

VOLUME 5 · PART 3

Palaeontology

OCTOBER 1962

PUBLISHED BY THE
PALAEOLOGICAL ASSOCIATION
LONDON

Price £3

THE PALAEOONTOLOGICAL ASSOCIATION

The Association was founded in 1957 to further the study of palaeontology. It holds meetings and demonstrations, and publishes the quarterly journal *Palaeontology*. Membership is open to individuals, institutions, libraries, &c., on payment of the appropriate annual subscription:

Institutional membership.	£5. 5s. (\$15.50)
Ordinary membership	£3. 3s. (\$ 9.50)
Student membership	£2. 2s. (\$ 6.50)

There is no admission fee. Student members will be regarded as persons receiving full-time instruction at educational institutions recognized by the Council. Subscriptions are due each January, and should be sent to the Treasurer, Professor P. C. Sylvester-Bradley, Department of Geology, The University, Leicester, England.

Palaeontology is devoted to the publication of papers (preferably illustrated) on all aspects of palaeontology and stratigraphical palaeontology. Four parts are published each year and are sent free to all members of the Association. Members who join for 1962 will receive Volume 5, Parts 1 to 4.

Volumes 1 (4 parts), 2 (2 parts), 3 and 4 (4 parts each) are still in print, and may be purchased separately at a cost of £2 (\$6) post free for each part; orders should be sent to the approved agents, Messrs. B. H. Blackwell, Broad Street, Oxford, England.

Manuscripts on all aspects of palaeontology and stratigraphical palaeontology are invited. They should conform in style to those already published in this journal, and should be sent to Mr. N. F. Hughes, Sedgwick Museum, Cambridge, England. A sheet of detailed instructions for authors will be supplied on request.

ADDENDUM

Plate 36 (Vol. 5, Part 2) : scale lines on figs. 1-3 represent 500μ ,
and those on figs. 4-7, 100μ .



THE PALAEOLOGY OF THE NAMURIAN ROCKS OF SLIEVE ANIERIN, CO. LEITRIM, EIRE

by the late PATRICIA J. YATES

ABSTRACT. On Slieve Anierin the Lower and Upper *Eumorphoceras* Stages of the Namurian contain an unbroken sequence of faunas; these are described in detail for the first time in Ireland. The simple geological structure enables marine bands to be collected in their undoubted order of superposition, in contrast to some equivocal sections elsewhere in Britain. Shale is the dominant rock type throughout the succession, but a thick grit, with coal seams, occurs in the lower part of E₂.

The faunas of the marine bands consist dominantly of goniatites and lamellibranchs, the most common goniatite genera being *Eumorphoceras*, *Cravenoceras*, and *Cravenoceratoides*, with *Anthracoceras* and *Dimorphoceras* abundant at certain levels. The goniatite species have relatively short time ranges and are unsurpassed for the recognition of zones and subzones. The lamellibranch species usually have longer time ranges, but are also shown to be valuable stratigraphically, supplementing the goniatites. The following new species and subspecies are described: *Eumorphoceras rostratum*; *E. bisulcatum erinense*, *ferrimoutanum*, and *leitrimense*; *Posidonia corugata elongata* and *gigantea*; *Caneyella membranacea horizontalis*; *Obliquipecten costatus*; *Posidoniella variabilis erecta*; and *Chaenocardiola bisati*.

Detailed stratigraphical correlations are made with beds of the same age in Ireland, the Pennine region in England, north-west Europe (notably Germany and Belgium), and North America. Some important revisions in correlation are suggested, and the remarkable extent of Namurian goniatite-lamellibranch faunas is demonstrated.

Editorial note. Miss Yates died on 7 August 1960 at the early age of twenty-eight, only five days before the examination of a thesis she had prepared for the Ph.D degree of the University of London. Since this work is a major contribution to Carboniferous stratigraphical palaeontology, it has been edited for publication (with the consent of her brother, Dr. E. M. Yates, Department of Geography, King's College, London) by Dr. W. H. C. Ramsbottom (Geological Survey Office, Ring Road Halton, Leeds 15) and Dr. Gwyn Thomas (Department of Geology, Imperial College, London, S.W.7). The title of the thesis has been retained for this paper, and the editors have not introduced material not known to the author or published since her death. Thanks are due to Mrs. Judith Creighton for undertaking the difficult task of sorting the author's manuscripts and cataloguing her extensive collections.

Repository. Copies of the author's thesis (containing some palaeontological descriptions not included in this paper) are in the Watts Library of Geology, and the author's collection is housed in the Murchison Museum, Department of Geology, Imperial College, London. Registration numbers without a prefix in the paper refer to specimens in this collection. Specimens in the Geological Survey Museum which are referred to in the text have the prefix GSM, and those from the British Museum (Natural History) the prefix BM.

Localities. Fossiliferous localities on Slieve Anierin, including those in P₁ and P₂, are shown on text-figs. 2, 3, and 4, and listed in the Appendix. Each Irish Ordnance Survey 6-inch sheet has been divided into sixteen quadrants; the figure in brackets following the sheet number is the number of the quadrant in which the locality referred to may be found, and is followed by the locality number, e.g. Leitrim 20(8)1, abbreviated to L20(8)1. It has been found necessary to renumber the specimens and localities mentioned in Yates (1961); a check list of the new numbers is given in the Appendix (section 2).

Abbreviations. The only departure from the normal custom of abbreviation of generic names to the initial letter is the use of *Ct.* for *Cravenoceratoides*, in order to avoid confusion with *C.* for *Cravenoceras*.

Authorship of species and subspecies. The authorship of the chief species and subspecies mentioned in this paper is as follows: *Anthracoceras glabrum* (Bisat), *A. paucilobum* (Phillips), *A. tenuispirale*

[Palaeontology, Vol. 5, Part 3, 1962, pp. 355-443, pls. 51-62.]

Demanet; *Cravenoceras africanum* Delépine, *C. cowlingense* Bisat, *C. gairense* Currie, *C. holmesi* Bisat, *C. leion* Bisat, *C. malhamense* (Bisat), *C. subplicatum* Bisat; *Cravenoceratoides bisati* Hudson, *Ct. edalense* (Bisat), *Ct. lirifer* Hudson, *Ct. nitidus* (Phillips), *Ct. nititoides* (Bisat), *Ct. stellarum* (Bisat); *Dimorphoceras looneyi* (Phillips); *Eumorphoceras angustum* Moore, *E. bisulcatum* Girty, *E. bisulcatum grasingtonense* Dunham and Stubblefield, *E. bisulcatum varicata* Schmidt, *E. girtyi* Elias, *E. hudsoni* Gill, *E. medusa* Yates, *E. medusa sinuosum* Yates, *E. plummeri* Miller and Youngquist, *E. pseudobilingue* (Bisat) emend. Moore, *E. pseudobilingue A* Bisat, *E. pseudobilingue C* Bisat, *E. pseudocoronula* Bisat, *E. rota* Yates, *E. sp. form A* Moore, *E. stubblefieldi* Moore; *Girtyoceras limatum* (Miller and Faber), *G. meslerianum* (Girty); *Goniatites elegans* Bisat, *G. falcatus* Roemer, *G. granosus* Portlock; *Kazakhoceras scaliger* (Schmidt); *Lyrogoniatites newsomi georgiensis* Miller and Furnish; *Neodimorphoceras hawkinsi* (Moore); *Nuculoceras nuculum* Bisat; *Sudetoceras alaskae* Gordon, *S. crenistriatum* (Bisat), *S. newtonense* Moore.

Actinopteria fluctuosa (Etheridge), *A. persulcata* (M'Coy); *Caneyella membranacea* (M'Coy), *C. wapanuckensis* (Girty); *Chaenocardiola footii* (Baily), *C. hahotoidea* (Roemer); *Dunbarella elegans* (Jackson); *Euchondria levicula* Newell; *Obliquipecten laevis* Hind; *Posidonia becheri* Bronn, *P. corrugata* (Etheridge), *P. lamellosa* (de Koninck), *P. trapezoedra* Ruprecht; *Posidoniella sulcata* (Hind), *P. variabilis* Hind; *Pseudamusium praetenuis* (von Koenen).

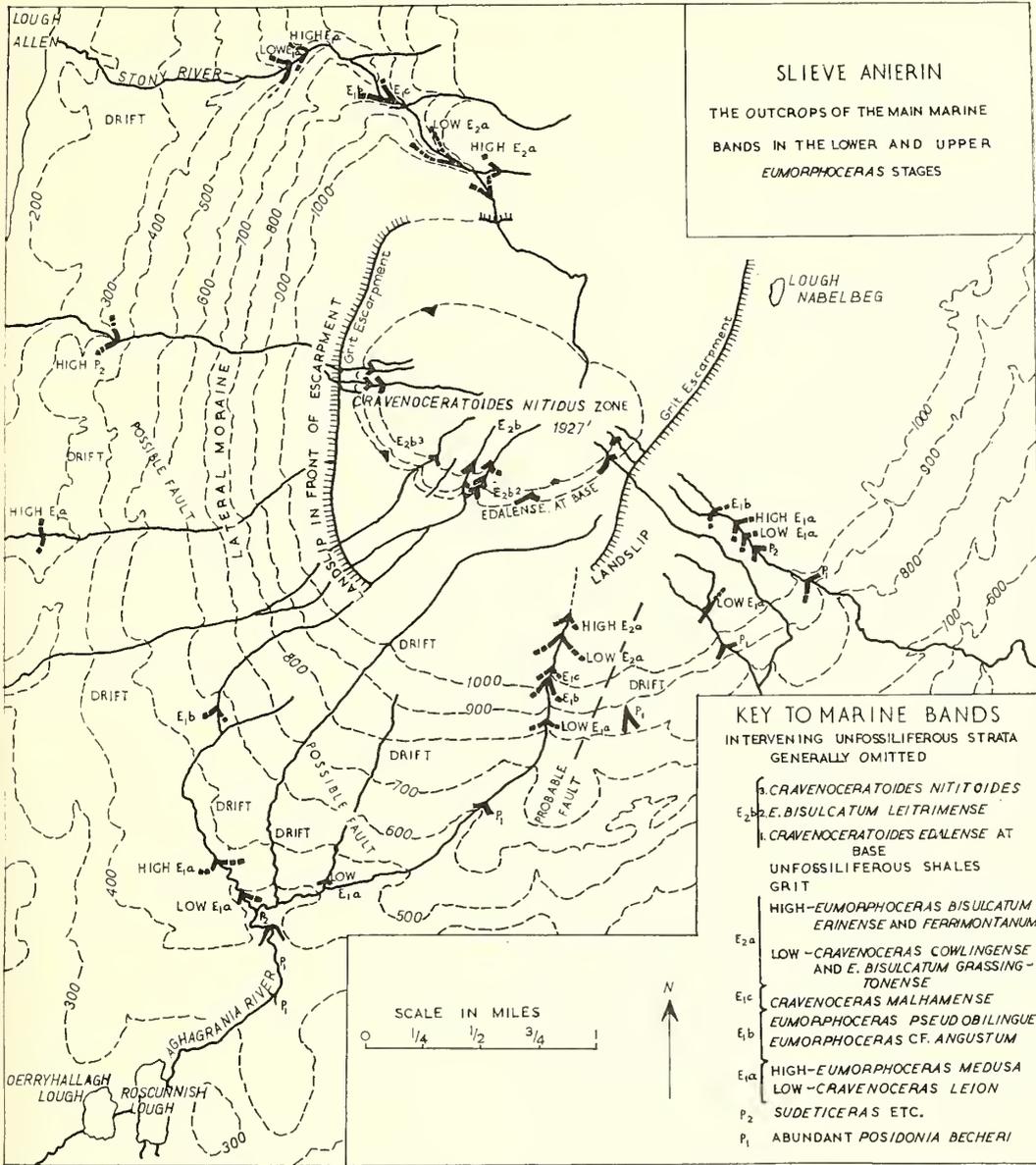
Leiorhynchus carboniferus polypleurus Girty, *Lingula parallela* Phillips, *Orbiculoidea nitida* (Phillips), *Productus hibernicus* Muir-Wood; *Thrinoceras hibernicum* (Foord), *Stroboceras subsulcatus* (Phillips), *Cycloceras purvesi* Demanet; *Mourlonia striata* (de Koninck); *Archaeocidaris urii* (Fleming); *Weberides* cf. *W. shumnerensis* (King); *Coleolus nanurcensis* Demanet.

THE goniatite zones established by Bisat had not been extensively applied in Ireland until Hodson (1954a) made the first attempts to interpret previous records and discover new fossiliferous localities in Co. Clare; this led to a fuller understanding of Upper Carboniferous palaeontology and palaeogeography in Ireland and gave this field of study a great stimulus.

The *Eumorphoceras* Stage has not previously been the subject of detailed study in Ireland. Smyth (1950) described part of E₂ in North Co. Dublin but as this was only a portion of a larger work the description was not detailed; furthermore the complex structural pattern made the interpretation of the succession difficult. Nevill (1957) described the Summerhill Basin, Co. Meath, but again no detailed study of the faunas was possible.

At Professor Hodson's suggestion a reconnaissance was made of Benbrack Mountain, which lies south of Cuilcagh (2,188 ft.) (see Padget 1953), on the borders of Co. Fermanagh and Co. Cavan, but although *Eumorphoceras bisulcatum* Girty (GSM 95317) was collected from the summit the exposures were thought to be too poor for further work. Slieve Anierin (1,927 ft.), which lies south-west of Benbrack in Co. Leitrim, proved to be more suitable, since a virtually continuous succession from basal P₁ up to E₂b is for the most part well exposed in stream sections, the E₁ and E₂ beds being particularly fossiliferous; moreover the area is fortunately not complicated structurally (text-fig. 1).

In the north of England there are many records of exposures of beds from the E₁ and E₂ Zones but no really continuous section is available except from borehole records. Hudson and Cotton (1943, pp. 142-73) described the E₁ and E₂ succession from a borehole in Alport Dale in Derbyshire. Although a borehole section is obviously of considerable value in establishing the order of superposition of many previously isolated records, there are equally obvious advantages in being able to collect over a continuous succession of beds, concentrating on particularly fossiliferous levels and obtaining a



TEXT-FIG. 1. Map of Slieve Anierin showing the outcrops of the main marine bands in the Lower and Upper *Eumorphoceras* Stages.

far wider picture of the fauna at such levels than can possibly be obtained from one borehole core. The value of the exposed succession on Slieve Anierin thus lies in the unbroken sequence of faunas which it provides. The fauna is described and figured, and correlations made with other areas.

Slieve Anierin lies in an area of Upper Carboniferous rocks which extends from the

southern tip of Lough Allen northwards for about 30 miles to the northern extremity of Lough Erne. At its greatest width this outcrop stretches for about 20 miles westwards from Swanlinbar in the east. The outcrop narrows northwards and is interrupted by a deep embayment of Carboniferous Limestone in the Belcoo area, to the north of which it widens again but rapidly narrows towards Lough Erne. Slieve Anierin lies at the southern end of this mass on the eastern side of Lough Allen.

Slieve Anierin is a flat-topped mountain with a prominent grit escarpment, which from a distance is easily mistaken for the summit of the mountain; in fact 200 feet of shales form a small residual outlier overlying the grit. The solid geology is virtually limited to stream sections by a thick obscuring mantle of peat bog and glacial drift below the grit escarpment (text-fig. 1), while high-level peat bog forms a thick mantle over most of the upland plateau above. The rocks are normally horizontal or only very gently dipping (up to about 5°), except in landslipped areas.

Previous work. Slieve Anierin was first mapped for the Geological Survey of Ireland by R. J. Cruise, and the results were published in 1876 on 1-inch Sheet 67. An explanatory memoir appeared in 1878, written by Cruise with palaeontological notes by W. H. Baily. The map shows Lower Coal Measures at the summit of the mountain overlying Millstone Grit, in which there are coal-seams; the slopes of the mountain below the Millstone Grit are mapped as Yoredale Beds (shales with ironstones).

Much of this memoir is devoted to the Arigna Mountains on the west of Lough Allen, including Kilronan to the south and Altagowlan further north, which are still being mined for coal. The coal from Kilronan was first used around 1788 to smelt the clay-ironstone bands which are very prolific in the lower shales. Despite glowing reports of the great economic possibilities of the coals on the Arigna Mountains by Griffith (1818) and by later authors, the history of the Connaught coalfield has hardly fulfilled early expectations. Du Noyer (1863) published a map of the mountains to the west of Lough Allen, gave the coal analyses earlier published by Kane (1845) and stated that the coalfield had 'little prospect of ever being properly developed'.

In the 1878 memoir it is stated that there are two coal-seams within the grit on Slieve Anierin corresponding with the lowermost (or Crow Coal) and the Middle Coal on the Arigna Mountains. Above the grit the Lower Coal Measures are said to be brown and black splintery shales attaining a considerable thickness and apparently without the top coal seam seen on Altagowlan. However, the Dail Commission of Inquiry into the Reserves and Industries of Ireland (1921, p. 132) reported that there was no information on the top coal but that it was said to exist on Altagowlan and on Slieve-an-Iarain but not on Kilronan. Altagowlan, being 300 feet higher than Kilronan, contains the upper strata including the third seam. On Slieve Anierin there is certainly no coal seam above the grit escarpment and it seems unlikely that it exists on Altagowlan either.

Boate (1652) said that 'The mountains on the east side of Lough Allen are so full of this metal, that thereof it hath got in Irish the name Slew Neren, that is, mountains of iron'. Hull (1878, p. 38) refers to Slieve-an-Ierain (or the Iron Mountain), and describes shales with rich beds of ironstone, regarded as the Yoredale Shales of the north of England, overlain by the Millstone Grit. He also refers (pp. 39, 40) to Gannister Beds or Lower Coal Measures, 600 feet in thickness, with two or three seams of coal and several beds containing marine genera such as *Phillipsia*, *Orthoceras*, *Goniatites*, *Productus*, *Pallustra*, *Orthis*, &c. These beds are said to occur on the tops of the hills bordering Lough Allen. They are now proved to be of E₂ age on Slieve Anierin.

In a later work Hull (1881, pp. 330-3) published a section, based on one given by Du Noyer (1863, p. 84, fig. 4), dealing with the area west of the Lough and showing three coal-seams on Kilronan and two on Altagowlan. Du Noyer's original section in fact carries the two seams on Altagowlan over to the other side of the Lough to Slieveanierin Mount. The recognition of this third seam on Kilronan by Du Noyer and by Hull thus appears to be at variance with the memoir, which places a third seam on Altagowlan but not on Slieve Anierin or Kilronan. The Memoir, in turn, differs from the Dail Commission which, although admitting that no information was available on this seam, placed it on Altagowlan and on Slieve Anierin.

Cole and Halissy (1924, pp. 31, 32) do not differentiate between Kilronan and Altagowlan but refer

only to Arigna. They mention only a lower and upper coal, the inference being that they only believed in the existence of two coal-seams, but this is never actually stated. They suggest (p. 32) that the upper coal is in true Coal Measures 'which here remain only as a capping to the highest hills'. Later Charlesworth (1953, p. 93) referred to a Leitrim Coalfield, specified three coal-seams and reproduced Hull's figure (originally taken from Du Noyer). He also subscribed to the view that some Lower Coal Measures occurred in this area. The succession on Slieve Anierin does not get higher than the Namurian.

The geology of Cuilcagh, to the west of Swanlinbar, was described by Padget (1953, pp. 17-27) but the details of the faunas given by him are disappointing, since they might be expected to correlate with the succession on Slieve Anierin. The great grit escarpment on Slieve Anierin corresponds to that on Cuilcagh, and yet the E_2 horizons which can be demonstrated to exist below the grit on Slieve Anierin do not seem to have been found on Cuilcagh. It is possible, however, that scree in the Sruh Croppa (the stream which Padget (p. 19) refers to as yielding the most complete succession) may have obscured the horizons below the grit which are better exposed on Slieve Anierin. Cuilcagh appears to have been a much more visited mountain than Slieve Anierin; Phillips (1836, introduction, p. 15) describes a visit made to Cuilcagh from Florence Court, the home of the Earl of Enniskillen, where he was staying with Sedgwick, Murchison, Griffith, Sir Phillip Egerton, and Agassiz.

Caldwell (1959, pp. 163-89, pl. 6), in his account of the Lower Carboniferous rocks of the Carrick-on-Shannon Syncline, describes the lithology and fauna of the Roscunnish Shales in the Aghagranian River; they are of P_1 and P_2 age and immediately underlie the author's basal E_1 beds.

The highest faunal band on Slieve Anierin is of E_2 age and thus the summit is in Namurian deposits and not in true Lower Coal Measures. The *Gastrioceras subcrenatum* Marine Band, which is the horizon used in western Europe to define the base of the Lower Coal Measures, has been detected in the Leinster Coalfield (Nevill 1956), where true Lower Coal Measures are in fact present, but on Slieve Anierin there is no indication of it or of stages H and R.

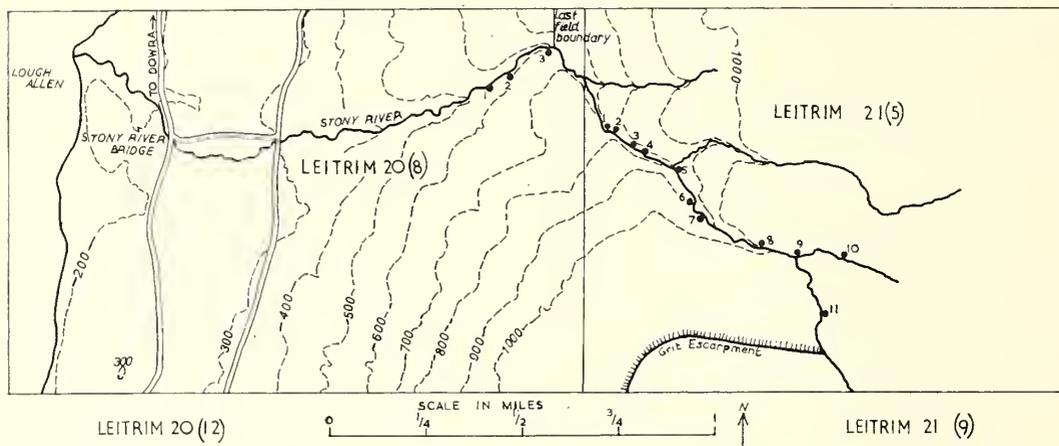
The Millstone Grit with Coal Seams of the Memoir (1878) is clearly the grit which forms the escarpment on the mountain. Since it can now be demonstrated that *Eumorphoceras bisulcatum* occurs beneath this grit and *Cravenoceratoides edalense* almost directly above it, the grit must therefore lie within E_2 . The *Ct. edalense* beds are considered to be at the level of *Ct. bisati*, which also occurs but is much less common. Hudson (1945) has placed the *Ct. bisati* subzone at the base of the *Ct. nitidus* zone. It is thus possible to assign the grit to E_{2a} or E_{2b} , but for convenience the *edalense* beds themselves are considered to be the base of E_{2b} and the grit assigned to E_{2a} . Both the grit and the beds above it are therefore placed in the Arnsbergian stage of the Namurian (Hudson and Cotton 1943, p. 152).

The two coal-seams within the grit marked on the 1-inch geological map may, with some difficulty, be traced along the grit escarpment on the western side of the mountain. On the southern flanks, however, they are completely obscured by drift deposits, but are misleadingly continued as broken lines on the map.

An attempt was made in 1957 to mine the lower coal-seam about 400 yards west of the Rocking Stone but the level was abandoned. The coal is poor in quality and the seams are probably impersistent. On the eastern side of the mountain there is another abandoned level to the west of the track on Leitrim 21(9). An old coal level is marked on the 6-inch map to the east of the track, but has not been found; it may be the one mentioned by Cruise (1878) as being above Aughacashel House and in the upper seam, which was found to be 1 foot thick. The level to the west of the track is certainly in the lower seam (about 3 ft. 6 in. thick). Coal-seams are not unknown from within the Millstone Grit series elsewhere, though they are usually poor in quality; e.g. the Bradley Coal

occurs within the Skipton Moor Grit, of E_1 age, in the Bradford and Skipton area (Stephens *et al.* 1953, p. 17).

