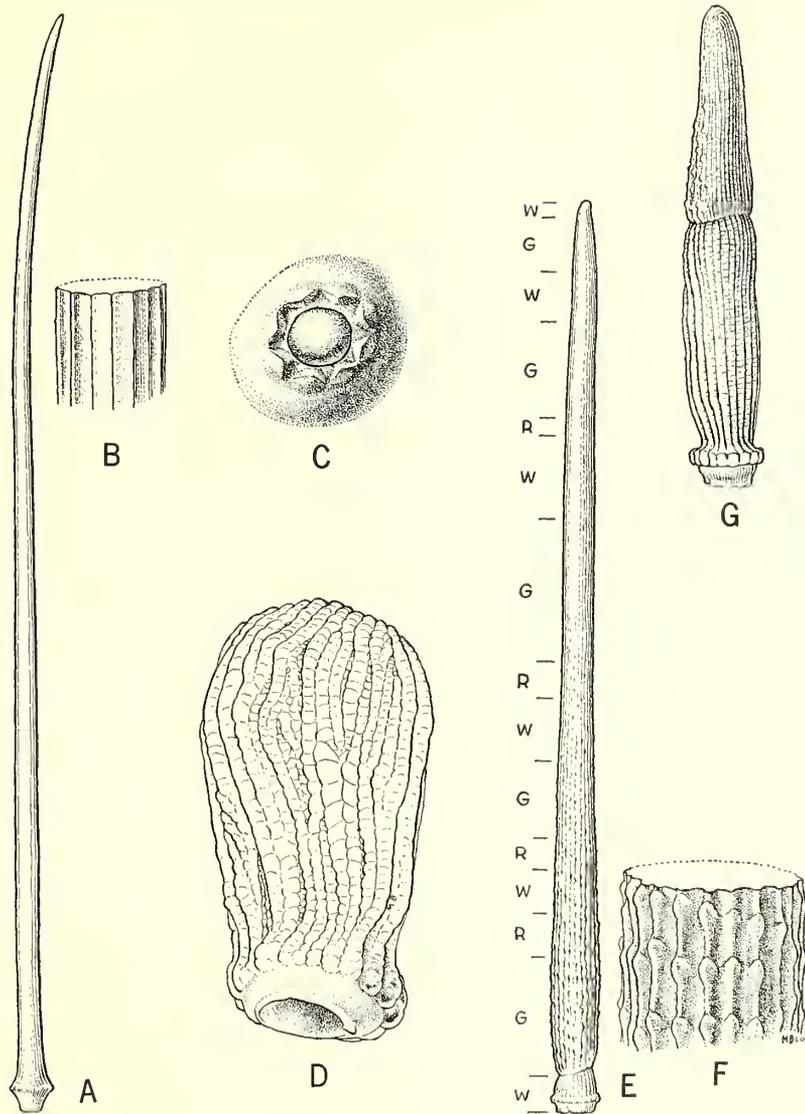
Holotype. UCMP 30751. *Paratypes* UCMP 30752–5.

Occurrence. Early Oligocene, upper half of the middle member of the Keasey formation, Oregon. UCMP localities A-5018 and A-8721. Fossils occur in grey, tuffaceous mudstone and fine-grained sandstone in the upper part of the Keasey formation exposed for about 200 yards along the west bank of the Nehalem River, approximately $\frac{1}{4}$ -mile upstream from secondary highway bridge and $\frac{1}{2}$ -mile upstream from town of Mist, Oregon.



TEXT-FIG. 5. Ambulacral and interambulacral detail of *Salenia schencki*, holotype, UCMP 30751, $\times 19.2$.

Discussion. *Salenia schencki* is characterized by crenulate primary ambulacral tubercles, nearly smooth primary interambulacral spines, and genital plates ornamented with about twelve serrated ridges radiating outward from the genital pore, and intercalated with smaller, discontinuous ridges which do not touch the genital pore.



TEXT-FIG. 6. A-C, *Salenia schencki*. D-G, *S. scrippsae*. A, Primary interambulacral spine, paratype, UCMP 30754, $\times 3.5$. B, Detail of ornamentation of paratype, UCMP 30754, $\times 21$. C, Primary ambulacral tubercle, paratype, UCMP 30753, $\times 36$. D, Primary ambulacral spine, paratype, UCMP 30759, $\times 48$. E, Primary interambulacral spine of ambitus, paratype, UCMP 30761, $\times 6$. Letters to the left of the figure indicate colour bands: W = white, R = red, G = green. F, Detail of ornamentation of paratype, UCMP 30761, $\times 24$. G, Primary interambulacral spine of oral surface, paratype, UCMP 30760, $\times 24$.

Salenia schencki compares with *S. tumidula* Clark as figured by Cooke (1959, p. 13, pl. 2, figs. 1-7) from the Paleocene Vincentown formation of New Jersey. These two species are somewhat similar in the overall size and shape of the corona, and in the radial pattern of the ridges on the apical plates, but *S. schencki* differs from *S. tumidula*

by having fewer radiating ridges on the apical plates and by the chevron pattern of these ridges. *S. schencki* differs further by having crenulated primary ambulacral tubercles with slightly convex bosses instead of slightly concave bosses, and by the somewhat larger periproct and peristome.