The so-called Yordale Beds extend down to the Lough edge on the west and to the top of the Carboniferous Limestone on the south and south-east. The term Yoredale is not particularly well chosen for these beds. The name was first used by Phillips (1836, pp. 36–37), with the type section in Wensleydale. Hudson (1926, pp. 125–35) subsequently amplified the term and described the Yoredale Beds as essentially a shallow-water series in which a rhythmic unit passing from shale through sandstone to limestone is continually repeated; goniatites are rare in these deposits. The shales on Slieve Anierin are in no way comparable with such a succession. At the base of the succession occur



TEXT-FIG. 2. Map showing the northern area of fossiliferous localities on Slieve Anierin, including the Stony River.

limestones, calcareous mudstones, and sandstones which are known to be of P_1 and P_2 age but from the base of the Namurian upwards shales were deposited continuously until the grit horizon. The only variation within this series is a greater concentration of clay ironstone bands at certain levels. They are a notable feature on Slieve Anierin; in the Stony River in particular the large nodules which weather out of these bands are seen plentifully in the river bed. Some bands in the shales are extremely fossiliferous and goniatites are very abundant, together with lamellibranchs. The succession has more in common with that described by Parkinson (1936, pp. 318–19) for the Upper Bowland Shales of the Slaidburn district of Yorkshire, where at least 400 feet of shales with goniatites and lamellibranchs as the common fossils succeed the P_2 beds. The onset of the Pendle Top Grit, however, occurs a short distance above *C. malhamense*, i.e. at a lower horizon than the grit on Slieve Anierin.

The 1-inch geological map shows some faulting of the grit and overlying shales but no supporting field evidence has been found. Impressive landslides have occurred along the western face of the mountain and at the south-western and south-eastern corners; the faults are all thought to be due to a failure to appreciate the magnitude of the landslipping. A fault shown on the 1-inch map between Slieve Anierin and the mountain to the north is continued as a broken line across the upper reaches of the Stony River but

the faunal band exposed at L21(5)11 does not appear to be displaced. Two faults have been inferred on the basis of displacement of faunal bands on the southern flanks of the mountain; it is impossible to do more than tentatively suggest the position of these faults (text-fig. 1).

Acknowledgements. It is my pleasant duty to acknowledge all the assistance I have received during the course of this work. Mr. W. S. Bisat has been a constant source of advice and encouragement on all matters relating to the goniatites; his unflinching interest has always been an invaluable stimulus. Dr. Gwyn Thomas has read and criticized this manuscript and has given much assistance over all aspects of this work. Mr. Murray Mitchell has provided easy access to material at the Geological Survey Museum, and in particular I am grateful for the ease with which I have been able to borrow specimens to photograph. Dr. W. H. C. Ramsbottom has also rendered assistance in discussion on several points. Professor Hodson must be thanked for my first introduction to the Namurian of western Ireland and for advice on photography. Thanks are also due to the Central Research Fund of the University of London for several grants towards field expenses. (The editors also wish to express their appreciation of the generous grant received from the Central Research Fund to defray the cost of the collotype plates in this paper.)

FAUNAL SUCCESSION

Throughout the succession lamellibranchs and goniatites are particularly abundant and in numbers of individuals and of species are dominant over all other groups.

The number of goniatite genera is small; *Eumorphoceras*, *Cravenoceras*, and *Cravenoceratoides* are the most important and their various species are representative of definite levels in the succession. *Anthracoceras* and *Dimorphoceras* are abundant at certain levels, but are considered to be less valuable because of the difficulties of identifying species when no sutural evidence is available; only one species of *Anthracoceras* is of real value in indicating a precise stratigraphical level.

At the horizons in which *Anthracoceras* or *Dimorphoceras* abound, other goniatite genera usually do not occur in any abundance and are sometimes absent. This probably reflects differences in the conditions under which the two groups of genera flourished, a phenomenon which has already been observed in deposits of this age. Hudson and Cotton (1943, p. 151) believed that the *Anthracoceras*—*Dimorphoceras* faunas could exist in sea water less saline than normal. Bisat, Duncan, and Moore (1931, p. 4), commenting on the occurrence of *Anthracoceras* in the Upper Limestone Series of Scotland and in the Coal Measures of England, believed that this genus could withstand conditions which could not be tolerated by other goniatite genera. In beds on Slieve Anierin in which *Dimorphoceras* and *Anthracoceras* abound, these goniatites are usually associated with *Posidonia* and *Posidoniella*. These two lamellibranchs also occur abundantly with the other goniatite genera but appear to be the only genera able to survive the conditions in which *Anthracoceras* and *Dimorphoceras* flourished. It seems, however, that *Anthracoceras* had greater powers of resistance to a less favourable environment than even these two lamellibranchs, since over considerable barren thicknesses of shale with only plant fragments and *Lingula*, a stray *Anthracoceras* can still occasionally be found, but no lamellibranchs.

It is a matter for conjecture why certain levels were so extremely fossiliferous and why conditions then were so suitable for goniatites and lamellibranchs. Hudson and Cotton (1943, p. 150) suggested that salinity was a controlling factor. At periods of maximum freshwater intake, and therefore low salinity, the faunas were unable to survive; at

periods when the freshwater intake was low and the salinity correspondingly high normal marine populations were able to flourish. An additional factor, however, has to be considered in the Slieve Anierin area, since the unfossiliferous shales frequently contain numerous clay-ironstone bands, often separated by only a few inches of shales. At these horizons the amount of iron in solution may well have made conditions intolerable for marine organisms, even those like *Dimorphoceras*, *Anthracoceras*, or *Lingula* which could tolerate low salinity.

At most of the fossiliferous levels in the Namurian beds on Slieve Anierin the number of individuals is usually very high whereas the number of species and genera is low. Two of the richest levels in genera and species are both in E₂ deposits. The lower yields about twelve species, the assemblage consisting entirely of goniatites and lamellibranchs, apart from some crinoidal debris and a nautiloid. The highest faunal band on the mountain is undoubtedly the richest in numbers of individuals, genera, and species, and in the diversity of the groups represented; apart from the ubiquitous goniatites and lamellibranchs there are brachiopods, trilobites, gastropods, fish remains, bryozoa, echinoid spines and plates, and crinoidal debris. It is also the most narrowly concentrated band, extending through only about 10–12 inches of rock. Other faunal bands, with far fewer species and consisting entirely of goniatites and lamellibranchs, extend through 10–12 feet of strata.

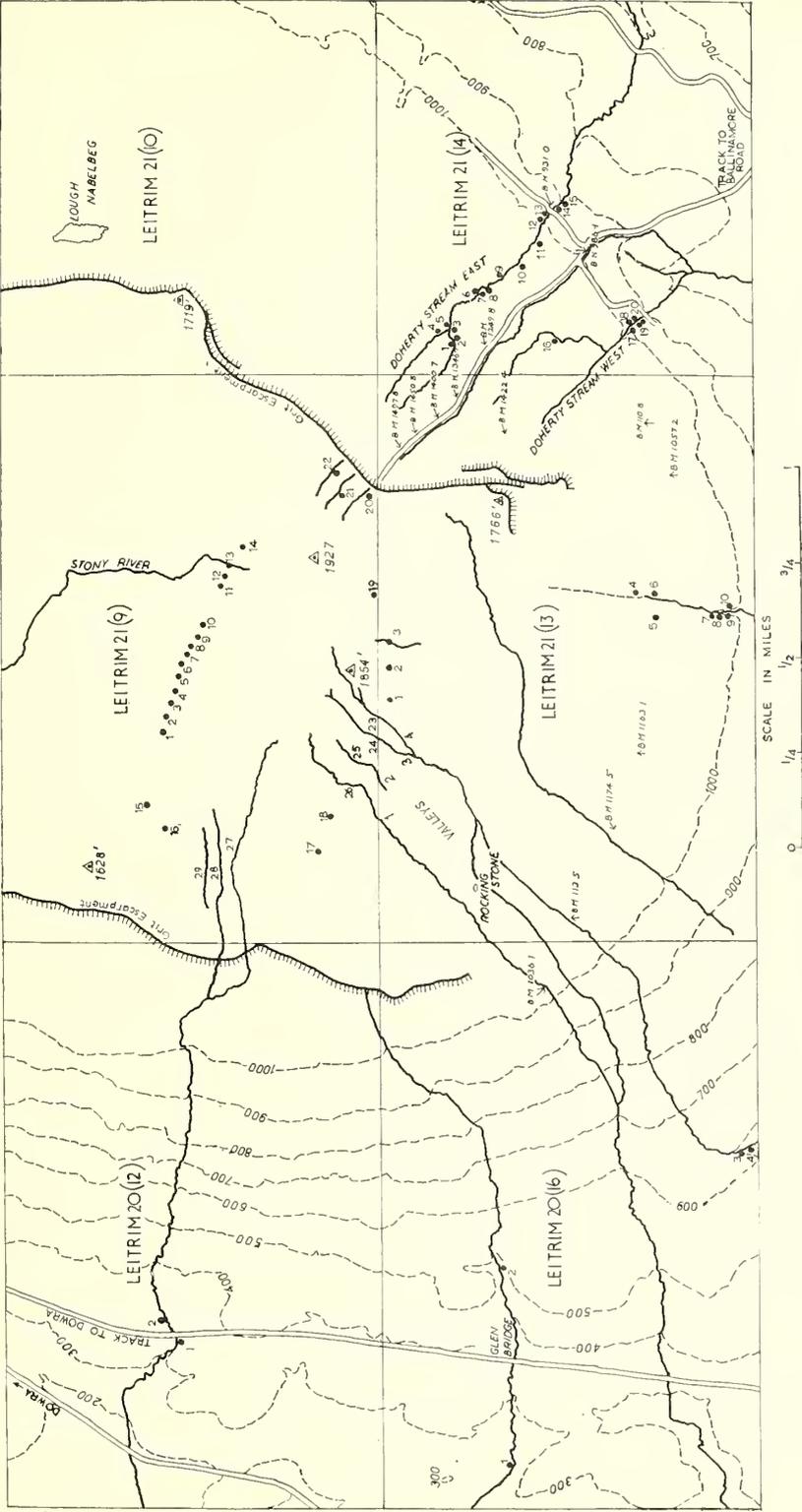
During P₂ times in the Slieve Anierin area, the deposition of argillaceous material became increasingly important and there was a diminution in the more calcareous shallower-water deposits which were laid down in P₁ and previous periods. By early Namurian times shales were the established lithological type. The shales of fossiliferous horizons are fairly solid and tough, and frequently split into large slabs, but those of the intervening unfossiliferous horizons are noticeably far more fissile and fragmentary, a slight tap with a hammer usually resulting in a cascade of small splinters of shale.

P₁-P₂ Faunas

The shales between the Carboniferous Limestone and the Millstone Grit were originally mapped as Yoredale Shales, but the succession in no way resembles the Yoredale succession in Yorkshire. In addition to the systematic study of the Namurian shales on Slieve Anierin, some collecting was also carried out in the Upper Viséan deposits (P₁ and P₂) which outcrop on the lower slopes of the mountain, chiefly on the southern and south-eastern sides, in order to trace the base of the Namurian (text-figs. 1, 3, 4).

Caldwell (1959, pp. 178–80) has given some details of the P₁ and P₂ beds in the Aghagrania River, where the succession is best seen, but the beds are only broadly divisible into the subzones established elsewhere on the basis of goniatites. Hodson and Moore (1959, pp. 384–96) were able to collect beautifully preserved goniatites in P_{1b} on Dough Mountain, farther north in Co. Leitrim, thus accentuating the very poor and scanty material available on Slieve Anierin at least in P₁.

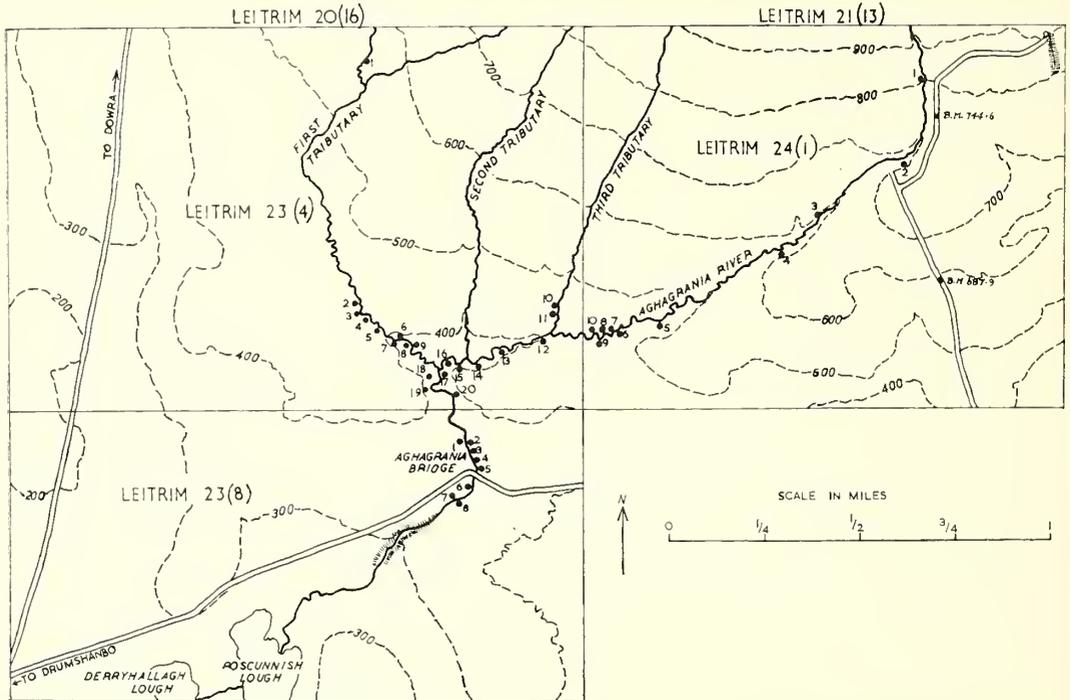
The succession in the Aghagrania River consists (see also Caldwell 1959) of alternations of shales, calcareous mudstones, mudstones, and muddy limestones. At Aghagrania Bridge a sandstone 20 feet thick is exposed. There is also an intercalation of decalcified limestone north of the bridge at L23(4)19, where the section is at least 30 feet high; there are many sandy seams, and the whole exposure has a curiously slumped appearance. *Goniatites*, broadly referred to the *striatus* group, has been collected below the



TEXT-FIG. 3. Map showing the central area of fossiliferous localities on Slieve Anierin.

sandstone south of Aghagrania Bridge, together with *Posidonia becheri*, *Thrinoceras hibernicum*, poor pleurotomariid gastropods, brachiopods, and orthoceratids. North of the bridge, above the sandstone intercalation but below the decalcified beds, *P. becheri* continues to be very abundant and occurs with rarer *Dunbarella elegans*, *Mourlonia striata*, rare spines of *Archaeocidaris urii*, and rare *Goniatites* cf. *G. falcatus*.

Above the decalcified beds there is a slight improvement in the faunas; softer mud-



TEXT-FIG. 4. Map showing the southern area of fossiliferous localities on Slieve Anierin, including the Aghagrania River.

stones are present at the base of L23(4)19 but shales become the dominant rock type at about 8 feet above the base of this section and, apart from occasional hard calcareous mudstone bands, apparently continue at least to the base of E_1 . At about 3 feet above the base of L23(4)19 *Leiorhynchus carboniferus polypleurus* occurs in abundance, while in a mudstone 3 feet above this again there are abundant examples of *Goniatites granosus* associated with *Sudeticeras* cf. *S. crenistriatum*. The genus *Sudeticeras* with crenulate radials is typical of P_2 deposits while *G. granosus* is very abundant in the *G. granosus* subzone (P_{2a}) elsewhere. At about 20 feet above the base of this section *Sudeticeras* sp. is abundant in shales, accompanied by very rare *G. granosus*, and with the first appearance of *Caneyella membranacea* s.l., which has not been seen lower in the succession. *P. becheri* does not occur at these P_2 levels, in contrast to its extraordinary abundance lower in the succession. *P. corrugata* becomes common in P_2 at about the same time as *Caneyella*, although it may also occur lower than *Caneyella*. *Dunbarella* continues into these P_2 levels. The problematical striated tube-like structure *Coleolus namurcensis*

Demagnet, which also occurs rarely in P_1 beds, is very abundant in the lower beds at L23(4)19. Another feature noted at about the level at which *Caneyella* appears in the upper part of L23(4)19 is the appearance of a thin, compressed and sharp-ventered goniatite referred to *Kazakhoceras* sp.; this species continues into E_1 and may in part be the same form as that mentioned and figured by Nevill (1957, p. 296, pl. 22, figs. 6, 7).

Two other exposures continue the succession. Locality L20(12)1 yields *C. membranacea* s.l. and *Sudeticeras* cf. *S. newtonense*. The presence of *Caneyella* indicates an horizon at least as high as the highest band at L23(4)19. *S. newtonense* is placed high in the succession of species of this genus (Moore 1950, p. 47). Locality L23(4)16 (which is close to L23(4)9, where basal E_1 beds are exposed) yields *C. membranacea* s.l. and *Lyrogoniatites newsomi georgiensis*. Bisat (1950, p. 12) refers the latter to a band at the top of the Viséan.

A clay-like band with a rich and varied fauna occurs at L23(4)17 and also high in the section at L23(4)15. At the latter locality, however, basal E_1 material occurs in the scree in front of the section and is believed to come from a horizon not far above the clay band which, although it has a rich fauna including two lamellibranch species which become very abundant in undoubted E_1 beds, does not itself include E_1 goniatites. The fauna of the clay band includes *Weberides* sp., *Chonetes* sp., *Lingula* cf. *L. parallela*, *P. corrugata*, *Pseudamusium* cf. *P. praetenuis* and *Obliquipecten costatus* sp. nov.

Various exposures are seen along the course of the Aghagrania River to the east of L23(4)18 and most are high in P_2 and below the basal E_1 band which is present at L23(4)9 and at high levels in L23(4)15. Farther north-east there are exposures of the decalcified beds seen just south of L23(4)19. The decalcified limestones are often extremely white and cherty, and rusty sands also occur. These beds have not been collected exhaustively but have yielded *Productus* sp. and crinoidal debris. A good exposure of these decalcified beds occurs at L24(1)1 with an excellent exposure of basal E_1 farther upstream at L24(1)1. Unfortunately the intervening exposures are inaccessible, but this is the part of the succession which is exposed, at least in part, at L23(4)19.

Farther north-east in Doherty Stream East (L21(14)14 and 15) there is a succession of alternating shales, mudstones, calcareous mudstones, and limestones similar to the succession south of Aghagrania Bridge. *P. becheri* and *Goniatites* of the *striatus* group (see Hodson and Moore 1959) occur. Beds very rich in *P. becheri* occur at L21(14)12. At L21(14)11 and in a deep gorge to the north-west, at least 40 feet of sandstone horizons and some sandy shales occur, containing only poor brachiopods and *Dunbarella* sp.; these beds have been correlated with the sandstone at Aghagrania Bridge. At L21(14)10 a hard calcareous mudstone occurs at the base, overlain by about 10 feet of pale, decalcified and sandy beds reminiscent of the decalcified beds seen in the Aghagrania River at L23(8)1.

In Doherty Stream East L21(14)9 yields only *C. membranacea* s.l., and is therefore some distance up in the P_2 succession. At L21(14)8 there is a rich faunal band which is the equivalent of that seen at L24(1)1 and is undoubtedly basal E_1 in age. The section in this stream is therefore broadly comparable with the main Aghagrania River section, although the good goniatite material above the decalcified beds is not exposed in it, the only faunal evidence for P_2 being *C. membranacea*.

In Doherty Stream West, rich *P. becheri* beds occur at L21(14)17 to 20 and are probably partly equivalent to those seen at L21(14)12 in the eastern stream. The overlying

40 feet of sandstones and soft sandy shales (with some coaly layers) are at an equivalent horizon to L21(14)11 in the eastern stream. No further exposures occur in Doherty Stream West until L21(14)16, where beds with *Cravenoceras leion* indicate an E₁ horizon.

It is suggested that the sandstone horizon seen at Aghagrania Bridge thickens north-eastwards in this direction, while the underlying limestones and calcareous mudstones are more numerous at the expense of the shale and mudstone horizons. It is not possible, however, to estimate whether the whole succession is actually thicker than in the Aghagrania River, since the top of the Cavetown Limestone which lies below the P₁ beds is not exposed; the Cavetown Limestone is well exposed in the lower reaches of Doherty Stream East. The north-easterly thickening of the P₁ sandstone would not be inconsistent with the appearance of a sandstone horizon at the base of the 'Yoredale Shales' on Cuilcagh (Padget 1953; and Irish Ordnance Survey Maps 67 and 56), where the lowest collected horizon in the Yoredale Shales is P₁b.

Pendleian and Arnsbergian faunas

The appearance of *Eumorphoceras* and *Cravenoceras* at the base of the Namurian is a striking event in the sequence of goniatite faunas and the former genus is used as a name for the basal division of the Namurian; beds are said to be of Lower or Upper *Eumorphoceras* Age (E₁ or E₂ respectively). Several of the stage names originally suggested by Bisat (1928, pp. 125-30) have now been replaced by others. The most important for the present study are Pendleian, proposed by Hudson and Cotton (1943, p. 152) to replace Bisat's Grassingtonian for beds of Lower *Eumorphoceras* Age, and Arnsbergian, proposed by the same authors for beds of Upper *Eumorphoceras* Age to replace Bisat's Lower Sabdenian.

These stages are further subdivided into zones and subzones:

Stage	<i>E₂ Zones and Subzones</i>	
	Zone	Subzones
Arnsbergian	<i>Nuculoceras nuculum</i>	{ <i>Nuculoceras nuculum</i> <i>Cravenoceratooides nititoides</i>
	<i>Cravenoceratooides nitidus</i>	{ <i>Cravenoceratooides stellarum</i> <i>Cravenoceratooides nitidus</i> <i>Cravenoceratooides bisati</i>
	<i>Eumorphoceras bisulcatum</i> s.s.	(Not divided)

This table is based on a portion of one published by Hudson (1945, p. 2). The inclusion of the *Nuculoceras nuculum* zone in the Sabdenian (*Homoceras* Age) is the practice adopted in the Bradford and Skipton Memoir (Stephens *et al.* 1953, p. 95) but does not concern the present work.

The succession of zones within the Pendleian Stage adopted in the same Memoir (op. cit., p. 91) is as follows:

<i>E₁ Zones</i>	
<i>Cravenoceras malhamense</i>	E ₁ c
<i>Eumorphoceras pseudobilingue</i>	E ₁ b
<i>Cravenoceras leion</i>	E ₁ a

The appearance of *Eumorphoceras* and *Cravenoceras* at the base of the Pendleian on Slieve Anierin is accentuated by the relative poorness of the P₃ and P₁ faunas in the area.

The genus *Girtyoceras*, from which *Eumorphoceras* probably evolved, is here absent from the P_2 and P_1 horizons, but elsewhere appears to have been fairly abundant at the end of P_2 times. Moore (1946, pp. 387–445, pl. 22–27) described several new species of *Girtyoceras* from horizons in Lancashire and Yorkshire ranging from B_2 to P_2 . Bisat (1936, pp. 533–4) suggested that *Cravenoceras* was probably derived from *Beyrichoceratoides*, which is found elsewhere in the Viséan zone B, and lingers on sporadically into E_1 but after P_1a is never common. In the Slieve Anierin area there are no deposits of B age, and P_1a beds (although probably present south of Aghagrania Bridge) yield only very poor *Goniatites* sp.

(a) *Cravenoceras leion* zone (E_1a). Reference has already been made to the clay band with a rich fauna devoid of goniatites which is believed to be just under the base of E_1 at L23(4)15 and 17. At L24(1)1 and at L21(14)8 the faunas consist of *Eumorphoceras pseudocoronula*, *E. rota*, *C. leion*, *P. corrugata*, *Chaenocardiola bisati* sp. nov., *Pseudamusium praetenuis*, *Kazakhoceras* sp. Above this rich fauna there are beds several inches thick with only *Caneyella membranacea*. *P. praetenuis* was also a prominent member of the clay band seen elsewhere without goniatites and believed to be slightly lower than this material. *Caneyella* was frequently abundant towards the top of P_2 where it was associated with *Sudetoceras*.