Salenia sp. aff. *S. mexicana* Schlüter

Text-fig. 4A; Plate 56, fig. 4

Hypotype. UCMP 30741.

Occurrence. Aptian-Albian, Alisitos formation, UCMP locality A-6278. From well-indurated, buff, weathering grey, silty sandstone in sea cliffs north of Punta San Isidro, Baja California, Mexico. Associated with numerous echinoids and pelecypods, small gastropods, sponges, an unidentifiable ammonoid, and several belemnoids.

Discussion. The single, partially crushed, incomplete specimen of *Salenia* collected from this locality is characterized by a strongly lobed apical system, narrow, somewhat sinuous ambulacra, and a large (diameter approximately 22 mm.) test. Except for its large size and the narrow, conic shape of the primary interambulacral tubercles, this specimen closely resembles the specimens of *S. mexicana* Schlüter described and figured by Böse (1910, p. 153, pl. 32, figs. 4-19) from the Vraconian (Albian) of La Encantada, Placer de Guadalupe, Chihuahua, Mexico. Maldonado-Koerdell (1953, p. 39) designated *S. mexicana* as a subspecies of *S. prestensis* Desor upon comparison of Böse's (1910) specimens with published figures of *S. prestensis*. In size the specimen resembles *S. texana* Credner, but can be distinguished by the strongly lobed apical system and the more widely spaced rows of primary ambulacral tubercles (see Cooke 1946, pp. 202-4, pl. 31, figs. 1-4 for a description of *S. texana*).

The fragmentary nature of the specimen from the Alisitos formation does not afford sufficient data to form an adequate conclusion regarding its affinities. From its size and the rather tenuous differences cited in the form of the primary interambulacral tubercles, it would appear that this specimen may represent a hitherto undescribed species closely resembling *S. mexicana*. However, until more complete and better preserved material is available, a more positive identification cannot be made.