At L23(4)9 and at L20(8)1 slightly later E_1 faunas occur. The most abundant goniatite is *C. leion*, mostly in the form of very small young individuals. Specimens of *Eumorphoceras* are extremely rare and are referred to *E. pseudocoronula*; at L20(8)1 a possible *E. cf. E. sp.* form *A* Moore also occurs. The fauna is dominated by *Obliquipecten costatus* sp. nov., which is so abundant that the beds are reminiscent of those in P_1 dominated by *P. becheri*. In the clay band just under the base of E_1 *O. costatus* sp. nov. was associated with other lamellibranchs, brachiopods, and trilobites; at this higher level in E_1 it is extremely abundant and continues through at least 2 feet of beds. *Chaenocardiola bisati* sp. nov. does not continue from the lower level at L24(1)1.

At L23(4)7 there are beds extremely rich in *E. pseudobilingue A* and *C. leion*, the latter of normal adult size; no lamellibranchs occur.

The sequence of faunas described so far is contained within about 10 feet of sediment, in contrast to some later levels where one fauna appears to continue through this thickness with little or no change. At the base of E_1 there is a rapid succession of faunas in a short vertical sequence, with scarcely any unfossiliferous sediments (see Table 1).

After *E. pseudobilingue A* the next species in ascending sequence to occur in great abundance is *Posidonia trapezoedra*, which extends through 10 feet of shales. This form is believed to be very close to *P. corrugata* seen lower in the succession but has strong radial corrugations in addition to the concentric folds, and a very characteristic outline as the name implies. In the lower part of its range it is associated with *Kazakhoceras* sp. which is believed to be the same form with a carinate venter as that seen high in P_2 .

The succeeding beds consist of a narrow band with *E. medusa*, which is closely related to *E. pseudocoronula* seen very near the base of E_1 . Stray specimens of *Kazakhoceras* sp. also occur at this level, with *P. trapezoedra* and *P. corrugata*, but the dominant lamellibranch is *Pseudamusium praetenuis*, which occurs sparsely with *E. pseudocoronula* near the base of E_1 . Very rare specimens of *C. leion* are still present. *E. medusa sinuosum* has

been collected at L23(4)2 from what is believed to be a later horizon and where it is still associated with *P. trapezoedra*; a rare example has also been collected at L20(8)2 where the beds are dominated by *E. medusa*, as at L21(14)6 and 7. The highest fossiliferous level in the *C. leion* zone apparently occurs at L23(4)2.

Some of the goniatites referred to as *Kazakhoceras* sp. may correspond to those referred to by Nevill (1957, p. 296, pl. 22, figs. 6, 7); they have a notched venter, and appear in P₂ and E₁. There are also some extremely large compressed specimens, so far only seen at L24(1)1, which have a sharp venter, an ornament very like a *Dimorphoceras* with two forward bows in the striae between the umbilicus and the venter, but which possess a definite nautiloid suture.

The series of faunas so far described occur in rapid succession within about 30 feet of beds. Within this comparatively small thickness of rock the genus *Eumorphoceras* shows a rapidly evolving series of species, reflecting a period of great activity following the inception of the genus. In contrast, *Cravenoceras* appears to have been more conservative, and one species, *C. leion*, which it has not been possible to subdivide, persisted with the several species of *Eumorphoceras* throughout the succession.

There follows a considerable thickness (up to about 100 feet) of unfossiliferous sediments. Ironstone bands are a feature of these beds, though they are not so frequent as later in the succession, and stand out from the shales which form dreary and steep exposures on either side of the Stony River.

(b) *Eumorphoceras pseudobilingue* zone (E₁b). This portion of the succession can be seen in the Stony River to the north, and in the headwaters of the Aghagrania River to the south, and close correlation exists between these two areas (text-figs. 1-4).

The unfossiliferous shales with ironstones are followed by beds with fairly abundant *Eumorphoceras* cf. *E. angustum*, but with the conservative *Posidonia* stock persisting together with the *Kazakhoceras* sp. from E₁a. The first species to appear above the unfossiliferous horizon at L21(5)1 and 2 is *P. trapezoedra*, which was also the last to be seen in E₁a. The two goniatite species have been collected not only in the Stony River at this level but also in the Aghagrania River at L21(13)9 and 10. No new species of *Cravenoceras* occur at this level nor indeed any evidence of the genus.

E. cf. *E. angustum* probably has its maximum abundance in the upper parts of the *P. trapezoedra* beds. In Doherty Stream East, at L21(14)5, it is seen abundantly with *P. corrugata*, *P. trapezoedra*, and *Kazakhoceras* sp. above a considerable thickness of unfossiliferous shales with clay-ironstone bands which succeed the last indications of the *C. leion* zone with *E. medusa* at L21(14)6.

Succeeding the beds with *E.* cf. *E. angustum* there are beds with abundant *E. pseudobilingue* s.s. occurring in large flat slabs of dark-grey shale characteristic of this level, e.g. at L21(5)4 (c. 20 feet), and L23(4)1. It is associated with less abundant examples of the two species of *Posidonia* seen lower in the succession; rare specimens of *Chaenocardiola footii* also occur.

Fifteen feet of similar beds occur in the Aghagrania River at L21(13)8; at the base occurs a thin band, which is also seen at L21(5)4, above the beds with *E. pseudobilingue* s.s.; it is dominated by *P. corrugata*, most of which are very small; it also yields rare *Chaenocardiola footii* and *Cycloceras purvesi*. At this level occur a few specimens of a *Eumorphoceras* which is neither *E. angustum* of the lower horizon nor *E. pseudobilingue*

s.s., which at L21(5)4 is collected directly below it. It is referred to as *E. pseudobilingue* C. The nature of the ribbing in these specimens is very like that of *E. pseudobilingue* s.s. but the decided groove at the shoulder is unlike the latter. The sparse collecting contrasts with the abundance of *E. cf. E. angustum* and *E. pseudobilingue* s.s. below. Between L21(13)9 and 10, and 8, there is an overgrown waterfall where collecting is difficult, and this is the level at which *E. pseudobilingue* s.s. occurs at L21(5)4.

Above the harder *pseudobilingue* material is a barren succession 8–10 feet thick, also seen at L21(14)1 and 4 in Doherty Stream East, with many horizons of very thinly leaved shales which still weather out into particularly large rectangular slabs. No clay-ironstone bands occur. They are overlain by the calcareous horizon with *C. malhamense* (E_1c).

(c) *Cravenoceras malhamense* zone (E_1c). Within 40 feet or less of beds it is possible to distinguish a lower group of goniatites which culminates in *E. pseudobilingue* s.s. followed closely by *E. pseudobilingue* C and an upper group in which there are no specimens of *Eumorphoceras* but in which the most common goniatite is *C. malhamense*, with far less common *Kazakhoceras scaliger*. As yet no undoubted specimens of *E. bisulcatum* have been seen and the beds are still regarded as Pendleian. Elsewhere in E_1 , e.g. in the borehole section from Alport Dale in Derbyshire (see Hudson and Cotton 1943, pp. 167–8), the *C. leion* zone is succeeded by the *E. pseudobilingue* s.s. zone and then the *C. malhamense* zone (E_1c). This division is also applicable on Slieve Anierin, where the last two zones are concentrated into a relatively thin sequence, though in the absence of faunal evidence it is impossible to determine the exact position of the unfossiliferous beds below *Eumorphoceras* cf. *E. angustum* within E_{1a} or E_{1b} . It is noticeable that on Slieve Anierin the beds with *Eumorphoceras* in E_{1b} do not contain any species of *Cravenoceras* and the reverse is true in the higher beds with *C. malhamense*. However, this was not so at the E_{1a} levels where the two genera occur in apparently equal abundance.

At the base of L21(5)5 a hard calcareous mudstone, 1 foot thick, yields *C. malhamense* and is overlain by fairly solid shales which fracture irregularly. At about 1 foot above the hard mudstone the shales become thinly leaved and contain abundant *Caneyella membranacea* through a thickness of about 3 feet of beds; *C. malhamense* is more sparse than in the lower calcareous horizon, and *Kazakhoceras scaliger* also occurs. The doubts over the true affinities of the latter are mentioned on p. 393 but as the ornament seems unmistakable and as it is clearly indicative of certain levels, Schmidt's specific name has been retained here. This is the lowest horizon at which this species has been collected during the present work. At L21(13)7 in the Aghagrania River it occurs with *C. malhamense* above *E. pseudobilingue* C; specimens of *Actinopteria persulcata* also occur, but this species has not been collected elsewhere on Slieve Anierin at this level.

The fossiliferous beds are succeeded by an unfossiliferous sequence 150 feet thick similar to the lower one separating the E_{1a} and E_{1b} fossiliferous levels, except that here the clay-ironstone bands are far more numerous and are often separated by only a few inches of unfossiliferous strata. Upstream from L21(5)5 the sections in the Stony River take on the dreary character (already seen below the *E. angustum* beds) of high exposures of very friable shales with frequent ironstone bands which diminish in frequency upwards, particularly through the upper 50 feet or so of beds.

(d) *Cravenoceras cowlingsense* fauna (Low E_2a). The next fossiliferous level is exposed in the Stony River, and can be traced along the sides of the valley high above the unfossiliferous sediments until at L21(5)9 it occurs at stream level and forms a prominent waterfall. Collecting from this horizon is easiest at L21(5)9, but it is also accessible at L21(5)8 some distance above the river bed. The same horizon is exposed in the Agha-grania River at L21(13)5 and 6; the former locality occurs high on the valley side and the total thickness is not exposed; at the latter the entire horizon is present, overlain by unfossiliferous beds.

The beds at these levels are more arenaceous than those lower in the succession but never show the large rectangular slabs which are characteristic of the *E. pseudobilingue* beds. The sequence is about 20 feet thick and the fauna, which is poor in species and also in individuals compared with lower and higher levels, remains the same throughout. It is dominated by *Cravenoceras*, and the specimens are all believed to belong to *C. cowlingsense* Bisat. One rare specimen displays a suture-line and it is very like the suture figured for this species by Hudson (1941, p. 281) from material collected by him in Mirkfell. A few rare specimens of *E. bisulcatum* s.l. were collected, and therefore this faunal band is the first in E_2 . The specimens are figured and described, and are compared with *E. bisulcatum grassingtonense* Dunham and Stubblefield (1944, pp. 258–60, pl. 11, figs. 4a–c). The only other goniatites at this level are poor specimens of Dimorphocera-tids which, in the absence of sutural evidence, are of little value.

A rare specimen of *Stroboceras subsulcatus* (Phillips) was also collected; this form was also noted at lower levels in E_1 . *Chaenocardiola footii* and the ubiquitous *P. corrugata* continue from lower levels, but *P. trapezoedra*, which occurs in great abundance lower down, has not been found at this level. *P. lamellosa* occurs but is never abundant, and might at first sight be easily mistaken for *P. becheri* from P_1 beds, though there are significant differences.

These beds are succeeded by 40–50 feet of very friable unfossiliferous shales, again with frequent clay-ironstone bands which are particularly abundant in the middle 20 feet of the sequence.

(e) *Eumorphoceras bisulcatum* fauna (High E_2a). The fauna of the next fossiliferous horizon is still dominantly a cephalopod-lamellibranch fauna, though a great deal of crinoidal debris occurs, for the first time above the more calcareous horizons of the Viséan. Sedimentation was slower at this time than in the earlier period when the beds with *C. cowlingsense* were being deposited.

The horizon, which is estimated to be only 6–8 feet thick, is rich both in numbers of species and individuals when compared with the lower fauna with *C. cowlingsense* as the dominant goniatite seen at L21(5)8 and 9, and at L21(13)5 and 6. The band is seen at three localities. At L21(5)10 the lower part of the band, of which about 4 ft. 6 in. are exposed, is seen at the top of the section overlying unfossiliferous friable shales. At the other two localities the base of the band is not exposed but the upper part and the overlying unfossiliferous sediments are seen; at L21(5)11 about 4 feet of the band occurs at stream level; at L21(13)4, where some excavation is necessary, about 2 feet are exposed in the valley side with unfossiliferous shales above.

There are slight faunal differences between the basal beds at L21(5)10 and the upper beds at the other two localities. Most of the fauna is common to all three localities; the

most abundant constituent is *E. bisulcatum*; *E. bisulcatum erinense* subsp. nov. is only seen in the lower beds associated with rare specimens of *E. bisulcatum ferrimontanum* subsp. nov., which succeeds it and which is dominant in the higher parts of the sequence at L21(13)4 and at L21(5)11, where the lower subspecies no longer occurs. Both subspecies are in many respects close to *E. bisulcatum* s.s. but significant differences exist; they appear to be closer to *E. bisulcatum* s.s. than to other subspecies, namely *E. bisulcatum grassingtonense* Dunham and Stubblefield, *E. bisulcatum varicata* Schmidt, and *E. bisulcatum* mut. B Schmidt.

The subspecies of *Eumorphoceras* are accompanied at this level by *Cravenoceras* cf. *C. gairense*, specimens of which are easily distinguished by means of three raised spiral lines around the umbilicus (a diagnostic feature, which is not seen in any other species of this genus). It has been collected at all three localities but is never as abundant as either subspecies of *Eumorphoceras*. *Kazakhoceras scaliger*, which occurs in E₁ with *C. nialhamense* and *Caneyella membranacea*, also occurs at the three localities. Its two associates do not survive E₁ times but *K. scaliger* apparently has a wider range. However, these are the only two levels at which this problematical species has been seen.

Anthracoceras glabrum occurs at the three localities but is decidedly more abundant in the lower levels at L21(5)10. Very rare specimens of the conservative *Stroboceras subsulcatus* also occur, contrasting with the more rapidly evolving goniatites.

Neither *C. membranacea* s.s. nor *C. membranacea horizontalis* subsp. nov. persist beyond E₁ beds, but at this level in E₂ an elongate subspecies of *P. corrugata* occurs, which it is thought may have been misidentified as *C. membranacea* by other authors; it is described as *P. corrugata elongata* subsp. nov. It is always associated with the ubiquitous *P. corrugata*, the most abundant species in the entire succession, and abundant specimens of the persistent *Chaenocardiola footii*, which occurs at several levels in E₁ and in E₂. The latter was not present in the faunas of the *C. leion* zone at the base of E₁, but *Chaenocardiola bisati* sp. nov. occurs at this level. *Chaenocardiola* never occurs in such swarms as some of the species of *Posidonia*, but it reaches its acme at this horizon.

Dunbarella aff. *D. elegans* is present, although this record does not conform with the horizon given by Jackson for the species; it is thought that the forms at this level are identical with those in P₁ and P₂. The species was not collected at any level in E₁ but is present again at this horizon in E₂.

(f) *The arenaceous interlude.* The very fossiliferous beds at L21(13)4, L21(5)11, and L21(5)10 are followed by about 100 feet of shales with clay-ironstone bands increasing in abundance upwards, overlain by a massive quartzitic grit, about 200 feet thick, which forms the prominent escarpment on the western and eastern sides of Slieve Anierin. Two thin coal-seams of poor quality occur within the grit; the lower is the most easily traced, and varies in thickness up to about 3 feet; the upper seam is only up to 1 foot in thickness, and is separated from the lower by about 50 feet of flagstones and sandy shales with plant remains. The lower part of the grit consists of the more massive beds but is usually the most obscured by the vast landslides which have occurred in front of the escarpment. About 75 feet of massive grits with some flagstones probably occur beneath the lower seam, while 25 feet of rusty arenaceous shales with ironstone nodules, followed by 50 feet of massive grit, overlies the upper seam.

It is clear that a great influx of fairly coarse arenaceous material entered the Namurian

seas in the area at this time, associated with advancing delta fronts which periodically allowed a coal swamp vegetation to flourish.

(g) *Cravenoceratoides edalense* and *Ct. bisati fauna* (E_2b1). The first fossiliferous horizon above the grit is exposed at L21(9)20, which is the nearest exposure to the top of the grit escarpment on the south-eastern side of Slieve Anierin; the intervening beds, about 40 feet thick, are obscured. At L21(13)3, on the south of the mountain where the grit is obscured by drift, the fossiliferous beds occur above 20 feet of unfossiliferous shales, the remainder being concealed.

The horizon is about 8 feet thick and consists of dark-grey to black shales which split into large regular slabs. The number of species is low but individuals are abundant. The commonest species is *Ct. edalense*. This is the first appearance of *Cravenoceratoides*, which is closely related to *Cravenoceras*, a frequent member of the faunas at lower horizons and which still continues to flourish at this level. Associated with *Ct. edalense*, but much more rare, is *Ct. bisati*; it shows an irregular and repeated bifurcation of the lirae instead of the single division seen in *Ct. edalense* s.s. No specimens of *Eumorphoceras* were seen at this level. The only other members of the fauna are *P. corrugata* and *P. corrugata elongata* subsp. nov.; the latter was also common in the high E_2a faunal band beneath the grit.

This horizon is believed to be in the *Ct. bisati* subzone (the lowest subzone of the *Ct. nitidus* zone) although it is here dominated by *Ct. edalense*, and *Ct. bisati* itself is only a rare member of the fauna. In the absence of evidence for precise dating, the shales above L21(13)4 and L21(5)11, the grit formation and the 40 feet of beds between the grit and the *Ct. edalense* band, can only be loosely assigned to either the top of the *E. bisulcatum* s.s. zone or the *Ct. bisati* subzone.

(h) *Cravenoceras subplicatum fauna* (E_2b1). The succession from the level of *Ct. edalense* to the summit of Slieve Anierin is exposed in its entirety in Valley 4 (L21(9)23). However, better collections can be made in Valley 3 (L21(9)24), despite the fact that the succession is slightly less complete, beginning higher at the level of *E. bisulcatum leitrinense* subsp. nov. The succession from *Ct. edalense* to *E. bisulcatum leitrinense* will therefore be described from Valley 4, and the rest of the succession from Valley 3 (see Table 2).

The *Ct. edalense* beds are succeeded by 8 feet of shales in which specimens are so abundant at certain levels that individual outlines become obscured. At other levels sediment is more abundant and the details of the fauna are consequently less obscure. Some of the best examples of *P. corrugata* s.s. have been collected at these levels, associated with *Posidoniella variabilis* and *P. variabilis erecta* subsp. nov. This is the first appearance of *Posidoniella* in the area.

The goniatites at this level belong to the genus *Cravenoceras*. At first the writer was inclined to assign these specimens, which are by no means good, to the *cowlingense* group, but many of the better ones are now compared with *C. subplicatum*.

The fauna undergoes a change in the succeeding 2 feet of beds. It is still a goniatite-lamellibranch fauna but now *Dimorphoceras* is the only goniatite. The difficulty of identifying the species of this genus without sutural evidence has already been mentioned, and the specimens at this level are therefore only tentatively attributed to *Dimorphoceras* cf. *D. looneyi*. This form dominates the fauna, and the only other fossils are

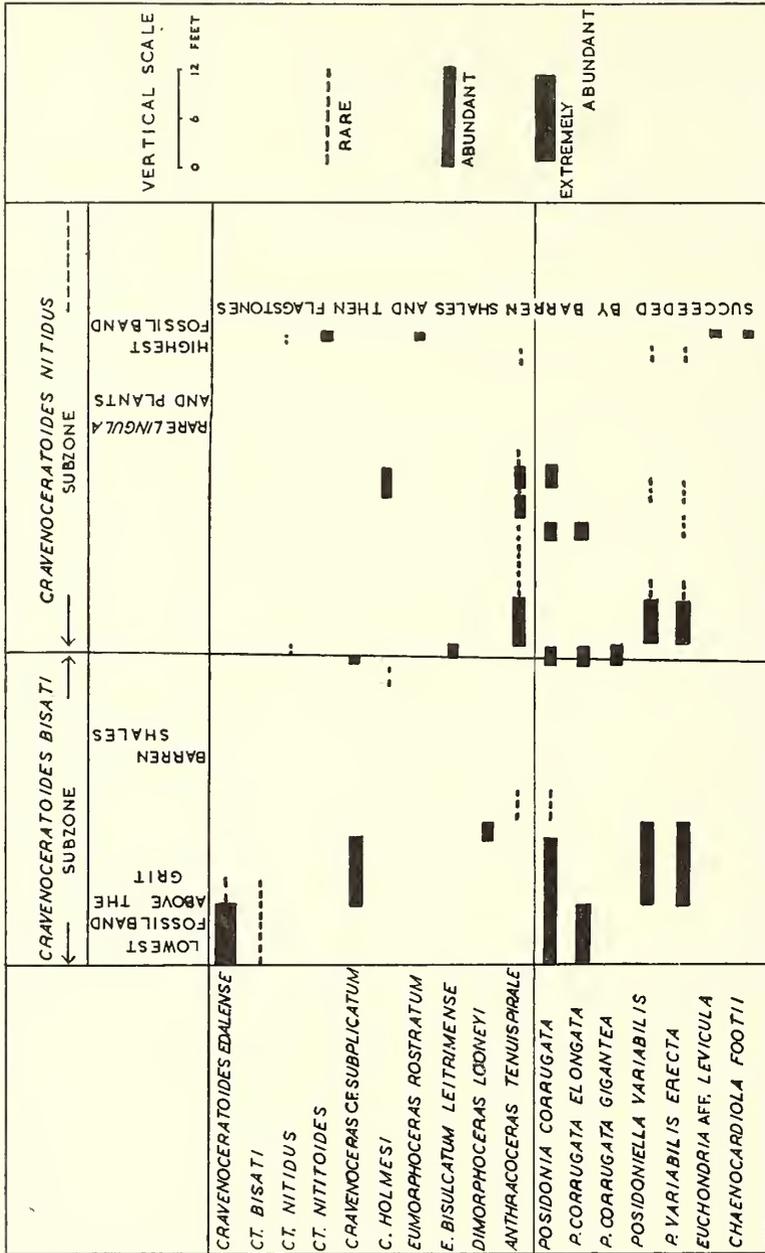


TABLE 2. Distribution of goniatites and lamellibranchs in the subzones of *Cravenoceratoides bisati* and *Cravenoceratoides nitidus* on Slieve Anierin, compiled from Valleys 3 and 4, L21(9)24 and 23.

Posidoniella variabilis and *P. variabilis erecta* subsp. nov., both of which were present at the lower level but subordinate to *Posidonia*.

Above this band there are about 4 feet of shales which are virtually barren except for very infrequent narrow seams of *P. corrugata* indistinguishable from those at lower levels, and occasional specimens of *A. tenuispirale*. The succeeding 12–15 feet of shales are completely barren, but they are overlain by a very fossiliferous band about 9 inches thick, crowded with fossils which frequently obscure each other. *P. corrugata* and *P. corrugata gigantea* subsp. nov. abound, but *P. corrugata elongata* subsp. nov. is slightly less common. Poorly preserved goniatites are present, and as in the case of the lower forms they are assigned to *C. subplicatum*.

In summary, the succession up to this point consists of about 16 feet of shales during the deposition of which a population rich in individuals but poor in species flourished. In the succeeding 2 feet *Dimorphoceras*, believed to be indicative of more brackish conditions, is the only goniatite. Thereafter, through about 16 feet of beds, conditions were unsuitable for goniatites, except for stray specimens of *Anthracoceras* and a few lamelibranch seams at the base. Overlying this portion of the succession is another fossiliferous horizon.

(i) *Eumorphoceras bisulcatum leitrinense fauna* (E_2b2). The description of the succession from this horizon to the top of Slieve Anierin is continued from Valley 3 (L21(9)24). *E. bisulcatum leitrinense* subsp. nov. extends through about 18 inches of sediment, and is associated with abundant specimens of *P. corrugata* s.s., its two subspecies *elongata* and *gigantea*, and less common examples of *Posidoniella variabilis*. The specimens of *Eumorphoceras* are mostly rather small and are not usually so well preserved as the forms occurring below the grit, and also at higher levels than *leitrinense*. This band is a very useful marker horizon and collections have been made from it at several other localities; it is thought that it may in fact represent the base of the *Ct. nitidus* subzone. At L21(9)19 *E. bisulcatum leitrinense* has been collected with very scanty pieces of *Cravenoceratoides* ornament, but the lirae on these fragments, although showing the bifurcations seen in the lower *Ct. edalense* s.s. material, are asymmetrical as in the two species *Ct. nitidus* and *Ct. nititoides*.