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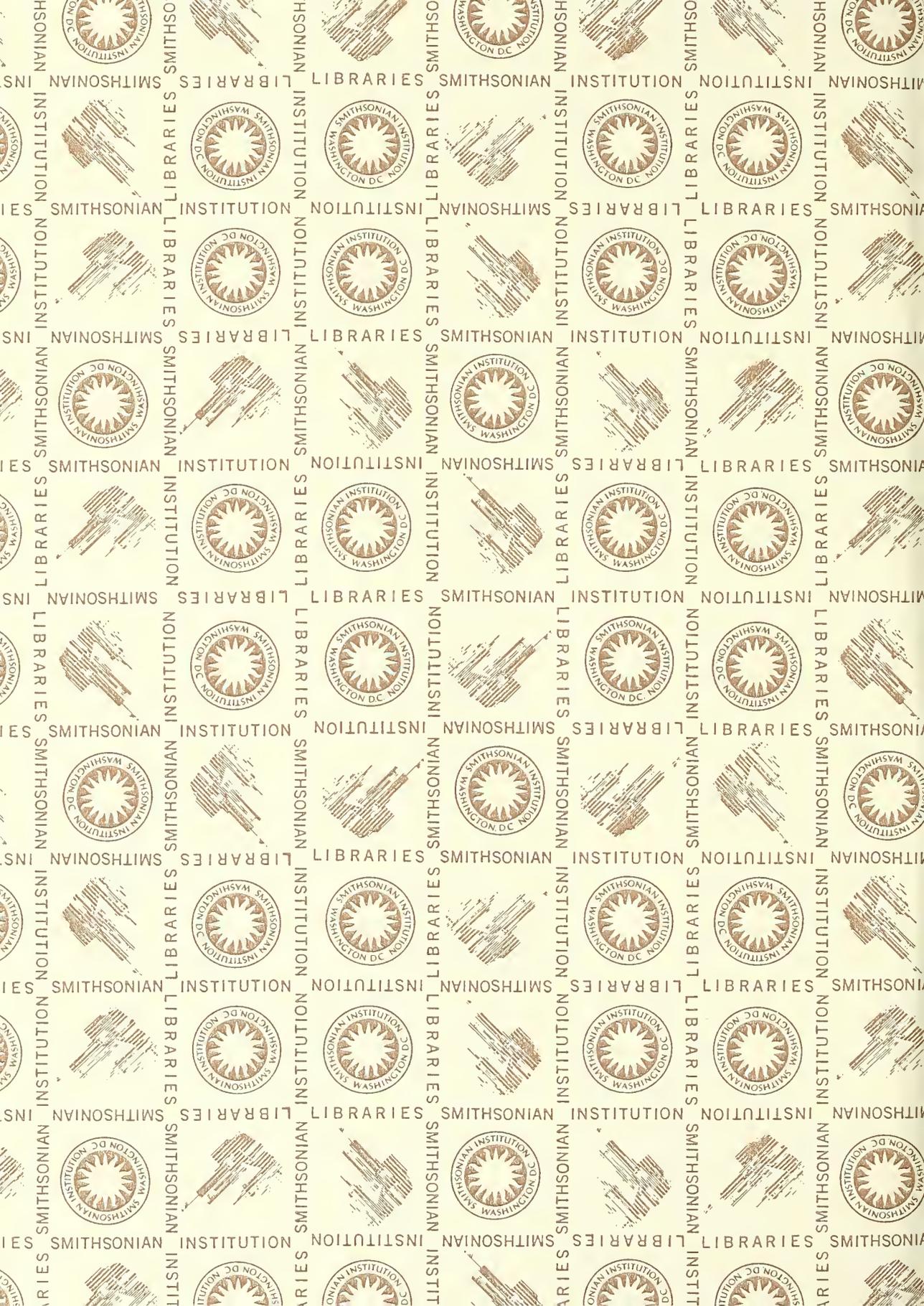
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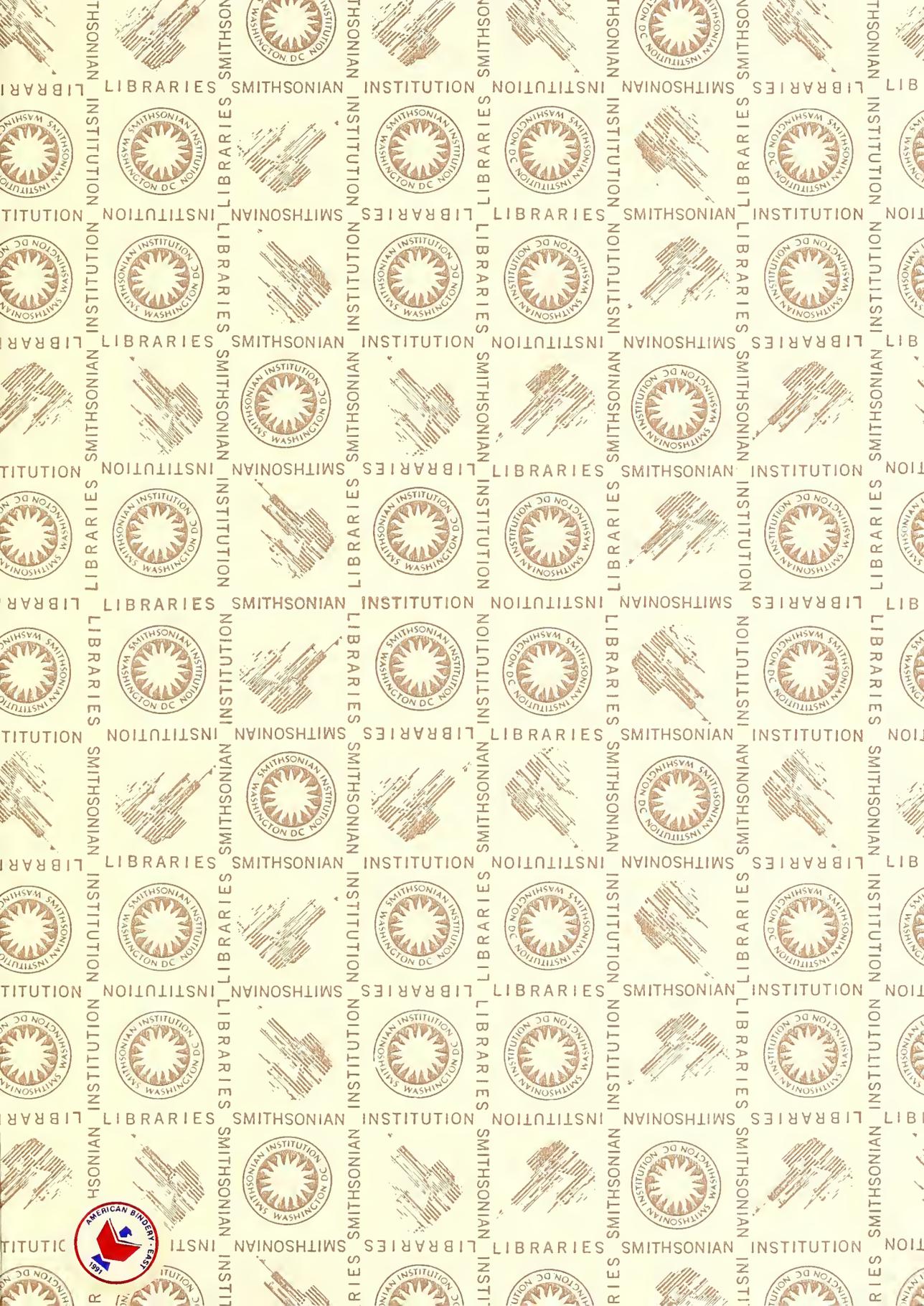
PALAEONTOLOGY

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