(j) *Anthracoceras tenuispirale fauna* (E_2b2). The *E. bisulcatum leitrinense* horizon is followed by 19 feet of shales, the only goniatite being *Anthracoceras tenuispirale*. This species has not hitherto been recorded in the British area but it occurs in abundance on Slieve Anierin. I am also informed by Dr. J. S. Jackson (*in litt.*) that the same species occurs in the Kingscourt inlier, Co. Meath. The possibility that specimens of *A. tenuispirale* from other areas have been wrongly identified as *Cravenoceras* cf. *C. holmesii* is discussed on p. 395.

On Slieve Anierin *A. tenuispirale* is usually associated with *Posidoniella variabilis* and *P. variabilis erecta* subsp. nov. It may also have been the species present with *E. bisulcatum leitrinense* but the material at this level is not sufficiently clear. Throughout the lower 5 feet of this 19-foot thickness of shales the proportion of fossils to sediment is about the same as in the lower *leitrinense* band so that individual specimens do not obscure each other; the lithology varies from pale brown decalcified siltstone to an intensely black siltstone.

In the next 7 feet of shales within the 19-foot sequence, fossils are very rare except for

a few specimens of *A. tenuispirale* and *Lingula* sp. Bisat (1933, pp. 412-14) believes *Anthracoceras* to be a semi-estuarine genus, and its scanty occurrence with *Lingula* here supports this contention. In the lower part of this 7-foot section *P. variabilis* is also present with *A. tenuispirale*, and seems to have been capable of withstanding a lower salinity than *Posidonia*.

After this barren interlude there is a thickness of about 2 ft. 6 in. in which *P. corrugata* and *P. corrugata elongata* are dominant, and *A. tenuispirale* and *Posidoniella variabilis* both rare. There follow two white sandstone bands, each about 4 inches thick and separated by about 8 inches of sandy unfossiliferous shales. This brief arenaceous interlude is succeeded by about 2 ft. 9 in. of beds in which *A. tenuispirale* is the only fossil present apart from internal moulds of minute mollusca and impressions of conodonts. In the upper 9 inches *Posidoniella variabilis* and *P. variabilis erecta* appear again. Conditions during the deposition of these 19 feet of shales therefore obviously fluctuated from semi-estuarine to littoral. At no point in the succession were clay-ironstone bands observed.

(k) *Cravenoceras holmesi* fauna (E_2b2). Succeeding these 19 feet of shales is a 15-inch band dominated by *C. holmesi*. At L21(9)13 a few internal moulds of this form were collected just below the *E. bisulcatum leitrinense* material but at L21(9)24 it appears for the first time as a very abundant component of the fauna about 20 feet above *leitrinense*. Associated with this species are very rare specimens of *A. tenuispirale* and a few rare *P. variabilis erecta*.

C. holmesi persists through the overlying 2 ft. 6 in. of shales and at certain levels is very abundant, but at other levels *A. tenuispirale* is dominant. At those levels at which *Cravenoceras* abounds specimens of *P. corrugata* and *P. corrugata elongata* are also common. *A. tenuispirale* occurs mostly in isolation, although sometimes in association with conodont impressions.

The next 3 feet of sediments are barren apart from rare *A. tenuispirale* and *Lingula* sp.; the upper 6 inches of this section has yielded no fossils at all. A narrow sandstone band then occurs, followed by 9 feet of beds containing *Lingula* sp., a narrow sandstone band and then 2 feet of shales with obscure ?*Anthracoceras* and *Posidoniella* and plant fragments only.

(l) *Cravenoceratoides nititoides* fauna (E_2b3). These less interesting deposits are terminated by a 6-inch band of decalcified mudstone in which fossils, though exceedingly abundant, are poorly preserved. This band, however, is the prelude to more rewarding material since it immediately underlies the richest faunal horizon on Slieve Anierin. The latter is only about 9 inches to 1 foot in thickness but the individuals are more abundant and there is less sediment than in the *leitrinense* band. The band is tough, pale brown in colour, completely decalcified, and loose slabs are frequently found in the streams winding through the peat on the upland area above the grit in front of the four main valleys on the south-western face of the mountain (text-figs. 1, 3).

The fauna consists of *Eumorphoceras rostratum* sp. nov., *Ct. nititoides*, rare *Ct. nitidus*, *Euchondria* aff. *E. levicula*, *Chaenocardiola footii*, *C.* cf. *C. haliotoidea*, *Dunbarella* aff. *D. elegans*, *Posidoniella* cf. *P. vetusta* (Sowerby), *Weberides* cf. *W. shumnerensis*, *Productus hibernicus*, *Orbiculoidea nitida*, *Mourlonia striata*, *Archaeocidaris urii*, crinoidal debris, *Stroboceras subsulcatus*, *Fenestella* sp., *Edestodus* sp.

This is the richest and most diverse band in the succession in terms of species present. Trilobites, brachiopods, gastropods, and echinoid plates and spines only occur elsewhere in the sequence in P₂ or very low E₁ levels. This is the only level at which any bryozoa have been seen.

After the accumulation of the thick grit formation the succession on Slieve Anierin up to the band just described has oscillated from decidedly marine horizons (e.g. those with *Ct. edalense*, *C. subplicatum*, and *C. holmesi*) to beds deposited under far more brackish-water conditions with *Dimorphoceras* or *Anthracoceras* alone at certain levels or associated with *Posidoniella variabilis*. Between the grit and the *Ct. nititoides* band clay-ironstones have not been observed but there are several thin sandstone horizons with *A. tenuispirale*, particularly in the brackish sequences.

Overlying the *Ct. nititoides* band there are 40 feet of barren sandy shales with clay-ironstone bands becoming more numerous towards the top. This is virtually a return to the lithology typically seen separating the various fossiliferous beds below the grit. The clay-ironstone horizons both below the grit and above the *Ct. nititoides* band occur as thin continuous beds as well as bands of nodules. The last solid beds seen under the peat deposits which cover the top of Slieve Anierin consist of about 12 feet of white or pale-buff flagstones with plant fragments.

SYSTEMATIC DESCRIPTIONS

Order AMMONOIDEA Zittel 1884

Suborder GONIATITINA Hyatt 1884

Superfamily GONIATITACEA de Haan 1825

Family GONIATITIDAE de Haan

Subfamily GIRTYOCERATINAE Wedekind

Genus EUMORPHOCERAS Girty 1909

Genotype: Eumorphoceras bisulcatum Girty 1909.

In his diagnosis of this genus Moore (1946, pp. 417-18) includes the following features: pronounced ribs as early as the second whorl and continuing into the late youthful stage; a ventro-lateral groove; a generally rounded venter; and a ventro-lateral salient and ventral sinus. In his original description Girty (1909, pp. 67-68) defined *Eumorphoceras* as lacking constrictions; however, species and subspecies have subsequently been described which show constrictions. Moore (1946, p. 393) has commented on this and added this feature to his diagnosis of the genus (p. 418), which now therefore includes some taxa with constrictions.

Eumorphoceras pseudocoronula Bisat

Plate 51, fig. 1

Eumorphoceras pseudocoronula Bisat 1950, p. 19, pl. 2, fig. 4.

Description. The umbilicus is widely open. There are prominent constrictions which after a short radial passage from the umbilicus soon curve smoothly forward to pass obliquely into the ventro-lateral groove. The edges of the constrictions are sharp and raised into ribs. Between each pair of constrictions there appear to be two or three ribs

which are strongly seen in the umbilical edge and close to it, but which fade some distance before the groove. The umbilical edge is beaded. The groove on the ventro-lateral area is divided into two by a strongly rounded ridge. The test ornament of delicate striae is seen in some specimens, and their course follows that of the constrictions as far as the groove. At the groove these striae have a prominent lingua, from which they curve backwards to a sinus on the venter. There are spiral striae in the ventro-lateral region.

Localities. This species is a very common member of a rich fauna at L24(1)1 and at L21(14)8.

Horizon. It is associated with *Cravenoceras leion* and *Eumorphoceras rota* (Yates 1961, pp. 57–58, pl. 6, figs. 6, 7). The stratigraphical level is E₁a.

Discussion. Although this form has already been described by Bisat, a description of the forms collected on Slieve Anierin is given here to facilitate comparison with the later closely related form of *E. medusa* (Yates 1961, pp. 54–56, pl. 6, figs. 1, 2). Specimen 7213 has been figured (op. cit., pl. 6, fig. 3).

Eumorphoceras pseudobilingue A Bisat

Plate 51, fig. 2; Plate 53, fig. 6

Eumorphoceras pseudobilingue A Bisat 1928, pl. 6 (facing p. 130).

Description. This form is sharply ribbed with a wide umbilicus and in this material no evidence of constrictions has been seen. The ribs are numerous and sharp; they are sickle-shaped and separated by wide interspaces; close to the shoulder ridge they have a well-marked and smoothly-curved forward swing and pass into the ventro-lateral furrow. The umbilicus has a raised and beaded edge. The ventro-lateral furrow is divided into two by a well-marked ridge. Both the two resulting furrows are well defined. The specimens with shell preserved show fine striae which follow the rib direction; spiral striae are strongly developed in the region of the ventro-lateral ridge.

Dimensions. 7016 (pl. 1, fig. 2): diameter 22 mm.; umbilical diameter 7 mm. 7017 (pl. 3, fig. 6): diameter c. 35 mm.; the ribbing is still strong on this large specimen though it is becoming more indistinct on the last visible piece of whorl.

Locality and horizon. The best examples on Slieve Anierin occur at L23(4)7. *E. pseudobilingue* A is associated with equally abundant examples of *C. leion* and is therefore an E₁a species.

Discussion. Moore (1946, p. 426) points out that although Bisat (1928) has divided *E. pseudobilingue* into three forms, *A*, *B*, and *C*, he has given no statement as to their differences, but apparently groups form *A* with *C. leion*. Moore also describes a form which seems to agree with one seen in younger beds on Slieve Anierin and it is therefore

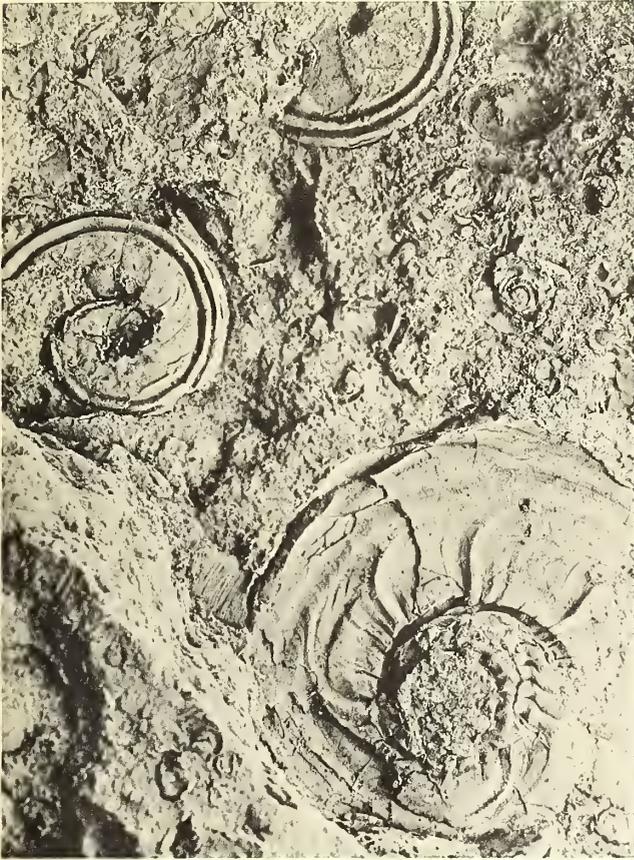
EXPLANATION OF PLATE 51

All specimens are from Slieve Anierin, Co. Leitrim, Eire.

Fig. 1. *Eumorphoceras pseudocoronula* Bisat. 7015c. External mould; also showing two internal moulds of *E. rota* Yates (7015a, b), $\times 3.5$.

Fig. 2. *Eumorphoceras pseudobilingue* A Bisat. 7016, external mould showing spiral ornament on the ventro-lateral ridge, $\times 4$.

Figs. 3–5. *Eumorphoceras pseudobilingue* (Bisat) emend. Moore. 3, 7039, showing wavy nature of narrow ribs, $\times 3.6$. 4, 7037, $\times 3.6$. 5, 7040, showing angular beaded venter of large specimen, $\times 2$.



1 × 3.5



3 × 3.6



4 × 3.6



2 × 4



5 × 2

useful and appropriate to describe the earlier form which agrees well with those figured by Nevill (1957, pl. 22, figs. 1–3) from the Summerhill Basin.

Eumorphoceras pseudobilingue (Bisat) emend. Moore 1946

Plate 51, figs. 3–5

Glyphioceras pseudobilingue Bisat 1922, *The Naturalist*, pp. 225–6.

Eumorphoceras pseudobilingue (Bisat) *partim*. Bisat 1924, pp. 99–100, pl. 10, figs. 1, 2.

Eumorphoceras pseudobilingue (Bisat); Schmidt 1934, p. 446, fig. 1. (non *Eumorphoceras pseudobilingue* (Bisat); Demanet 1941, pp. 135–6, pl. 5, figs. 11–14.

Eumorphoceras pseudobilingue (Bisat) emend. Moore 1946, pp. 426–9, pl. 23, fig. 2; pl. 25, fig. 3; text-fig. 27.

Description. The very early whorls have not been seen. At 12 mm. diameter the ribbing is strong and there are about 13/half whorl. The following description is based on many specimens of which 7037 (Pl. 51, fig. 4) is a typical example. At *c.* 20 mm. there is a ventro-lateral ridge and a wide umbilicus. The venter is broad but the mid-venter becomes raised and angular. It is not certainly known at what diameter this angularity of the mid-venter appears, but it is a well marked character by *c.* 25 mm. Large fragments show a distinct notching of the mid-ventral ridge (Pl. 51, fig. 5). The ribs in this species have a typically wavy character. In the adult whorl they are thin and sharp, separated by wide interspaces. In the earliest part of the whorl they are sharp on the umbilical edge and continue over the greater part of the flank. Near the ventro-lateral ridge they curve forward and terminate at the ridge. At this stage there is one quite noticeable bend in the course of the ribs close to the umbilical edge. As the whorl advances the ribs fade over most of the flank and are sharp only in the immediate neighbourhood of the umbilicus. They swing strongly forward just after leaving the umbilical edge but then disappear. At very advanced diameters there are still indications of the ribs at the extreme umbilical edge, and they persist when the ventro-lateral ridge has all but disappeared.

Dimensions. 7037: diameter *c.* 20 mm. (Pl. 51, fig. 4). 7038: diameter *c.* 25 mm. Most of the specimens approximate to these dimensions but crushing has obscured many, making their exact measurement impossible.

Localities. L23(4)1 and L21(5)4.

Horizon. L23(4)1 is isolated but is probably in low E₁b. At L21(5)4, which is also in low E₁b, the fauna occurs a little distance above beds with *Eumorphoceras* cf. *E. angustum*, *Posidonia corrugata*, and *P. trapezodra*; the latter horizon is separated by a considerable thickness of unfossiliferous rusty shales from the highest faunal band in the *C. leion* zone (E₁a).

Discussion. The Slieve Anierin examples are considered to conform to the lectotype (GSM 72972) from Little Mearley Clough described by Moore (1946), and other specimens deposited by Moore at the Geological Survey Museum from Cow Close Syke, Malham. Moore gives no stratigraphical placing beyond assigning an E₁ age. A few feet above this form on Slieve Anierin occur forms referred to *Cravenoceras* aff. *C. malhamense*, *Kazakhoceras scaliger*, and *Caneyella membranacea*. The figure given by Schmidt (1934, p. 446, fig. 1) shows a similarity in the wavering nature of the ribbing and the ridge which develops in the mid-venter. Demanet (1941, pp. 135–6, pl. 5, figs. 11–14) has forms which do not resemble either the Irish specimens or Moore's material. They

apparently have a far smaller umbilicus, the ribbing disappears at far smaller diameters and there is apparently a strong shoulder groove. These specimens do not resemble *Eumorphoceras pseudobilingue* A.

Eumorphoceras pseudobilingue C Bisat

Plate 52, figs. 1, 2

Eumorphoceras pseudobilingue C Bisat 1928, pl. 6.

Description. There is a marked groove on the ventro-lateral area which persists to advanced diameters. At 10 mm. diameter (umbilical diameter 3 mm.) there are ribs which are strongly defined at the umbilical edge but which lose their strength over the flanks. In their thinness and wide interspacing they resemble those of *E. pseudobilingue* s.s., but lack the typical wavering character of the ribs in that species although they still show a kink near the umbilical edge. At this stage there are slight constrictions. By 15 mm. diameter the ribs are seen only at the extreme umbilical edge and no constrictions are seen. The ventro-lateral groove is still strong.

Dimensions. 7041: diameter 15 mm. (Pl. 52, fig. 1). 7042: diameter 10 mm. (Pl. 52, fig. 2). 7043: diameter c. 8 mm. 7044: diameter c. 10 mm.

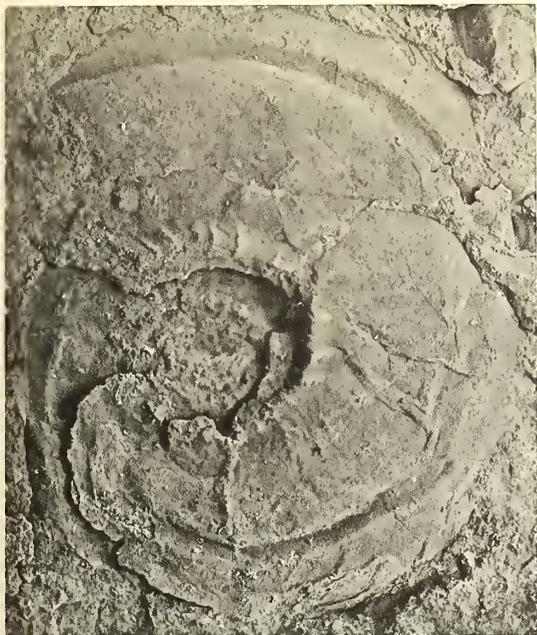
Localities. L21(5)4, low E₁b; L21(13)8, high E₁b.

Horizon and associated fauna. These forms have all been collected from a very thin band immediately above beds with *E. pseudobilingue* s.s., which are in turn above beds containing *Eumorphoceras* cf. *E. angustum*. They are associated with rare specimens of *Chaenocardiola footii* and gregarious small individuals of *Posidonia corrugata*.

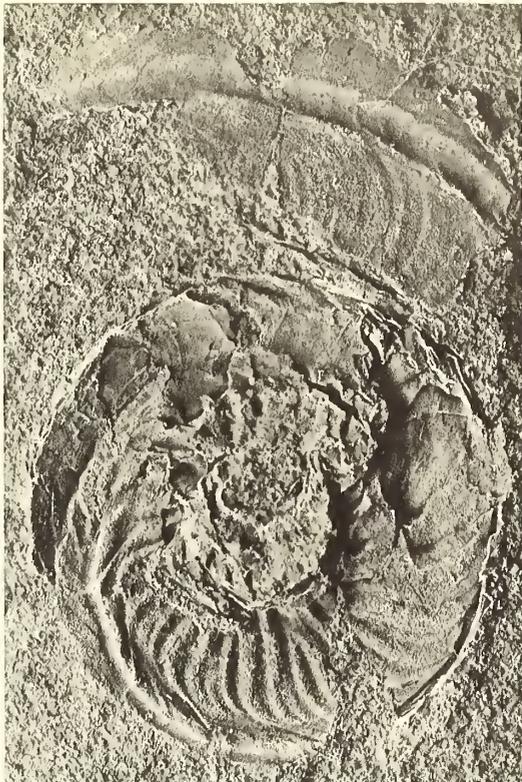
Discussion. This species has points of similarity with *E. angustum* Moore (1946, pp. 424–6, pl. 24, figs. 1–7; text-fig. 26), namely the early fading of the ribs and the comparatively small umbilicus; however the ribs, although fading early, are still quite strong at diameters at which in *E. angustum* they are little more than plications. In *E. pseudobilingue* C there is an undoubted groove in the ventro-lateral area which contrasts strongly with the poorly developed ridge seen in this area in *E. angustum*. A large distorted specimen at about 22 mm. diameter still shows the ventro-lateral groove. A comparison has also been made with *E. hudsoni* Gill, originally described by Moore (1946, pp. 419–20, pl. 24, figs. 2, 2a) as *Eumorphoceras* sp. form B aff. *Sagittoceras costatum* Ruprecht. Moore states that in this species the groove in the ventro-lateral

EXPLANATION OF PLATE 52

- All specimens are from Slieve Anierin, Co. Leitrim, Eire.
- Figs. 1, 2. *Eumorphoceras pseudobilingue* C Bisat. 1, 7041, showing early loss of ribs and strong ventro-lateral groove, $\times 5.5$. 2, 7042, $\times 6$.
- Figs. 3, 4. *Eumorphoceras bisulcatum grassingtonense* Dunham and Stubblefield. 3, 7047, the inner whorls show rib bifurcation and a relatively early reduction in their strength; the outer whorl is preserved as an internal mould showing a strong groove only, $\times 5.3$. 4, 7046, fragment showing two constrictions, $\times 7$.
- Fig. 5. *Eumorphoceras bisulcatum ferrimontanum* subsp. nov. 7055, paratype, showing ribs only at the umbilical edge, merging into finer striae over the flanks, $\times 4$.
- Fig. 6. *Cravenoceratoides nitidus* (Phillips). 7094, external mould showing relatively large umbilicus and asymmetrical lirae, $\times 4$.



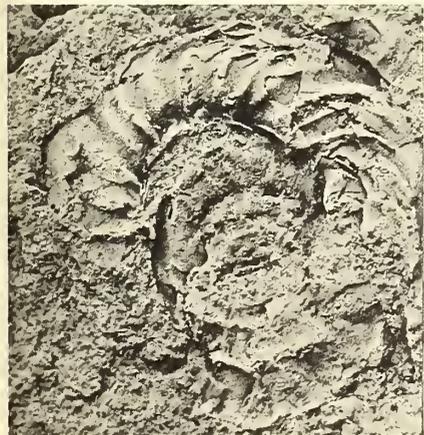
1 x 5.5



3 x 5.3



2 x 6



4 x 7



6 x 4



5 x 4

area continues up to about 20 mm. On the holotype (GSM 72650) at 11 mm. diameter there appears to be very little sign of a groove, but only a slight ridge. This ventro-lateral groove does not appear as a very strong feature on GSM 72649, 72651-5, all collected from Carla Beck, near Skipton. *E. pseudobilingue* C has a strong groove, and a smaller umbilicus than *E. hudsoni*.

The Slieve Anierin specimens are, however, similar to *E. pseudobilingue* s.s. The thin ribs with wide interspaces are common to both but in *E. pseudobilingue* C the ribs fade earlier and do not show the wavy character seen in the ribs of *E. pseudobilingue* s.s. The ribs (see 7041, Pl. 52, fig. 1), before fading on the flanks, show the same kink after leaving the umbilicus as is seen in *E. pseudobilingue* s.s. In the latter, however, there is a definite ridge in the ventro-lateral area. Bisat has mentioned but never described or figured *E. pseudobilingue* C (1928, pl. 6). Slieve Anierin forms have so far been referred to *E. pseudobilingue* A and to *E. pseudobilingue* s.s. At the Geological Survey Museum GSM Z1 5777, collected in Little Mearley Clough, has been labelled *E. pseudobilingue* C, but the specimens are very poor though they appear to possess a groove on the ventro-lateral area. There are also slabs collected by Parkinson from Studforth Gill, Tosside, 5 miles south-west of Settle, Yorkshire, which are said to be high *E. pseudobilingue* C. On these slabs only one specimen, GSM Z1 5775, resembles the Slieve Anierin examples; although poor it has a groove on the shoulder. On the other slabs the examples appear to be closer to *E. pseudobilingue* s.s. It has been decided (with Bisat's approval, *in litt.*) to refer these examples from Slieve Anierin below *Cravenoceras malhamense* to *E. pseudobilingue* C.

Eumorphoceras bisulcatum grassingtonense Dunham and Stubblefield

Plate 52, figs. 3, 4

Eumorphoceras bisulcatum Girty mut. *grassintonensis* Dunham and Stubblefield 1944, pp. 258-60, pl. 11, figs. 4a-c.

Description. At a diameter of about 10 mm. the umbilical diameter is about 3.5 mm.; in 7045 at this diameter there are about fourteen strong ribs in slightly under half a whorl; these ribs are strong and slightly swollen at the umbilical edge, where they seem to project over the edge; there are two clear constrictions in this specimen. At a diameter of about 7 mm. 7046 shows one clear constriction and a rib forking very close to the umbilical edge just before the constriction. In 7047 at 12 mm. diameter the ribs show raised, swollen tips at the umbilical edge but they are very muted across the rest of the flank; at 19 mm. diameter over the flank (which is all this specimen shows at this diameter) only growth lines are seen. At this, the largest diameter seen, the shoulder groove is still strong. From above these constrictions are not very strong; they are most easily seen at their break into the shoulder groove. This is also true in the type specimen GSM KD423. This feature is also commented on by Currie (1954, p. 582) in describing *E. bisulcatum* aff. *grassingtonense* Dunham and Stubblefield.

Dimensions. 7047: greatest diameter 19 mm., diameter of inner ribbed part 12 mm. (Pl. 52, fig. 3). 7046: diameter 7 mm. (Pl. 52, fig. 4). 7045: diameter 10 mm.

Localities. L21(13)6 and L21(5)8.

Horizon. Low E₂a. This is the earliest record on Slieve Anierin of *E. bisulcatum*. It occurs very scantily

indeed, the dominant goniatite at this level being *Cravenoceras cowlingense*. *Dimorphoceras* sp. is also present. Lamellibranchs are not common and include *Chaenocardiola footii*, *Posidonia lamellosa* and *P. corrugata*.

Discussion. The material at this level is very scanty and *Cravenoceras* individuals far exceed *Eumorphoceras* in abundance, but as this is the lowest horizon at which *E. bisulcatum* occurs they are particularly important specimens. At 10.5 mm. diameter *grassingtonense*, described by Dunham and Stubblefield (1944, pp. 258–60), has an umbilicus of 4.0 mm. and about sixteen ribs in half a whorl. Specimen 7048 corresponds approximately to these figures; only two constrictions have been seen in this specimen but others may be concealed between these two. 7046 shows a bifurcation of the ribs at a point immediately before the single clear constriction. Rib bifurcation is a feature of *grassingtonense*, in which at 10.5 mm. diameter there are about five constrictions with five ribs between them, but the number is not constant. The ribs of *grassingtonense* are said to 'take origin at the margin in a raised tubercle', and this feature is seen in the Slieve Anierin material. In the original description of this mutation it is stated that the diameter at which the ribbing becomes reduced is not known. In 7047, at about 12 mm. diameter, the ribs are still strong at the edge of the umbilicus but less apparent on the flank. At this diameter also bifurcations in the ribs appear to be slightly commoner and to take place further over the flank.

Eumorphoceras bisulcatum erinense subsp. nov.

Plate 53, figs. 1, 2; Plate 54, fig. 7

Description. The ribs are strong and numerous. They continue across the flanks almost to the shoulder groove; very close to the latter they bend forward rather sharply. After a short oblique passage forward they end at the groove. The ribs are still apparent at a diameter of 14 mm. in 7049 and the umbilical diameter is about a third of the total diameter. In some specimens the ribs are still strong at 18 mm. over most of the flank (see 7050) and the shoulder groove is also still strongly defined.

Holotype. 7049c (counterpart 7274): the large specimen, diameter 14 mm. (Pl. 53, fig. 1). *Paratypes.* 7049a, b: two small specimens on the same slab, diameter 8 mm. and 9 mm. (Pl. 53, fig. 2). 7050: diameter 17–18 mm. (Pl. 54, fig. 7). 7052: diameter 12 mm.

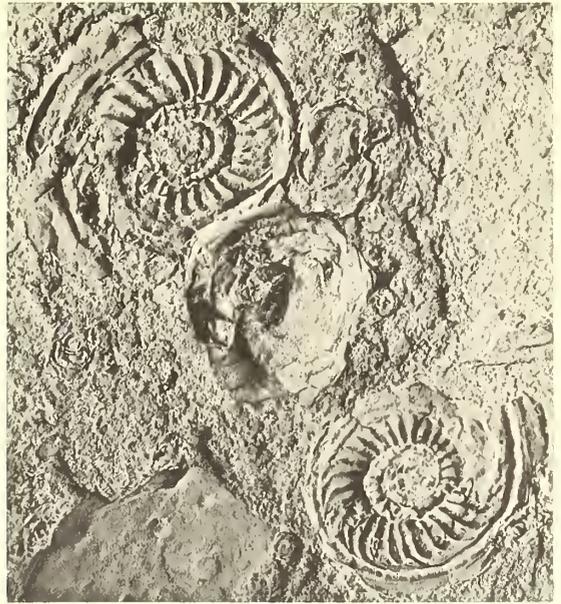
Type locality and horizon. This subspecies has so far only been collected from one locality, L21(5)10, which is thought to be very close to L21(13)4 and L21(5)11 in stratigraphical level, which is high E₂a. The associated fauna at the three localities is the same, and *E. bisulcatum ferrimontanum* subsp. nov. occurs at L21(5)10 with *erinense*, but less abundantly. At the other localities mentioned only *ferrimontanum* is present.

EXPLANATION OF PLATE 53

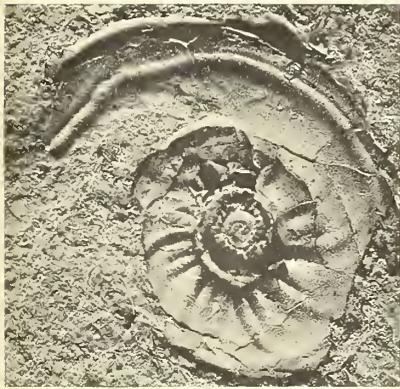
- Except for fig. 3, all specimens are from Slieve Anierin, Co. Leitrim, Eire.
 Figs. 1, 2. *Eumorphoceras bisulcatum erinense* subsp. nov. 1, 7049c, holotype, showing geniculate aspect of ribs, $\times 4.3$. 2, 7049a, b, paratypes, external moulds, $\times 4$.
 Fig. 3. *Eumorphoceras* cf. *E. bisulcatum ferrimontanum* subsp. nov. Edge Marine Band, Cononley Beck, 200 yds. S. 47° W. of Cononley Church, Yorks. GSM GM3675, $\times 4.25$.
 Figs. 4, 5. *Eumorphoceras bisulcatum leirimense* subsp. nov. 4, 7060, holotype, showing constrictions with 2–3 short intervening ribs, $\times 5.3$. 5, 7063, paratype, $\times 9.4$.
 Fig. 6. *Eumorphoceras pseudobilingue* A Bisat. 7017, external mould, $\times 3$.



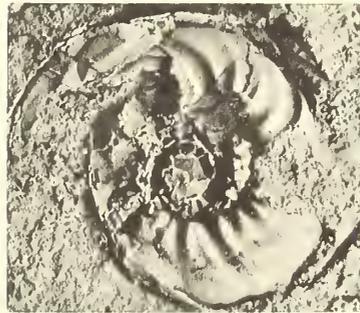
1 x 4.3



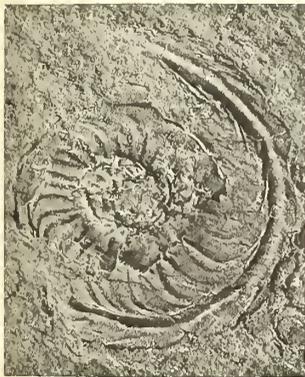
2
x 4



4 x 5.3



5 x 9.4



3 x 4.25



6 x 3

Discussion. This subspecies resembles *E. bisulcatum ferrimontanum* subsp. nov. in some respects. Both forms have abundant and strong ribs, but in *erinense* they persist to much larger diameters. The groove is strong to large diameters in both subspecies. Apart from the greater persistence of the ribs in *erinense* there is also a difference in their appearance when compared with those of *ferrimontanum*. In *erinense* they pass almost to the groove before bending forward rather sharply to pass obliquely into the groove. The result is a geniculate appearance and a larger radial portion to the rib. In these specimens of *erinense* although the ribs persist to about 18 mm. diameter they merge distally into the finer striations on 7049c where the geniculation begins at about 14 mm. diameter. In 7050 they are strong over about three-quarters of the flank and then degenerate. At a diameter of at least 25 mm. 7053 has a marked ridge at the shoulder with a slight furrow on its lateral and ventral side. As with *ferrimontanum* there are differences when compared with *E. bisulcatum* Girty s.s. The geniculate aspect of the ribs in *erinense* is closer to Girty's figures than the ribs in *ferrimontanum*. Occasional indications of rib bifurcation are seen in *erinense* but these do not seem to follow any definite pattern. They are not mentioned in Girty's description (1909, pp. 68-70) nor by Miller and Youngquist (1948, pp. 662-4). The umbilicus of the type specimen of *E. bisulcatum* s.s. is smaller than that seen in *erinense*.

Eumorphoceras bisulcatum ferrimontanum subsp. nov.

Plate 52, fig. 5; Plate 53, fig. 3; Plate 54, figs. 1-4

Description. Most of the specimens are rather small. The ribs are strong from the earliest whorls. By the time a diameter of 12 mm. has been reached the ribs are sharp on the immediate umbilical edge only. At smaller diameters the ribs pass over the flanks with a slightly forward trend towards the shoulder groove. They have a slight twist at the umbilical edge. Close to the groove they curve forward and are much less distinct, merging into finer growth striae. They pass forwards to form a lingua in the ventro-lateral region. The rounded termination of the lingua is situated on the ventral side of the shoulder groove. There are indications also of spiral ornament in this region. The shoulder groove is seen to advanced diameters (see 7054 and 7055). The groove is strong, with the inner and the ventral wall showing about equal angles of slope. At a radius of 15 mm. 7056 shows a ridge at the shoulder with a strong furrow still on its lateral side and a far fainter furrow on the ventral side. So far no undoubted constrictions have been seen in these specimens. The umbilical diameter is about a third of the total diameter at 14 mm. diameter. The ribs in 7057 number about 17/half whorl. There is evidence of at least nine ribs in the small fragment of the umbilicus seen in 7055.

Holotype. 7054 (counterpart 7048): diameter 18 mm. (Pl. 54, fig. 1). *Paratypes.* 7058: incomplete, 227 mm. (Pl. 54, fig. 2). 7059: diameter 11 mm. (Pl. 54, fig. 3). 7055 (Pl. 52, fig. 5). 7057: diameter 14 mm. (Pl. 54, fig. 4).

Type locality and horizon. This form is abundantly represented on Slieve Anierin at L21(13)4, the type locality, and at L21(5)11. The horizon is high E₃a. The rich associated fauna includes *Cravenoceras* cf. *C. gairense*, *Kazakhoceras scaliger*, *Chaenocardiola footii*, *Dunbarella elegans*, and several varieties of *Posidonia corrugata*.

Discussion. In this form the ribs apparently fade away relatively early. 7058 is almost smooth apart from the growth-lines and the faint indication of ribs at the umbilical

edge. The lingua is relatively deep (see 7055 and 7054). The rib counts are fairly large. These examples are obviously broadly referable to *E. bisulcatum* Girty. Unfortunately Girty's description (1909, pp. 68–70, p. 11, figs. 15–19c) is based on specimens of about 10 mm. diameter and the later stages well seen on the Slieve Anierin specimens have not been discussed in detail beyond the statement that the ventro-lateral groove persists for longer than the ribs. From Girty's plates it seems that his specimens apparently have rather more geniculate ribs than are seen in the author's material. Moore (1946, pp. 430–3) describes a form which he refers to *E. bisulcatum* Girty s.l. but it does not agree with the present subspecies. The latter is probably close to the form *E. bisulcatum* as described by Girty, but differs in the less geniculate nature of the ribs. Most of the Irish specimens have an umbilical diameter of about a third of the total diameter. The type specimen of *E. bisulcatum* (refigured by Moore 1946, pl. 25, figs. 5a–d) has an umbilical diameter of about 25 per cent of the whole. The inability to compare very closely the specimens at slightly more advanced stages is also a difficulty. However, since this form occupies a definite level and appears to be distinct in at least one feature it is proposed to name it *E. bisulcatum ferrimontanum*.

Subspecies of E. bisulcatum. The three subspecies of *E. bisulcatum* which have been described may look very similar superficially but a study of many specimens collected from beds whose order of superposition is known with certainty is valuable and shows that three subspecies of this species do exist. Two of these occur on approximately the same level and are stratigraphically higher than the third. For the sake of clarity the salient features of these three subspecies and their order of appearance are summarized.

(a) Specimens collected at L21(13)6 and L21(5)8 from a low E₂a horizon show:

1. About sixteen ribs in half a whorl.
2. Constriction (at least at small diameters).
3. Rib-bifurcation (more frequent at advanced diameters and taking place farther from the umbilical edge).
4. Ribs which are somewhat swollen at the umbilical edge and project over it.
5. Ribs fading over the flanks at 12 mm. diameter.
6. An umbilical diameter which is about 35 per cent of the whole.
7. The groove still strong at the largest diameter seen.

These are identified as *E. bisulcatum grassingtonense*.

(b) The high E₂a band at L21(5)10 yields specimens attributable to a subspecies showing:

1. Geniculate ribs.
2. Ribs still apparent at 17–18 mm.

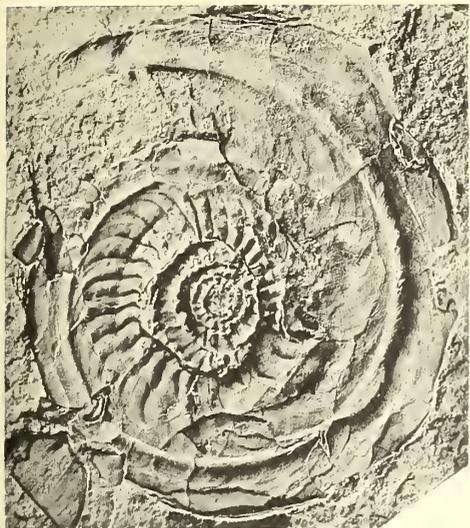
EXPLANATION OF PLATE 54

All specimens are from Slieve Anierin, Co. Leitrim, Eire.

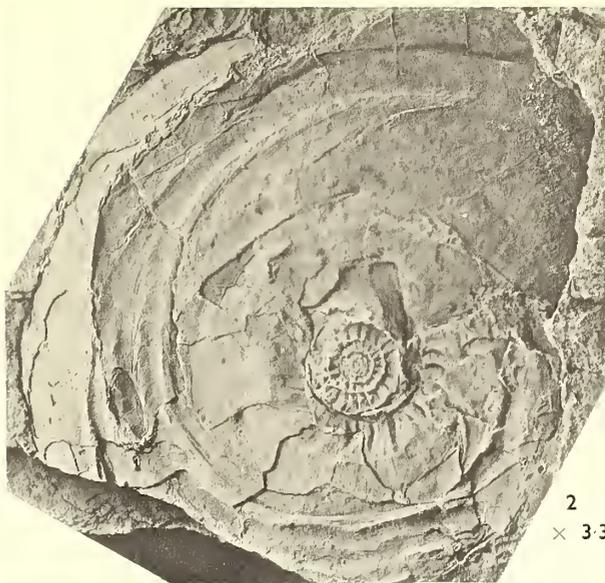
Figs. 1–4. *Eumorphoceras bisulcatum ferrimontanum* subsp. nov. 1, 7054, holotype, external mould showing early failure of ribs, and spiral ornament on the ventro-lateral area, $\times 3.75$. 2, 7058, paratype, external mould, with the ventro-lateral groove still seen over most of the specimen although the ribbing has been lost, $\times 3.3$. 3, 7059, paratype, external mould, $\times 5$. 4, 7057, paratype, external mould, $\times 4.75$.

Figs. 5–6. *Eumorphoceras bisulcatum leitrimense* subsp. nov. 5, 7065, showing constrictions persisting over the venter, $\times 8$. 6, 7064, paratype, $\times 4.75$.

Fig. 7. *Eumorphoceras bisulcatum erinense* subsp. nov. 7050, paratype, showing geniculate ribs to relatively large diameter, $\times 3.75$.



1 x 3.75



2
x 3.3



3 x 5



5 x 8



6 x 4.75



4 x 4.75



7 x 3.75

3. An umbilical diameter about 33 per cent of the whole.
4. Constrictions not apparent.
5. Occasional indications of rib bifurcation.
6. Groove persistent to advanced diameters. At very large diameters a ridge appears with a shallow groove laterally and ventrally.

These are identified as *E. bisulcatum erinense* subsp. nov. Rare examples of the following subspecies are also present.

(c) Specimens collected from the high E₂a band at L21(5)11 and L21(13)4 show:

1. No bifurcations or constrictions.
2. An umbilical diameter which is about 33 per cent of the whole.
3. Ribs fading on the flanks at about 12 mm.
4. The groove persisting to advanced diameters; at very advanced diameters there is a ridge at the shoulder with a strong groove laterally.
5. About seventeen ribs in half a whorl.

These are identified as *E. bisulcatum ferrimontanum* subsp. nov.

All these early examples of *E. bisulcatum* show features of resemblance to *E. bisulcatum* s.s. A close relationship exists between the three subspecies despite the several distinguishing features which each has developed. The earliest subspecies, *grassingtonense*, resembles the much later *ferrimontanum* in the early fading of the ribs on the flanks, but no rib bifurcations and constrictions have been seen in the latter and the umbilical diameter may be slightly smaller in *ferrimontanum* at comparable diameters. *Erinense* and *ferrimontanum* are alike in umbilical diameter but the ribs persist to greater diameters in *erinense* and are rather geniculate in aspect. The latter shows an occasional rib bifurcation, a link with *grassingtonense*. All three subspecies in common have a strong shoulder groove persisting to the large diameters but at very large diameters in *erinense* and *ferrimontanum* a ridge appears on the shoulder. A strong furrow is present laterally of this ridge in *ferrimontanum* but there appears to be a less strong furrow each side of the ridge in *erinense*. Comparably large diameters of the lower form *grassingtonense* are not available for comparison. There is still a groove at c. 20 mm. in this subspecies. The distinguishing features are the relative persistence of the ribs, their aspect, and whether or not they show bifurcations. Constrictions have so far only been seen clearly in *grassingtonense*, the earliest form.

Eumorphoceras bisulcatum leitrimense subsp. nov.

Plate 53, figs. 4, 5; Plate 54, figs. 5, 6; Plate 55, fig. 5

Description. These specimens are all rather small. Constrictions are clearly seen. 7060 is the best specimen and shows in the earlier part of the last whorl three short ribs between the constrictions. Later there appear to be only two ribs between the constrictions. The intermediate ribs are short and do not extend to the ventro-lateral groove. This groove is strong to advanced diameters. Fragments of shell devoid of all indications of ribs or constrictions are not uncommon and represent an extremely gerontic stage of this subspecies. The umbilicus is not large; at small diameters it is about 29 per cent of the total diameter. A few short ribs persist at the umbilical edge after the last constrictions, and are rather fat and stubby. At least in the early stages the constrictions are strong over the venter; unfortunately the venter at later stages has not been seen.

Holotype. 7060: diameter 10 mm.; umbilical diameter 2.5–3 mm. (Pl. 53, fig. 4). *Paratypes*. 7061: diameter 16 mm. (Pl. 55, fig. 5). 7062: diameter 10 mm. 7063: diameter 5 mm. (Pl. 53, fig. 5). 7064: diameter 7–8 mm.; umbilical diameter 1.5–2 mm. (Pl. 54, fig. 6).

Type locality and horizon. Basal beds at L21(9)27, western exposure. It also occurs in basal beds at L21(9)28 and in Valley 3 (L21(9)24) and Valley 4 (L21(9)23). The E₂b2 horizon on which this form occurs is above beds rich in *Ct. edalense* and well below the top faunal band. Associated with this form are several variants of *Posidonia corrugata*, and *Anthracoceras* cf. *A. paucilobum*.

Discussion. From a consideration of specimens 7060 and 7064 it appears that in the last constrictions seen, there are only two intervening short ribs, of which either one or both coincide with the actual edge of the constriction, which is raised and rib-like close to the umbilicus. In the earlier part of the last whorl, which shows these intermediate short ribs, one of these, the first to develop, coincides with the edge of the constriction. The constrictions show a strong forward curve in all cases.

Not many subspecies of *E. bisulcatum* with constrictions have been described. H. Schmidt (1934, p. 455) defines *E. bisulcatum varicata*; this form, at a diameter of 12 mm., has seven ribs reducing to four between the constrictions. The constrictions are shown on his figure (op. cit., p. 449, fig. 29) to continue strongly over the venter and the umbilicus looks quite large compared with the Slieve Anierin material. The short intermediate ribs are the same in both cases but in the German specimens there are greater numbers of intermediate riblets between the constrictions.

E. bisulcatum grassingtonense Dunham and Stubblefield (1944, pp. 258–60) has constrictions which number about five/whorl and usually have about five ribs between them. However these intermediate ribs are not short but geniculate, and reach to the ventrolateral groove. Also there is occasionally the appearance of a bifurcation. The type specimen of this form does not show any constrictions over the venter and the form is obviously distinct from the Slieve Anierin material. The constrictions are less obvious in *grassingtonense*. The only form so far described which bears any resemblance to the author's specimens is *E. bisulcatum varicata*, but the former can be distinguished by means of the very low number of intermediate riblets between the constrictions.

The varieties of *E. bisulcatum* from the Scottish limestones (see Currie 1954, pp. 581–4, pl. 4, figs. 5–7) do not seem to resemble this subspecies. GSM Da 1593, 1594, and 1599, collected from a section in the left bank of the stream, 150 yards south-east of Low Stubbing and 820 yards N. 10° W. of Holy Trinity Church, Cowling, are thought to be the same as the Slieve Anierin form.

EXPLANATION OF PLATE 55

All specimens are from Slieve Anierin, Co. Leitrim, Eire.

Figs. 1–4. *Eumorphoceras rostratum* sp. nov. 1, 7066, paratype, showing one rib bifurcation and the shallow groove between the curve of the flank and the ridged edge of the venter, $\times 3.8$. 2, 7067a, holotype, external mould, $\times 3.5$. 3, 7067b, paratype, $\times 6$. 4, 7068, paratype, $\times 3$.

Fig. 5. *Eumorphoceras bisulcatum leitrimense* subsp. nov. 7061, paratype, external mould showing persistent ventro-lateral groove but early loss of ribs and constrictions, $\times 4.6$.

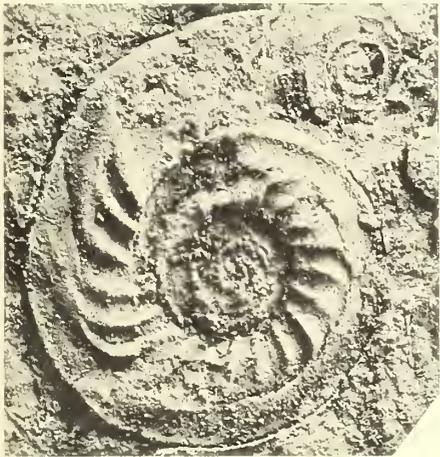
Fig. 6. *Cravenoceras leion* Bisat, 7076, fragment of internal mould showing two constrictions and the acute edged umbilicus, $\times 4$.



1 x 38



2 x 35



3 x 6



6 x 4



4 x 3



5 x 46

Eumorphoceras rostratum sp. nov.

Plate 55, figs. 1-4

Description. These specimens are very strongly ribbed from the smallest diameters seen. The largest complete specimen at 27 mm. diameter still shows very strongly developed ribs. At 10 mm. diameter there are about eleven ribs in half a whorl. Occasionally a rib forks (e.g. in specimen 7066). At 18 mm. diameter there are about fourteen ribs in half a whorl. The ribs pass strongly and radially (with a forward trend) over the flank for about half to two-thirds of the distance between the umbilical edge and the shoulder groove. They then begin to curve forwards, and thereafter lose their strength and merge into growth lines which pass forwards into an extremely deep lingua over the strong ridge at the shoulder. There is a shallow concavity between the curve of the flank and the strong ridge which marks the junction of the curved flank and the venter (the venter is usually embedded but the ridge at the edge of the flank apparently passes straight down into, and is the edge of, the flattened venter).

Holotype. 7067a (counterpart 7211): diameter 27 mm. (Pl. 55, fig. 2). *Paratypes.* 7067b (counterpart 7212): small specimen on this slab, diameter 10 mm. (Pl. 55, fig. 3). 7066: diameter 20 mm. (Pl. 55, fig. 1). 7068: diameter 20 mm. (Pl. 55, fig. 4). 7069: diameter 20 mm.

Type locality and horizon. Valley 4, L21(9)23; also Valley 2, L21(9)25. All the specimens were collected from a very prominent fossiliferous horizon which is the highest on Slieve Anierin, E₂b3. They are members of a very abundant fauna which includes *Ct. nititoides*, *Chaenocardiola footii*, *Weberides* cf. *W. shumnerensis*, &c., and which occurs about 40 feet above *E. bisulcatum leitrinense* subsp. nov.

Discussion. The distinguishing features of these specimens are the very pronounced lingua in the growth-lines; the early merging of strong ribs into fine growth-lines which often takes place about half-way across the flank; the strong ridge at the junction of venter and flank; and the very shallow depression between this ridge and the gently curved flank. The ribs are still strong at large diameters. No constrictions have been seen. Moore (1946) has described specimens of *E. bisulcatum* s.l. from Samlesbury Bottoms, River Darwen, Lancs., where they are associated with *Nuculoceras nuculum*. They therefore occur at a higher horizon than the Slieve Anierin specimens. A study of Moore's specimens in the Geological Survey Museum results in the conclusion that the forms are not the same. In GSM 72603 (Moore 1946, pl. 22, fig. 3) there is a definite groove at the shoulder and the ribs persist across the flanks to this groove. 7067b from Slieve Anierin is approximately the same size for comparison and is distinctly different. The strong ribs have merged into growth-lines and start their forward swing to the lingua about half-way across the flank; also, there is no prominent shoulder groove but only a slight dip on the flank side of the sharp edge which lies between flank and venter. The test is seen in the specimens described by Moore and shows spiral lirae (GSM 72602, pl. 27, fig. 2). These have not been seen in the Slieve Anierin material, but the vagaries of preservation may well be responsible for this absence. A point of similarity is that the ridge (at the margin of the flank) which slopes down to the venter is also present in Moore's material, but in the latter is flanked by a decided groove which is already present by 3 mm. diameter.

Miller and Youngquist (1948, pp. 665-7, pl. 100, figs. 1-4, 20, 21) have defined the species *E. plummeri*, which they believe closely resembles the form described by Moore.

From their plate and descriptions the same distinctions from the Slieve Anierin specimens as those for Moore's material are valid.

Subfamily HOMOCERATINAE Spath
Genus CRAVENOCERAS Bisat 1928

Genotype: *Cravenoceras malhamense* (Bisat 1924). Bisat originally defined this genus in 1928 but subsequently described it far more fully (1932, pp. 27–36, pl. 1, 2). Within the genus he separated two groups, one around forms like *C. leion* Bisat and *C. malhamense* (Bisat) with delicate non-dichotomizing striae, and another group with stronger dichotomizing ornament and including such forms as *C. edalense* Bisat and *C. nitidum* (Phillips). Hudson (1941, p. 282, footnote) later separated off the latter group as a new genus, *Cravenoceratoides*, but left the other group as *Cravenoceras*.

Cravenoceras cf. *C. gairense* Currie

Plate 56, figs. 1, 2

Cravenoceras gairense Currie 1954, pp. 577–9, figs. 8–10; text-figs. 6*b*, *c*.

Description. This form is interpreted as moderately globose. The umbilicus is not large and probably occupies about a quarter or less of the diameter. The ornament consists of fine non-bifurcating striae, having a distribution of three or four per 1 mm. at about 6 mm. from the umbilical edge. The striae are radial with a very slight forward trend from the umbilicus. There are three raised spiral ridges around the umbilicus; in the impressions they are seen in reverse as impressed furrows separated by low curved ridges. The spiral ridges are raised above the general curvature of the flanks to form a rim around the umbilicus.

Dimensions. The specimens are generally too fragmentary for accurate measurement; the following are relatively complete, although squashed, specimens. 7082 (counterpart 7256): diameter *c.* 8 mm.; umbilicus 2 mm. 7083 (counterpart 7257): diameter *c.* 8 mm.; umbilicus 2 mm. (Pl. 56, fig. 1).

Localities and horizon. The specimens were all collected at localities L21(13)4, L21(5)11, and L21(5)10, which are all thought to be at approximately the same stratigraphical level and represent a high E₂ horizon.

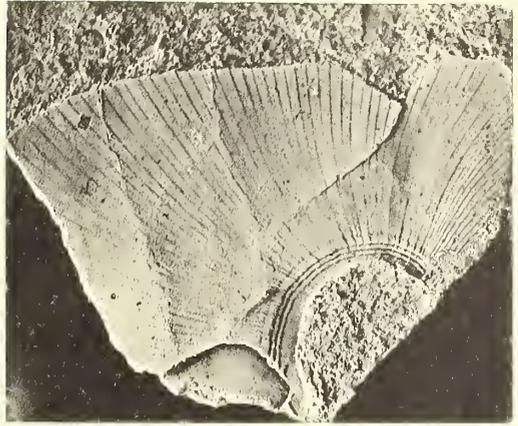
Discussion. This distinctive species has been described by Currie from the Gair Limestone of Lanarkshire, and other specimens from the Calmy Limestone of Lanarkshire are also mentioned. Currie (1954, p. 532) has given a table showing the possible stratigraphical relationships of the Scottish deposits, from which it appears that the Calmy Limestone and the Gair Limestone are both higher in E₂ than the beds on Slieve Anierin

EXPLANATION OF PLATE 56

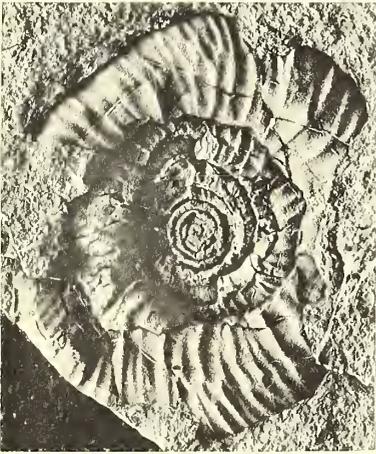
- All specimens are from Slieve Anierin, Co. Leitrim, Éire.
Figs. 1, 2. *Cravenoceras* cf. *C. gairense* Currie. 1, 7083, $\times 5.25$. 2, 7084, fragmentary external mould showing spiral ornament around the umbilicus, $\times 5$.
Figs. 3, 4, 6. *Cravenoceratoides* cf. *Ct. bisati* Hudson. 3, 7103, showing irregular bifurcating lirae, $\times 4.5$.
4, 7104, external mould showing repeated bifurcation of lirae, $\times 3.5$. 6, 7105, external mould showing irregular bifurcation of lirae, $\times 4$.
Fig. 5. *Cravenoceratoides edalense* (Bisat). 7101, part of internal mould with a constriction, and an external mould showing the symmetrical lirae with one bifurcation, $\times 5.3$.
Fig. 7. *Chaenocardiola footii* (Baily). 7174, external mould, $\times 6.5$.



1 × 5.25



2 × 5



3 × 4.5



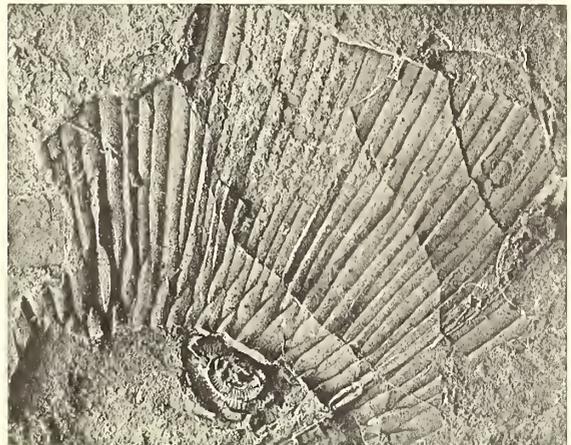
4 × 3.5



7 × 6.5



5 × 5.3



6 × 4

are believed to be. The fauna associated with *C. gairense* in the Scottish limestones is rather similar to that which occurs at a higher level on Slieve Anierin within the *Ct. nitidus* zone E₂b. Currie (*in litt.*, 1959) admits the great similarity of the Irish material to her specimens but is unwilling to go any further with shale impressions only. The specimens are therefore probably best identified as *Cravenoceras* cf. *C. gairense*. Currie mentions a specimen in the Geological Survey Museum (GSM RM77) which resembles her species but apparently lacks the middle spiral line. In addition GSM JS1479 and JS1492 from Crickton, Glam., appear to be very close to *C. gairense*. GSM JS1121 from near Ilston, Glam., is also close.

Cravenoceras subplicatum Bisat

Plate 57, fig. 1

Cravenoceras subplicatum Bisat 1932, pp. 30–31, pl. 1, fig. 5.

Description. The shape of these specimens is not easy to interpret but is apparently a slightly flattened cadicone. The ornament consists of very fine non-bifurcating striae, which are radial with no backward deflection near the umbilical edge. The umbilicus is about a quarter or slightly more of the total diameter. There are two noticeable features in these specimens. The first is seen on 7085, which shows the impressions of rather widely spaced striae over the venter and more sharply incised impressions of some of the striae at the umbilical edge. The other feature is seen on the internal mould 7086, which shows a tendency to form undulations of the surface which fan outwards from the umbilicus and fade away over the flanks and venter. Each of these undulations bears on its surface several striae, one of which usually appears somewhat more prominently than those on either side of it.

Dimensions. All the specimens are small and imperfectly preserved, and it is difficult to give accurate dimensions; the diameters are considered to be from 10–14 mm.

Localities and horizon. Most of the specimens have been collected from Valley 4, L21(9)23, from an E₂b1 level between the *Ct. edalense* beds and beds with *E. bisulcatum leitrinense* subsp. nov. They are particularly common in a band just beneath that containing the latter. They are associated with *Posidonia corrugata* and its subspecies. Less perfect examples have been collected from just above the *Ct. edalense* beds. Good specimens have been collected at localities L21(9)1–14.

Discussion. These specimens are very abundant and in view of their stratigraphical position it is important to decide on their affinities. They contrast with *C. cowlingsense* Bisat (1932, pp. 29–30, pl. 1, figs. 1–3) in the absence of any backward deflexion in the ornament; also the ornament is rather finer (at any rate at these diameters though possibly larger specimens would show a coarser ornament). They differ from *C. holmesii* Bisat (1932, p. 31, pl. 1, fig. 6) in the absence of a rim around the edge of the umbilicus. Two features of the Slieve Anierin material have been particularly noted and despite the differences in preservation both features are revealed in an examination of the type material of *C. subplicatum*. The holotype, GSM 49963 (from Birstwith Beck, near Hampsthwaite, Yorks.), of about 11 mm. diameter, shows very fine striations with periodically sharper plications at the umbilical edge. These become less obvious away from the umbilicus but there is still a tendency for periodic striae on the flanks and venter to be stronger than their adjacent ones, which are frequently so faint as to be

barely perceptible. As a result of this the stronger striae stand out and give the impression of a very widely spaced ornament (seen in 7085). The other feature, already described in 7086, may possibly be associated with slightly larger size. GSM Z1 5806, a topotype of *C. subplicatum*, with a diameter of about 13 mm., shows the plications at the umbilical edge, but in this case there is apparently a raising up of several striae, and this bundle fans outwards away from the umbilicus and fades over the flanks and venter back into the normal convexity.

Genus CRAVENOCERATOIDES Hudson 1941

Genotype: *Cravenoceratoides nitidus* (Phillips).

Cravenoceratoides nitidus (Phillips)

Plate 52, fig. 6

Goniatites nitidus Phillips 1836, pp. 235–6, pl. 20, figs. 10–12.

Homoceras nitidum (Phillips); Bisat 1924, p. 106.

Cravenoceras nitidum (Phillips); Bisat 1932, pp. 34–35, pl. 2, fig. 3.

Cravenoceratoides nitidus (Phillips); Hudson 1946, pp. 376, 383, pl. 21, fig. 11; pl. 21a, figs. 1a–c.

Description. The shape is apparently cadicone. The umbilicus is rather wide, and about a third of the diameter. The ornament consists of radial bifurcating lirae. In the external impressions these can be seen to be asymmetrical (canted). The bifurcation in the lirae at a diameter of 14 mm. is about 1 mm. from the edge of the umbilicus; at the same diameter the lirae are about two per mm. on the venter. There is no forward arching in the lirae even in the largest specimens. The tendency in this species is for the bifurcation to stay uniformly close to the umbilical edge, with little or no tendency to migrate over the flank as growth advances.

Dimensions. 7094: diameter 14 mm., umbilicus 4.5 mm. (Pl. 52, fig. 6). 7095: diameter 28–30 mm., umbilicus c. 9 mm. 7096: diameter c. 22 mm., umbilicus 7.5–8 mm.

Locality and horizon. All the specimens so far collected come from the highest faunal band, E₂b₃, in Valley 3, L21(9)24. The fauna at this level is very rich in *Ct. nititoides*, *E. rostratum* sp. nov., *Euchondria* aff. *E. levicula*, *Chaenocardiola footii*, *Weberides* cf. *W. shunnerensis*, &c. The specimens of *Ct. nititoides* are more abundant than *Ct. nitidus*.

Discussion. This species is distinguished from *Ct. nititoides* by the larger umbilicus and the lack of the forward curve in the lirae, which in *Ct. nitidus* are radial. In all the examples of *Ct. nititoides* examined there is a tendency for the bifurcation of the lirae to

EXPLANATION OF PLATE 57

All specimens are from Slieve Anierin, Co. Leitrim, Eire.

Fig. 1. *Cravenoceras subplicatum* Bisat. 7087, external mould showing in the later whorls striae which are more widely spaced and stronger at the umbilical edge, $\times 4.25$.

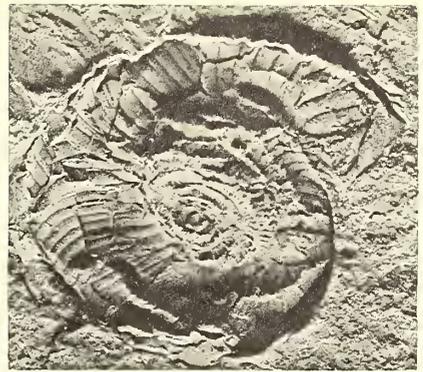
Fig. 2. *Cravenoceratoides edalense* (Bisat). 7102, external mould showing singly bifurcating symmetrical lirae, $\times 5$.

Fig. 3. *Anthracoeras tenuispirale* Demanet. 7129, crushed specimen showing spiral ornament, $\times 16$.

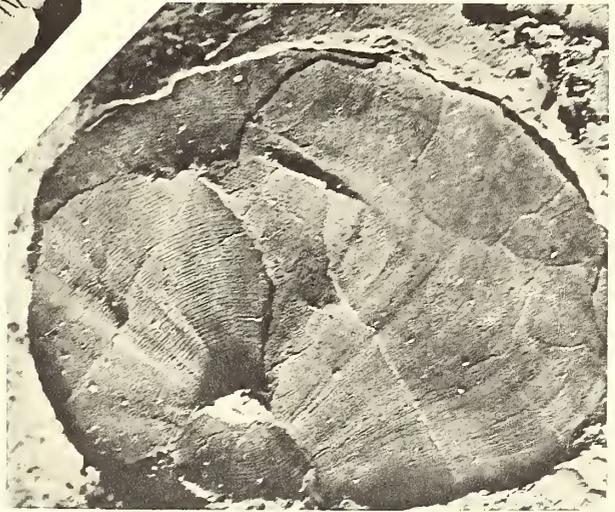
Figs. 4, 5. *Cravenoceratoides nititoides* (Bisat). 4, 7099, external mould showing bifurcating asymmetrical lirae tending to curve forward over flanks, and the small umbilicus, $\times 3.3$. 5, 7097, $\times 5$.



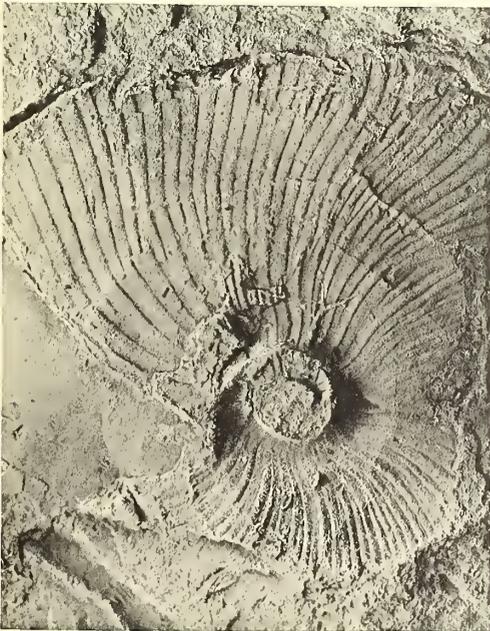
1 × 425



2 × 5



3 × 16



4 × 33



5 × 5

move over the flank during ontogeny. This is hardly seen at all in *Ct. nitidus* where the position of the bifurcation stays close to the umbilical edge. In both species the lirae are asymmetrical (canted), in contrast to the symmetrical lirae (tented) of *Ct. edalense* and *Ct. bisati* (Hudson, 1946). Schmidt (1934, p. 449, fig. 42) figures *Cravenoceras* cf. *C. nitidum* (Phillips) from Germany, and his figure shows an umbilical diameter of about a third of the total diameter, but the bifurcations are not very clear on the drawing, which cannot be compared with the present specimens. The latter are closely comparable, however, with the lectotype of *Ct. nitidus*, BM C279a, which has been figured by Hudson (1946, pl. 21a, figs. 1a-c).

Cravenoceratoides nititoides (Bisat)

Plate 57, figs. 4, 5

Cravenoceras nititoides Bisat 1932, p. 35, pl. 2, fig. 2.

Cravenoceras nititoides Bisat; Schmidt 1934, p. 450, fig. 47.

Cravenoceras nititoides Bisat; Demanet 1941, pp. 143-4, pl. 6, figs. 6-8.

Cravenoceratoides nititoides (Bisat); Hudson 1941, p. 282.

Cravenoceratoides nititoides (Bisat); Hudson 1946, pp. 375, 376, 383, pl. 21, fig. 8.

Description. This species occurs crushed, but if undeformed it would probably be a slightly flattened cadicone. The plications bifurcate once, the bifurcation occurring a short distance over the flanks away from the edge of the umbilicus. The plications have a very slight forward swing over the flanks and are asymmetrical (canted). The umbilicus is small.

Dimensions. 7097: diameter 11 mm. (Pl. 57, fig. 5). 7098a: large specimen, diameter 18 mm., umbilical diameter 3 mm. 7098b: one small specimen, diameter 11 mm., umbilical diameter 2 mm. 7099 (counterpart 7261): very squashed, umbilicus 3.5 mm. (Pl. 57, fig. 4). 7100: diameter 24 mm., umbilicus 4 mm.

Locality. All the specimens were collected from the highest faunal band on Slieve Anierin, and mainly from Valley 3, L21(9)24. The band, which is about 9 inches thick, is exposed at stream level almost at the upper end of this valley. Above the band there are about 40 feet of unfossiliferous rusty shales which are followed by about 12 feet of white, flaggy sandstones with plants.

Horizon. This band, which is of E₂b₃ age, is rich in fossils; *Ct. nititoides* is very common and occurs with *E. rostratum* sp. nov., *Chaenocardiola footii*, *Euchoudria* aff. *E. levicula*, *Weberides* cf. *W. shunnerensis*, *Productus hibernicus*, plates and spines of *Archaeocidaris urii*, *Stroboceras subsulcatus*, *Fenestella* sp., &c.

Discussion. In his original description Bisat distinguishes this form from *Ct. nitidus* by the fact that 'the plications are somewhat forwardly arched on the conch in adolescence, becoming radial in the adult'. Also the umbilicus is smaller in *nititoides* than in *nitidus*. The canted (asymmetrical) nature of the plications in these two species distinguishes them from sharply symmetrical (tented), plicated forms such as *Ct. edalense* or *Ct. bisati*. *Ct. stellarum* also has typically tented plications. The holotype of *Ct. nititoides* from Pace Gate Beck, near Bolton Abbey, is remarkably like the forms from Slieve Anierin. Tonks (1925, pp. 251-2) originally described the Pace Gate Beck section and the fauna, as on Slieve Anierin at this level, includes *E. bisulcatum*, trilobites, and a *Productus*. Unfortunately there are no exposures at this locality now and very little of the original material is available apart from the holotype of *nititoides*.

Cravenoceratoides edalense (Bisat)

Plate 56, fig. 5; Plate 57, fig. 2

Cravenoceras edalense Bisat 1928, p. 132, pl. 6, 6a, figs. 4, 4a.*Cravenoceratoides lirifer* Hudson 1946, pp. 380–5, pl. 21, figs. 1–3, 5–7.

Description. This form shows a planulate stage in the very early whorls, but with advancing development an increasingly globose shape is assumed. In most examples a wide and deep umbilicus reveals the early planulate whorls. The degree of involution is not very great even at the very advanced stages. There is a strong and bifurcating ornament; the lirae are sharply defined and symmetrical. Hudson (1946, p. 383) uses the expression 'tented' for such lirae. The early planulate whorls show much finer and closer ornamentation. The venter is broad with little or no indication of a ventral sinus in the lirae. In these specimens it is rather difficult to determine the exact position of the bifurcation of the lirae; in many the single bifurcation appears very close to the umbilical edge, but in others it appears to be nearer the edge of the broad venter.

Dimensions. The rather imperfect preservation of these globose forms results in distortion of their original dimensions and accurate measurements are difficult to make. The diameters of the shells have not been measured, except in the less deformed planulate stages, which are up to 5–6 mm. approximately.

Localities and horizon. All the specimens have been collected from the shales in the lower part of Valley 4, L21(9)23, and from localities L21(13)2, L21(13)3, and L21(9)20. They occur in the first fossiliferous horizon above the thick grit, E₂b1. They are associated with subspecies of *Posidonia corrugata*.

Discussion. Bisat (1928) originally figured *Cravenoceras edalense*, and subsequently refigured it (1932, p. 33, pl. 1, figs. 4a, b). The specimens refigured in 1932 were later placed by Hudson (1946) in a new species, *Cravenoceratoides bisati*. Hudson also erected the new species *Cravenoceratoides lirifer* (1946, pp. 380–5, pl. 21, figs. 1–3, 5–7). The specimens separated by Hudson from *Ct. edalense* s.s. as *Ct. bisati* are distinguished by an irregular and repeated bifurcation of the lirae. This character is seen also in the figures given by H. Schmidt (1934, p. 448, figs. 23, 24) of *Cravenoceras edalense*. These forms appear to be specifically distinct from *Ct. edalense* s.s., in which there is only one bifurcation, but the writer has been unable to recognize any way of separating *Ct. edalense* s.s. from *Ct. lirifer*, and since the species predated *Ct. lirifer* the name of *Ct. edalense* seems more applicable to the abundant examples which occur on Slieve Anierin.

Cravenoceratoides cf. *Ct. bisati* Hudson

Plate 56, figs. 3, 4, 6

Cravenoceratoides bisati Hudson 1945, pp. 376–80, pl. 21, figs. 4, 10; text-fig. 1a.

Description. These specimens are similar in general shape to *Ct. edalense* but are distinguished by an irregular bifurcating ornament. In addition to the tendency for repeated bifurcation there is a tendency for the neighbouring branchlets from two bifurcating lirae to run together and continue as one lira, which may subsequently be seen to bifurcate. This is best seen in specimens 7103 (Pl. 56, fig. 3) and 7105 (Pl. 56, fig. 6).

Localities and horizon. These specimens occur at the same localities as *Ct. edalense* s.s. and on the same horizon, E₂b1, but they are not so abundant.

Superfamily DIMORPHOCERATACEAE Hyatt 1884

Family DIMORPHOCERATIDAE Hyatt 1884

Genus KAZAKHOCERAS Ruzhencev 1947

Kazakhoceras scaliger (Schmidt)

Plate 59, fig. 4

Dimorphoceras? scaliger Schmidt 1934, p. 458, fig. 2.

Description. Compressed and involute forms with a sharp venter and minute umbilicus. The most obvious feature is the lattice or reticulate pattern which covers the surface and which is unmistakable even in very small fragments of the shell. This lattice pattern bears no relationship to the growth-lines, which can frequently be seen with it. The growth-lines are suggestive of a member of the Dimorphoceratidae; the strong umbilical bow is well seen in 7108 with lattice ornament also.

Dimensions. 7109 (counterpart 7249): diameter 21 mm. 7112: radius 11 mm. (Pl. 59, fig. 4). 7110: diameter 14 mm. 7111 (counterpart 7246): radius 30 mm.

Localities and horizons. These specimens have been collected from two levels on Slieve Anierin. At the lower level seen at L21(13)7, and at L21(5)4 and 5, they are associated with *Cravenoceras* aff. *C. malhamense*, *Caneyella membranacea*, and *Chaenocardiola footii* in E_{1c}. At the higher level seen at L21(5)11 and at L21(13)4 the fauna is a larger one and includes *Cravenoceras* cf. *C. gairense*, *E. bisulcatum erinense* subsp. nov., *E. bisulcatum ferrimontanum* subsp. nov., *Posidonia corrugata* and subspecies, *Chaenocardiola footii*, and *Dunbarella elegans*. The species is more abundant at this higher level, which is considered to be in high E_{2a}.

Discussion. In his original description of this form H. Schmidt (1934, p. 458) doubts whether the lattice pattern is true ornament, and expresses the belief that it may be the wrinkled layer. I believe the lattice pattern is ornament, but it is impossible to be definite on this issue without studying solid specimens capable of dissection. The species is found on Slieve Anierin only at the two levels indicated above, with its greatest abundance undoubtedly in the E_{2a} horizon. Schmidt's original examples were apparently from E₁ beds, as are those from the lower level on Slieve Anierin. Ruzhencev (1947) erected *Kazakhoceras* to include forms like *Neodimorphoceras* but with differences in the suture and with a sharply keeled venter. The Slieve Anierin specimens with the lattice pattern are tentatively placed here. Many specimens with this lattice ornament in the Geological Survey Museum collection have been identified as *Neodimorphoceras hawkinsi* (Moore). In particular the material from Holbeck (Stephens *et al.* 1953, p. 28) has been referred to this species, but on examination these specimens appear to be the same as those which I have referred to *K. scaliger*. Schmidt (1934, pp. 458; 446, fig. 2) does not comment on the suture of his species. Neither does Moore (1958, pp. 225-6) make any comment on the ornament of *K. hawkinsi*, nor does he include *K. scaliger* in the synonymy of his species. In the absence of any definite sutural proof that these two forms are conspecific, I prefer to retain the specific name *scaliger* for specimens showing the lattice pattern. This practice has some stratigraphical value since the specimens only occur on two horizons. Moore (1958, p. 225) records *K. hawkinsi* from P₂ and E₂ horizons and says that it is impossible to distinguish between the specimens from two such widely different levels. *Neodimorphoceras* cf. *N. scaliger* is recorded by Hudson and Cotton (1943, p. 163) at the base of E₂ and in the *C. malhamense* E_{1c} zone (op. cit.,

p. 167), and these are the same two levels at which the species has been found on Slieve Anierin.

Genus ANTHRACOCERAS Frech 1899

Anthracoceras tenuispirale Demanet

Plate 57, fig. 3; Plate 58, fig. 4; Plate 59, fig. 1

Anthracoceras tenuispirale Demanet 1941, pp. 148-9, pl. 6, fig. 18; pl. 7, figs. 1, 2.

Description. A very involute species with a small umbilicus. The shell is ornamented with delicate radiating lirae, which when first seen are evenly curved over the flanks but progressively develop a lingua on the ventro-lateral area. With high magnification it is possible to distinguish a spiral ornament on the very early part of the shell which fades as the radial ornament becomes important. The spiral ornament is seen to be dominant on specimens up to 6 mm. diameter, at which stage the radial ornament is appearing. Thereafter the radial ornament becomes increasingly important, with a high and moderately deep lingua forming by 9 mm. diameter (7127). Indications of constrictions are present in the spirally striated specimens; 7128 shows at least three such constrictions.

Dimensions. 7126: diameter 6 mm. (radials more or less smoothly curved and just appearing). 7128 (counterpart 7357): diameter 6 mm. (radials more or less smoothly curved and just appearing) (Pl. 58, fig. 4). 7129: diameter 5 mm. (spirals only) (Pl. 57, fig. 3). 7130: diameter 3.5 mm. (spirals only). 7131: diameter 8 mm. (radials beginning to show the lingua). 7132: diameter 10 mm. (radials beginning to show the lingua). 7127: diameter 9 mm. (radials showing definite lingua) (Pl. 59, fig. 1).

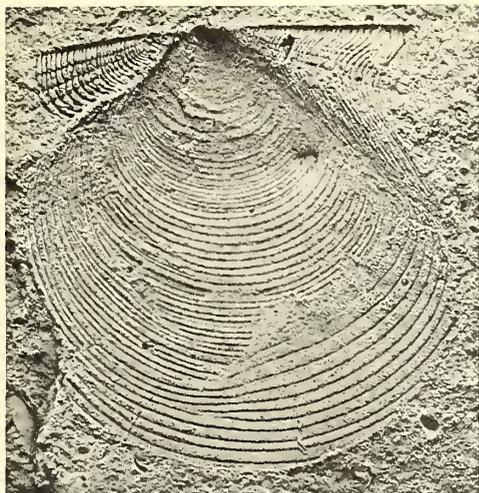
Localities and horizon. Most of the specimens were collected in Valley 3, L21(9)24. The species occurs in abundance in E₂b2 between the band with *E. bisulcatum leitrinense* subsp. nov. and the top faunal band with *E. rostratum* sp. nov. and *Ct. nititoides*. It is associated with *C. holmesi*, *P. corrugata*, *Posidoniella variabilis*, and *P. variabilis erecta* subsp. nov.

Discussion. These specimens undoubtedly show the characteristics of Demanet's species, which has so far only been described from Belgium. Demanet apparently believes that the spirals are a feature of the inside of the test and the radials the outside. He comments that in some specimens the two forms of ornament may be seen superimposed. The author's specimens, though numerous, are inconclusive on this point. If the spirals are internal ornament then the outside of the shell would seem to have been without ornament until about 5-6 mm., when the first radials appear in the author's material. Currie, with experience of better material of *Anthracoceras*, states (*in litt.*) that the spiral ornamentation she has seen in other species has been a feature of both the inside and the outside of the test.

EXPLANATION OF PLATE 58

All specimens are from Slieve Anierin, Co. Leitrim, Eire.

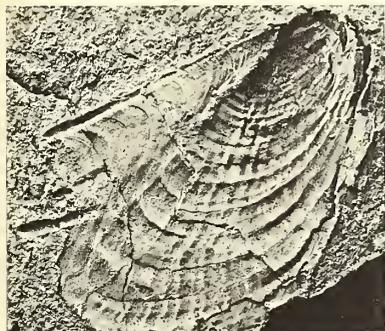
- Figs. 1, 2. *Euchondria* aff. *E. levicula* Newell. 1, 7165, external mould of right valve with no radial ornament, $\times 7.25$. 2, 7158, internal mould of left valve with external ornament impressed upon it, $\times 6$.
 Fig. 3. *Actinopteria persulcata* (M'Coy). 7223, external mould of left valve, $\times 4$.
 Fig. 4. *Anthracoceras tenuispirale* Demanet. 7128, showing spiral striae with indications adorally of the radial ornament, $\times 20$.
 Fig. 5. *Posidonia corrugata* (Etheridge). 7144a, left valve, $\times 6.5$.



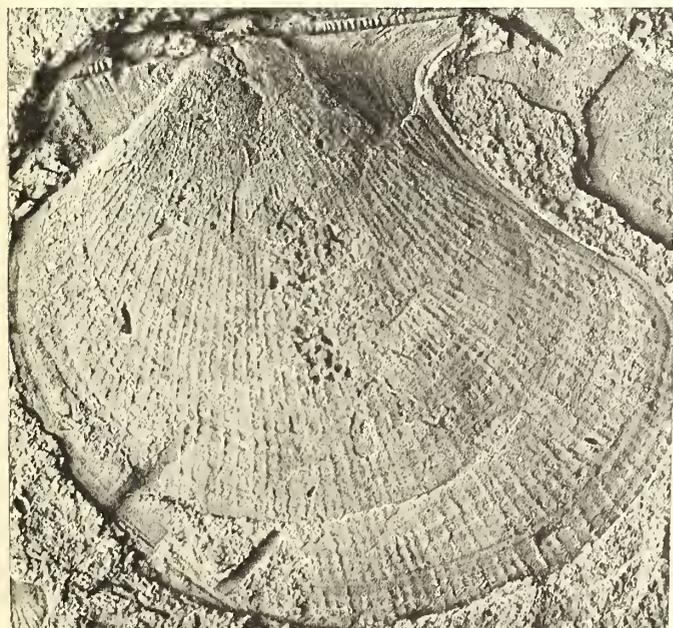
1 × 7.25



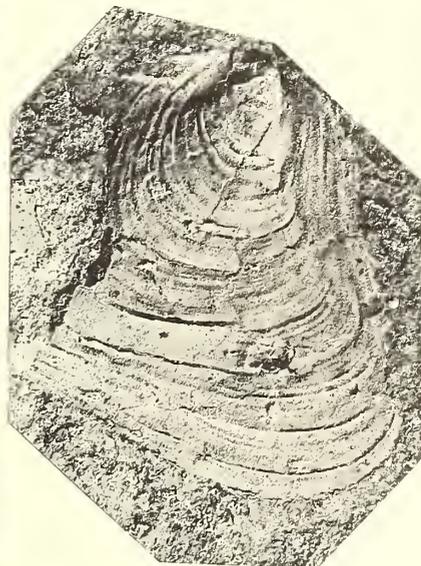
4 × 20



3
× 4



2 × 6



5 × 6.5

In view of the great abundance of *A. tenuispirale* on Slieve Anierin at E₂b levels it seems remarkable that it has not been described from beds of the same age elsewhere. The very high magnification that is needed to see these early spirals makes it very likely that such specimens have been assigned to *A. paucilobium* (Phillips) or *A. glabrum* Bisat, which it closely resembles in other respects.

GSM CS891 from the Colsterdale Marine Band (E₂b) in a stream section 300 yards west of Ivin Waite, west of Pateley Bridge, Yorks., although labelled as *Cravenoceras* cf. *holmesii* is seen to be *A. tenuispirale* when suitably magnified. Bisat has seen a photograph and agrees with me (*in litt.*, 1960) that this is the case. He also comments that this raises the question of whether some other records of *C. holmesii* in the literature may not in fact also be *A. tenuispirale*. This occurrence is interesting in that it is thought to occur at a similar level to that on which the species is so abundant on Slieve Anierin.

Class LAMELLIBRANCHIATA Blainville 1816

Family PTERINOPECTINIDAE Newell 1937

Genus POSIDONIA Bronn 1828

Posidonia corrugata (R. Etheridge jun.)

Plate 58, fig. 5; Plate 60, fig. 4

Posidonomya corrugata Etheridge 1873, pp. 103–4.

Posidonomya corrugata Etheridge; Etheridge 1874, pp. 304–5, pl. 13, figs. 4, 5 (*non* fig. 6).

Posidonomya corrugata Etheridge; Hind 1901, pp. 30–31, pl. 6, figs. 1, 2, 5.

Posidonomya corrugata Etheridge; Weigelt 1922, pp. 93–95, fig. 17.

Posidonomya corrugata Etheridge; Schmidt 1934, p. 446, fig. 8; p. 451, fig. 52.

Posidonia corrugata (Etheridge); Ramsbottom 1959, p. 406.

Description. The hinge-line is short. The height and greatest antero-posterior measurement are approximately the same. The umbo is prominent and nearer the anterior end of the hinge from which it is separated by a narrow anterior wing, which in some specimens is slightly concave but in most is flattened. The anterior margin descends from the hinge-line at first vertically but soon swings forward obliquely to this short vertical piece; farther downwards the direction of the anterior margin changes from this forward swing to a steeper one and it then curves round smoothly into the ventral margin.

The posterior margin is oblique, and both it and the ventral margin show a considerable degree of backward extension. The surface of the valve bears strong concentric corrugations as well as less prominent growth lines.

Dimensions. 7144a (counterpart 7277): left valve, height 9 mm., greatest antero-posterior measurement 10 mm. (Pl. 58, fig. 5). 7144b, c (counterpart 7277): two left valves, height 8 mm., greatest antero-posterior measurement 7 mm. 7145 (counterpart 7278): two left valves, height c. 9 mm., greatest antero-posterior measurement 13 mm. (Pl. 60, fig. 4). 7146: right valve, height 7–8 mm., greatest antero-posterior measurement 7–8 mm. 7147 (counterpart 7282): left valve (also deformed right valve), incomplete greatest antero-posterior measurement 8 mm.

Localities and horizons. This species has been collected abundantly at numerous horizons ranging from P₂ to E₂. The localities on Slieve Anierin are too numerous to list separately. Specimens are particularly abundant in the shales above the grit in E₂, and they are frequently the only forms present. The abundance is often such that good individual specimens are very difficult to obtain. Some of the best examples were collected in E₂b1 shales almost immediately above the *Ct. edalense* beds in Valley 4,

L21(9)23. Locality L23(4)5 lies in the *C. leion* zone but the specimens are in every way like the ones from E₂.

Discussion. R. Etheridge jun. (1873, pp. 103–4) described this species as being very variable. In his view nearly all the adult specimens have radial ribs in addition to the concentric corrugations. The most common form of *P. corrugata* in Ireland is dominated by concentric corrugations. Specimens do exist with radial corrugations but these are not the most common and have been given specific rank as *Posidonomya trapezoedra* by Ruprecht (1937, pp. 30–31). Subspecies of this typical *P. corrugata* occur at certain horizons and are described below. They are always associated with *P. corrugata* as interpreted above.

Posidonia corrugata elongata subsp. nov.

Plate 60, fig. 1

Description. The specimens ascribed to this subspecies resemble *P. corrugata* in the possession of a narrow anterior wing and a short hinge-line. The more dorsal part of the anterior margin also resembles *P. corrugata* in that it descends vertically for a short distance and then swings forward. Thereafter, however, the anterior margin differs in following a backward course in its passage into the ventral margin and in being approximately parallel to the oblique posterior margin. The corrugations of the valves are in every way similar to those in *P. corrugata*.

Holotype. 7148a (counterpart 7216a): probably incomplete, height 10 mm., antero-posterior measurement 6 mm. (Pl. 60, fig. 1). *Paratype.* 7220: height c. 12 mm., antero-posterior dimension c. 8 mm.

Type locality and horizon. This subspecies is most common in E₂ but similar forms have been observed in lower beds. Some of the best examples were collected from the high E_{2a} horizon exposed at L21(13)4, the type locality, and at L21(5)11, and also from the E_{2b2} beds with *E. bisulcatum leirimense* subsp. nov. in Valley 4, L21(9)23.

Discussion. Specimens of this subspecies differ from the typical *P. corrugata* in being longer and narrower in shape. This difference in aspect is produced by the more backward passage of the ventral portion of the anterior margin, and also the steeper posterior margin. In some respects this subspecies might be confused with the more oblique specimens of *Caneyella membranacea* but in the latter the umbo is not so close to the anterior margin as in *elongata*, where the anterior ear is extremely narrow as also in the typical *P. corrugata*. Radial ribbing is usual in *C. membranacea* whereas it has not been clearly observed in *elongata*; if present in the latter it is faintly seen only on the more ventral part of the shell. The anterior margin in *C. membranacea* descends more or less vertically for some distance before curving round into the posteriorly inclined part of the margin,

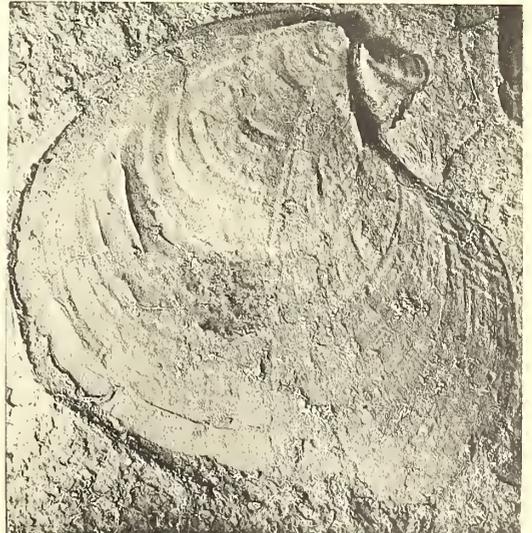
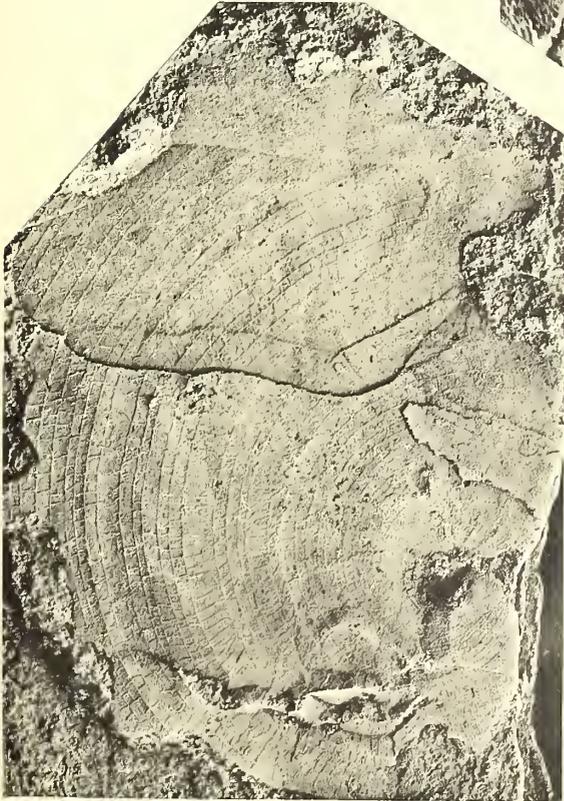
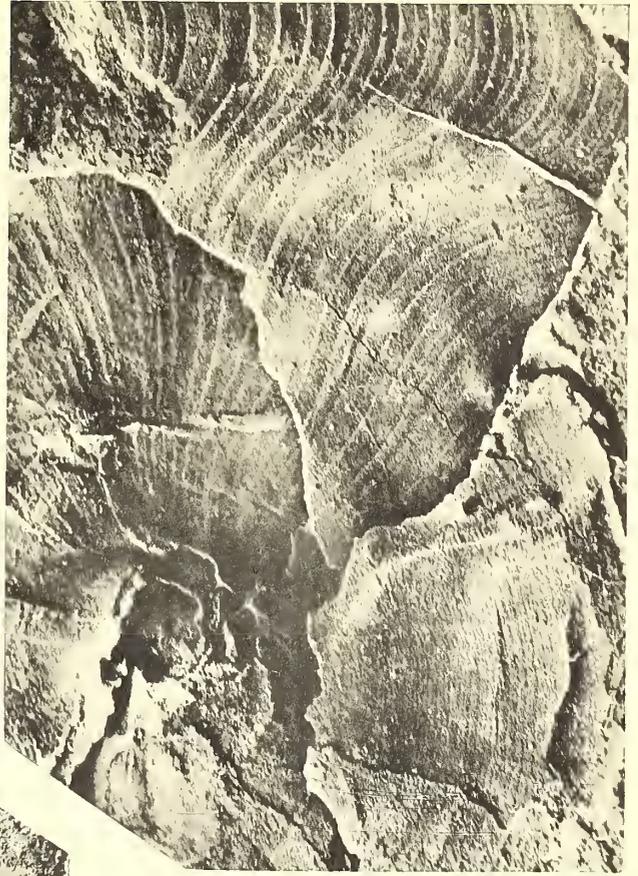
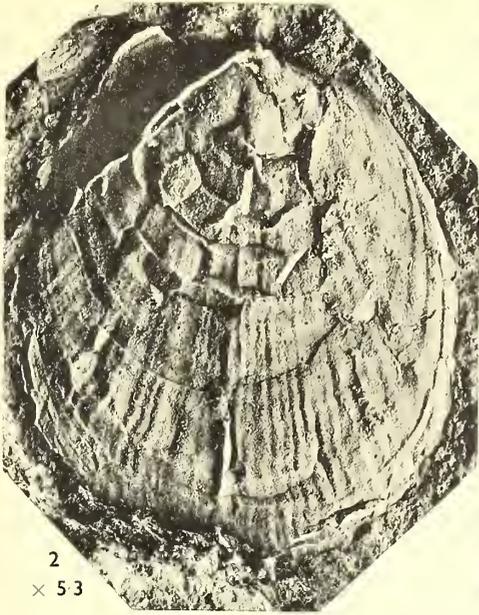
EXPLANATION OF PLATE 59

All specimens are from Slieve Anierin, Co. Leitrim, Eire.

Fig. 1. *Anthracoeras tenuispirale* Demanet. 7127, showing spiral ornament in the early whorls, and radial ornament in the adult whorl, $\times 20$.

Figs. 2, 3. *Obliquipecten costatus* sp. nov. 2, 7217, paratype, left valve, showing radial ornament, $\times 5.3$. 3, 7219, holotype, right valve, $\times 2$.

Fig. 4. *Kazakhoceras scaliger* (Schmidt). 7112, showing brickwork-like pattern, $\times 7$.



YATES, Namurian lamellibranchs and goniatites

while in *elongata* it descends in an anterior direction obliquely to the hinge-line before curving back.

Posidonia corrugata gigantea subsp. nov.

Plate 60, fig. 2

Description. This subspecies is larger and more coarsely and irregularly corrugated than *P. corrugata* or *P. corrugata elongata*. Like the latter the more ventral portion of the anterior margin descends obliquely backwards but in this subspecies it is less oblique. There is considerable backward extension of the posterior and ventral margin. The posterior margin is less steep than in *elongata*. The height and antero-posterior measurement in this subspecies are approximately the same as in *P. corrugata*. The concentric corrugations are somewhat coarser and more irregular than in the other forms.

Holotype. 7149; height 22 mm., antero-posterior measurement *c.* 20 mm. (Pl. 60, fig. 2). *Paratype.* 7150 (counterpart 7353); height 20 mm., antero-posterior measurement *c.* 16 mm.

Type locality and horizon. The best specimens have been collected in Valley 4, L21(9)23, the type locality, and Valley 3, L21(9)24. This form has so far only been seen in E₂ beds. It appears to be most common in the E₂b2 beds containing *E. bisulcatum leirrimense* subsp. nov. or just below these in E₂b1. It is also present in the slightly lower *Ct. edalense* beds, E₂b1.

Discussion. Apart from the large size and the coarse ornament this subspecies appears to combine some of the features of the normal *P. corrugata* and of *P. corrugata elongata*. In the posterior margin, which is less steeply inclined than in *elongata*, it resembles *P. corrugata*. The anterior margin resembles that of *elongata* though it is less oblique and steeper, and only slightly backwardly inclined. As a result of its large size this subspecies is particularly vulnerable to fracture and complete specimens are rare.

Genus CANEYELLA Girty 1909

Caneyella membranacea (M'Coy)

Plate 60, fig. 3

Posidonomya membranacea M'Coy 1844, p. 78, pl. 13, fig. 14.

Posidonomya membranacea M'Coy; Hind 1901, pp. 33-34, pl. 5, figs. 18-23.

Posidonomya membranacea M'Coy; Schmidt 1934, p. 446, fig. 10; (*non*) p. 448, fig. 28.

Posidonomya (Posidonia) membranacea M'Coy; Demanet 1941, pp. 80-81.

Posidonia membranacea (M'Coy); Smyth 1950, p. 317, pl. 17, fig. 6.

Caneyella membranacea (M'Coy); Ramsbottom 1959, p. 406, pl. 71, fig. 14.

Description. The hinge-line is of moderate length, with the umbo about midway along or slightly anterior. The posterior margin is very oblique to the hinge-line and passes ventrally and backwards in an almost straight line. The anterior margin at first descends approximately vertically and then curves round to pass obliquely backwards in a path approximately parallel with the posterior margin. The surface of the valve is ornamented with concentric folds and with finer growth-lines. There is also a radial ornament of obscure radial folds, of varying strength, which pass from the umbo across the valve

and terminate on the ventral margin; they are most obvious over the central area of the valve.

<i>Dimensions</i>	<i>Length—greatest distance measured parallel with the hinge-line</i>	<i>Greatest distance from the umbo to a point opposite on the ventral margin (measured parallel with the posterior margin).</i>
7154 (counterpart 7247)	c. 17 mm.	c. 31 mm.
7051 (counterpart 7266) (Pl. 60, fig. 3)	c. 22 mm.	c. 38 mm.

Localities and horizons. These are given in the description of *C. membranacea horizontalis* subsp. nov. below, and the two forms are considered together in the discussion of that subspecies.

Caneyella membranacea horizontalis subsp. nov.

Plate 61, fig. 5

Description. In this subspecies the posterior margin is not so obviously oblique to the hinge-line, instead the two lie in practically a straight line. The growth lines, however, terminate on the anterior part of this long straight apparently dorsal margin, and the actual length of hinge-line is about the same as in *C. membranacea*. After the initial vertical descent the anterior margin curves round to describe a course approximately parallel with the straight dorsal edge. The ornament in this subspecies is the same as in *C. membranacea* except that the radial folds tend to be stronger.

<i>Dimensions</i>	<i>Length—greatest distance measured parallel with the hinge-line</i>	<i>Greatest measurement from the umbo to a point opposite on the ventral margin (measured parallel with the posterior margin)</i>
7157, holotype, (Pl. 61, fig. 5)	25 mm.	22 mm.
7156	36 mm.	32 mm.

Type locality and horizons. L21(14)9, the type locality, and L23(4)19 are both considered to be high P₂; at the latter, 20 feet above the base of the section, *C. membranacea* and *C. membranacea horizontalis* are associated with *Goniatites granosus*, *Dimbarella elegans*, and *Sudeticeras crenistriatum*.

Some of the best examples on Slieve Anierin have been collected from localities L21(5)5 and L21(13)7, which are believed to be at about the same horizon, i.e. E₁c; at both these localities *C. membranacea* and *C. membranacea horizontalis* have been collected with *Cravenoceras* aff. *C. malhamense*, *Kazakhoceras scaliger*, and, about 20 feet above, *E. pseudobilingue* s.s.

Discussion. *C. membranacea* is a very variable species, but it is possible to separate two extreme forms according to the angle made by the posterior margin with the hinge-line. The forms figured by Hind and the original type from the Skerries, Co. Dublin

EXPLANATION OF PLATE 60

All specimens are from Slieve Anierin, Co. Leitrim, Eire.

Fig. 1. *Posidonia corrugata elongata* subsp. nov. 7148a, holotype, right valve showing dorso-ventrally elongated form, $\times 7$.

Fig. 2. *Posidonia corrugata gigantea* subsp. nov. 7149, holotype, left valve, $\times 2.8$.

Fig. 3. *Caneyella membranacea* (M'Coy). 7155, showing posterior margin oblique to hinge-line, $\times 3$.

Fig. 4. *Posidonia corrugata* (Etheridge). 7145, two left valves, $\times 4$.

Fig. 5. *Posidoniella variabilis* Hind. 7173a, b, c, internal moulds, $\times 4$.



1 x 7



3 x 3



2 x 2.8



5 x 4



4 x 4

(refigured by Hind 1901, pl. 5, fig. 18), are of the more oblique form considered as *membranacea* s.s. The specimens illustrated by Demanet (1938, pl. 10, figs. 5, 10, 11) are nearer to *horizontalis*; so also is the specimen figured by Ramsbottom (1959, pl. 71, fig. 14). On Slieve Anierin the two forms usually occur together and so far have not been found in E₂. All Demanet's records are from E₁ (1941, p. 81). Schmidt (1934, p. 448, fig. 28) figures the species in beds with *Ct. edalense*; the very narrow anterior wing suggests that this may be *Posidonia corrugata elongata* or *P. corrugata gigantea*, both of which occur near this level on Slieve Anierin. Smyth (1950, p. 317) reports the species in E₂, but here again I believe the specimen may be more correctly regarded as a subspecies of *P. corrugata*. Ramsbottom (1959, p. 406) placed the species in the genus *Caneyella*, which he defined as including costate and non-costate species with a relatively long hinge-line, with the umbo usually towards the anterior end. It is believed that *horizontalis* is rather more abundant in the P₂ horizon than in the E_{1c} band, where *membranacea* s.s. is dominant.

Family EUCHONDRIIDAE Newell 1937

Genus EUCHONDRIA Meek 1874

Euchondria aff. *E. levicula* Newell

Plate 58, figs. 1, 2

Euchondria levicula Newell 1937, p. 107, pl. 1, figs. 6, 7; pl. 19, figs. 5, 10, 11, 18.

Description. Left valve. The hinge length is about half or slightly less than half of the greatest antero-posterior measurement. The umbo is slightly anterior of the mid point of the hinge-line. The shell has a postero-ventral extension. The anterior wing is small and defined from the body of the valve by a strong downfold which passes from the umbo to the anterior margin. The posterior wing is larger than the anterior but has no distinct fold marking it off externally. The anterior margin of the anterior wing is very gently curved, the posterior margin has a deep embayment below the hinge-line which swings outwards in to the postero-ventral extension. The surface of the valve is ornamented with radiating costae. These are regularly spaced at about 4-5/mm. They are crossed by concentric fila in which the spacing is a little more variable, from 5-7/mm. The intersection of the two results in a cross-hatched pattern of ornamentation on the left valve. The fila continue on to the ears and there are also three to four costae on the anterior ear. The posterior ear has about five costae. It is not always easy to determine these numbers with absolute certainty as the costae do not appear to be as strong on the ears as on the body of the valve but they are definitely present in small numbers. Along the hinge margin specimen 7158 (Pl. 58, fig. 2) shows a line of denticles, which may represent the position of a row of ligamental pits.

Right valve. This valve lacks the postero-ventral extension. There is less discrepancy between the greatest antero-posterior measurement and the hinge length; with increase in size the discrepancy increases slightly. The anterior wing is defined by a deep furrow from the umbo to the anterior margin. This wing, although small, is very convex. The posterior wing is not defined by a furrow but is clearly distinguished by the sharp descent in the umbonal region from the convexity of the valve to the flat wing. There are no radiating costae on this valve. The fila are very clearly seen in external impressions, the

spacing being about 8/ mm. Although costae are absent from the valve they are present on the ears. The anterior ear has three or four costae and the posterior four to five costae.

<i>Dimensions</i>	<i>Dorso-ventrally</i>	<i>Antero-posteriorly</i>
7160, left valve	10 mm.	c. 12-13 mm.
7161a, large left valve	c. 13 mm.	c. 15 mm.
<i>b</i> , small left valve	c. 10 mm.	c. 12 mm.
<i>c</i> , broken right valve	10 mm.	
7162, incomplete left valve	c. 14 mm.	
7163a, right valve	15 mm.	15 mm.
<i>b</i> , left valve	5 mm.	5 mm.
<i>c</i> , on lower side, right valve	9 mm.	9 mm.
7164, incomplete right valve	10 mm.	
7165, right valve (Pl. 58, fig. 1)	8.5 mm.	9 mm.
7158, left valve (Pl. 58, fig. 2)	13 mm.	15 mm.
7159a, left valve	16 mm.	18 mm.

Localities and horizon. This species has only been found in the topmost faunal band on Slieve Anierin, E₂b₃, associated with *Ct. nititoides* and *E. rostratum* sp. nov. Numerous specimens were collected in Valley 3, L21(9)24.

Discussion. The genus *Euchondria* (Meek 1874, pp. 488-9), as understood by Newell (1937, pp. 102-5), is typified externally by the costae and fila on the left valve, which by their intersection produce a distinctive cross-hatched ornament, and the absence of costae in the right valve, which is smooth, possessing only obscure concentric fila. The ligament area has a series of ligamental pits both before and behind the median resilifer. These two features, namely discrepant ornament on the two valves and the multiple resilifers, are taken to be the chief characters of the genus.

Newell (1937, p. 102) has erected a family for these forms, in which he also places *Crenipecten*. He describes several species of *Euchondria*, of which *E. levicula* Newell (1937, p. 107, pl. 19, figs. 5, 10, 11, 18) looks very like the specimens from Slieve Anierin. The latter seem slightly different in the distinctness of the fila in the right valve and the very deep anterior auricular sulcus in this valve, but the left valve seems indistinguishable from *E. levicula*. Newell (*in litt.*) agrees with the differences just mentioned but believes that the Irish specimens should be regarded as very closely related to *E. levicula*. They are therefore identified as *Euchondria* aff. *E. levicula*. There appear to be no previous records of this genus in the Carboniferous rocks of either England or Ireland. The holotype and topoparatypes come from the Hushpuckney black and grey shales, Swope formation (Missouri subseries), at Devil's Backbone, near Winterset, Iowa. Apart from the fact that this is the first record of this species outside America it is interesting also

EXPLANATION OF PLATE 61

All specimens are from Slieve Anierin, Co. Leitrim, Eire.

- Figs. 1, 2. *Chaenocardiola bisati* sp. nov. 1, 7184, holotype, external mould showing low number of relatively sharp ribs separated by wide flat interspaces, $\times 4.5$. 2, 7185, paratype, internal mould, $\times 5$.
 Fig. 3. *Chaenocardiola* cf. *C. haliotoidea* (Roemer). 7183a, *b*, two internal moulds, $\times 3.5$.
 Fig. 4. *Posidoniella variabilis erecta* subsp. nov. 7129b, holotype; 7129c, *d*, paratypes, an internal mould and two external moulds respectively, showing the near vertical anterior margin, $\times 6$.
 Fig. 5. *Caneyella membranacea horizontalis* subsp. nov. 7157, holotype, external mould of right valve showing hinge-line and posterior margin in more or less continuous line, $\times 5$.



that it occurs in a rather different lithology from the American specimens. These (Newell, *in litt.*) are almost invariably found in dark to black shales, associated with pyrite, and he believes they were adapted to a low pH and strongly reducing conditions. The Slieve Anierin specimens occur in a decalcified calcareous shale with a fauna including other lamellibranchs, goniatites, a productid, crinoidal debris, trilobite remains, and occasional echinoid spines and plates. The genus does not occur beneath this band in shales of lithology similar to Newell's description.

Newell states (*in litt.*) that the denticles along the hinge margin in the Slieve Anierin forms (see particularly the left valve 7158 (Pl. 58, fig. 2) and less obviously the right valve 7163c) tend to confirm an idea that he has had for several years that these are not ligament grooves but rather hinge denticles which are found in the juvenile stages of many modern scallops.

External impressions of this species provide the clearest details of the external ornament but inevitably show nothing of the ligamental area. Natural moulds of the interior, with details of the external ornament impressed upon them, have frequently been preserved and these are less sharp in the details of the ornament. In 7158, a left valve, an internal mould of the ligamental area is seen along the dorsal margin of an internal mould with external ornament impressed upon it; this opinion is confirmed also by Newell. Specimen 7165 (Pl. 58, fig. 1) is the impression of a right valve in which there seems to have been breakage of the valve during the life of the shell and a subsequent repair of the damage after which the growth-lines return to the normal pattern. Specimen 7166 shows the moulds of a right and a left valve closely associated, and once more internal moulds have the external ornament impressed upon them.

Family AVICULOPECTINIDAE Etheridge jun., emend. Newell 1937

Genus OBLIQUIPECTEN Hind 1903

Obliquipecten costatus sp. nov.

Plate 59, figs. 2, 3; Plate 62, fig. 5

Description. Right valve. The hinge-line is short. The posterior margin makes an obtuse angle with the hinge-line and is gently curved and smoothly continuous with the ventral margin. The anterior margin is concave below the anterior ear but soon becomes very convex forwards. The anterior ear is very distinct in this valve and is extended above the hinge-line (this feature is well seen in 7167). There are apparently two broad undulations of the surface of the ear. The posterior ear is very small indeed. The extension forward of the valve becomes more apparent with the increase in size of the specimen; it is very marked in the holotype but less apparent in some of the smaller paratypes. Growth-lines are seen on all the specimens and are particularly sharp on the ears. There is also a distinct radial ribbing of the surface. On some of the larger right valves (notably the holotype) the ribbing is stronger on the anterior part of the shell and rather muted over the rest of the surface. In the more dorsal part of the shell the convexity of the valve decreases very sharply posteriorly but ventrally there is a much more gradual change.

Left valve. In this valve the anterior ear is defined by the broad umbonal fold. The anterior margin of the ear is apparently smoothly continuous with the anterior margin of

the valve. The posterior wing is again very small. The growth-lines and radial ribbing are as in the right valve, except that in the largest specimens of the left valve seen the ribs are still apparently strong all over the surface with no particular attenuation in the anterior region.

Holotype. 7219 (counterpart 7265): right valve, dorso-ventrally 40 mm. (incomplete), antero-posteriorly 45 mm. (Pl. 59, fig. 3). *Paratypes*. 7169: right and left valve, dorso-ventrally 21–22 mm., antero-posteriorly 18 mm. (Pl. 62, fig. 5). 7217: left valve, dorso-ventrally 14 mm., antero-posteriorly 12 mm. (Pl. 59, fig. 2). 7167 (counterpart 7168a): right valve, incomplete. 7168b: left valve, other side of slab bearing counterpart of 7167, dorso-ventrally 30 mm., antero-posteriorly 28 mm.

Type locality and horizon. L20(8)1; also L23(4)8. *O. costatus* appears to be particularly abundant in E_{1a}, where it has been found with *Cravenoceras leion* and *Eumorphoceras* cf. *E. sp.* form *A* Moore; the latter occurs at the type locality L20(8)1. The species occurs, however, at other horizons in E beds but never so abundantly.

Discussion. *Obliquipecten* is characterized, in Newell's opinion (1937), by 'the remarkable extent to which the opisthocline obliquity has been carried and the nearly complete loss of the posterior auricle'. There can be no doubt that the Slieve Anierin specimens are members of this genus but they are specifically distinct from the only described species *O. laevis* Hind, which is described by that author (1903) as being smooth apart from the growth-lines. Newell describes the species as 'nearly smooth save for a few fine radiating costae on the anterior part of each valve and a few coarse fila on the anterior auricle of the right valve'. The Slieve Anierin specimens are considered to be specifically distinct by reason of their ribbed character. Demanet (1941, pp. 84–86) identified specimens in the E₁ deposits of Belgium as *Obliquipecten* aff. *O. laevis* Hind but described these forms as smooth apart from concentric growth-lines.

Family MYALINIDAE Frech
Genus POSIDONIELLA de Koninck 1885

Posidoniella variabilis Hind

Plate 60, fig. 5

Posidoniella variabilis (Brown MS.) Hind 1897, pp. 100–1, pl. 7, figs. 7–9.
Posidoniella variabilis Hind; Ramsbottom 1959, p. 405, pl. 71, fig. 10.

Description. Convex forms in which the umbo is pointed and terminal. The usual aspect is rather mytiloid. Internal moulds are frequent and are either smooth or bear somewhat irregular concentric corrugations, which appear to be more frequent nearer the ventral edge of the valves and absent or poorly seen in the more dorsal part of the valve under the umbo. The hinge-line is short and the anterior margin descends obliquely backwards making an acute angle with the hinge-line. The posterior margin is approximately parallel with the anterior, but rather more curved than the anterior. External impressions of the shell show fine concentric growth-lines and a few obscure corrugations.

Dimensions. 7172: dorso-ventrally 9.5 mm., antero-posteriorly 6 mm. 7173a, b, c: largest specimen, dorso-ventrally 8 mm., antero-posteriorly 6.5 mm. (Pl. 60, fig. 5).

Localities and horizon. Specimens have been collected abundantly on Slieve Anierin at many levels in E₂ shales above the grit from the level of the *Cravenoceras subplicatum* fauna, E₂b1, upwards.

Discussion. The author's specimens agree closely with the species *P. variabilis*. Ramsbottom (1959, p. 405) has selected a lectotype from Hind's original specimens and figured it (op. cit., pl. 71, fig. 10). He believes that of the several Millstone Grit species referred to *Posidoniella*, only *P. variabilis* rightly belongs to that genus. However, although many of my forms agree closely with *P. variabilis* there are others in which the mytiloid aspect is not present and a squarer form has been assumed. This change in shape is reflected in the nearly vertical downward descent of the anterior margin, in contrast to the oblique backward passage of the margin in undoubted *P. variabilis*. The Slieve Anierin form resembles *P. laevis* (Brown) (Hind 1897, pl. 6, figs. 12-14, 24), but in Ramsbottom's opinion (*in litt.*) Brown's original specimen had an anterior wing and therefore cannot belong to *Posidoniella*. However, in E₂ shales on Slieve Anierin forms with a vertical anterior margin undoubtedly exist. From a study of many specimens it seems likely that in fact *P. variabilis* and the squarer form represent two extremes of variation, since many specimens are difficult to assign to either end of the series. It seems desirable to name this squarer form, since the two end-forms of the series are so distinct, and this can most appropriately be done by designating it as a subspecies of *P. variabilis*. The name *P. variabilis erecta* subsp. nov. (Pl. 61, fig. 4) is proposed for those forms in which the anterior margin descends vertically; holotype, 7129*b*, paratypes, 7129*c*, *d*.

Demanet (1941, pp. 76-77, pl. 2, fig. 3) records *P. variabilis* within the *Dimorphoceras* cf. *D. looneyi* horizon, which corresponds with one of the periods of dominance of *P. variabilis* on Slieve Anierin. However, Demanet considers that the oblique anterior margin is a constant feature. H. Schmidt (1934, p. 44, fig. 45) also records this species in beds with *D. looneyi*.

Family PTERIIDAE Meek 1864
Genus ACTINOPTERIA Hall 1884
Actinopteria persulcata (M' Coy)

Plate 58, fig. 3

Pteronites persulcatus M' Coy 1851, p. 170.

Actinopteria persulcata (M' Coy); Hind 1901, pp. 23-25, pl. 4, fig. 14.

Description. The umbo is swollen but not quite terminal on the hinge-line, there being a narrow expansion anterior to it. The anterior margin runs obliquely backwards to the curved ventral margin. The posterior margin is smoothly continuous with the ventral margin but is ultimately concave beneath the hinge-line. The posterior wing is a long isosceles triangle in shape (with its apex at the umbo and its base the concave portion of the posterior margin). It is flattened compared with the convexity of the rest of the valve. The surface of the valve and the wing show concentric lines of growth which are quite widely spaced and reflect clearly the concavity of the posterior margin ventral to the hinge-line. There are also radial corrugations of the surface of the valve which seem to be absent on the wing in all the specimens seen. They are strongest on the middle of the valve and show a slight offset of their courses at the growth-lines. There is a long posterior extension of the hinge-line area, that of each valve being concave towards its fellow of the opposite valve. They are all unfortunately broken in this material and it is therefore impossible to tell how far this extension reached beyond the body of the valve.

Externally this extension first appears faintly as a convex ridge just below the dorsal edge of the valve at about 5 mm. behind the umbo, but is a distinctly rounded ridge just below the dorsal margin at 7 mm. from the umbo. It then continues to the posterior margin and beyond.

Dimensions. 7223 (counterpart 7250): dorso-ventrally 10 mm., antero-posteriorly 12 mm. (Pl. 58, fig. 3).

Locality and horizon. L21(13)7, about six specimens. The horizon is E₁c. The specimens are associated with *Caneyella membranacea*, *Kazakhoceras scaliger*, *Chaenocardiola footii*, and *Cravenoceras* aff. *C. malhamense*.

Discussion. This is not a common species on Slieve Anierin. I compared the form initially with *Actinopteria fluctuosa* (Etheridge) (Hind 1901, pp. 25–26, pl. 5, figs. 8–12). However, R. B. Wilson, who has been working on these species, informs me (*in litt.*) that he considers that *A. fluctuosa* should now be included in *A. persulcata*, and this practice is followed here. In Scotland the species is particularly abundant at the P₁–P₂ boundary, although starting in Zone D. It therefore has a long range, since in Ireland it occurs on a high E₁ horizon.

?Family CONOCARDIIDAE Neumayr

Genus CHAENOCARDIOLA Holzapfel 1889, emend. Beushausen 1895

Chaenocardiola Holzapfel 1889, pp. 61–62.

Chaenocardiola Holzapfel; Beushausen 1895, pp. 364–5.

Chaenocardiola Holzapfel emend. Beushausen 1895; Hind 1900, pp. 474–6, pl. 52, figs. 5–7.

Chaenocardiola Holzapfel emend. Beushausen 1895; Demanet 1941, pp. 67–69, pl. 1, figs. 5–7.

Little appears to be known about the internal structure or the true affinities of this very distinctive genus. Hind mentions a certain resemblance to *Conocardium*. Demanet refers it to the family Conocardiidae Neumayr. Hind further states that he believes the genus is more nearly related to the Cardiidae. It is impossible to make any comment on the affinities of the Carboniferous specimens to be described.

The most obvious generic features are the very strong forward curvature of the umbones and the slightly concave area just beneath the umbo on each valve. The ribbing is strong and continues from the umbo to the ventral margin and the valves are ribbed on the inside of the shell, though this usually fades before the umbo and is strongest on the ventral margin. Hind (1900, p. 476) mentioned fine striations parallel to the upper edge and interpreted them as the site of the ligament. These fine striations parallel to the upper edge have also been seen on internal moulds in many of the Slieve Anierin specimens.

Chaenocardiola footii (Baily)

Plate 62, fig. 3

Lunulacardium footii Baily 1860, pp. 18–19, fig. 9.

Conocardium footii (Baily); Etheridge 1888, p. 281.

Chaenocardiola footii (Baily); Hind 1900, pp. 475–6, pl. 52, figs. 5–7.

Chaenocardiola haliotoidea Roemer; Schmidt 1934, p. 446, fig. 7.

Chaenocardiola footii (Baily); Demanet 1941, pp. 67–68, fig. 5, ?fig. 6.

Description. The shape is approximately semicircular. The dorsal margin is gently convex but rather more sharply so at the anterior end where it descends to the umbo.

At the posterior end the dorsal margin is truncated sharply by the posterior margin, which curves quickly round into the ventral margin. At the anterior end of the shell there is a slight concavity of the surface immediately beneath the umbones. The original form does not appear to have been very convex. The umbo appears to be incurved. Strong ribs radiate from the umbo across the body of the valve and are crossed by fine concentric lines of growth. The ribs are about twenty-five in number on most specimens but may vary up to thirty.

Dimensions. 7174: largest on slab, height 6 mm., length 9.5 mm. (Pl. 62, fig. 3). 7175a: height 13 mm., length 16 mm. 7175b: height 13 mm., length 17 mm. 7176: height 3.5 mm., length 5 mm. 7177a-d: a, height 5 mm., length 11 mm.; b, height 5 mm., length 9 mm.; c, height 4 mm., length 9 mm.; d, height 10 mm., length 15 mm. 7148b: height 8 mm., length 12 mm. 7178: height 11 mm., length 15 mm. 7179: height 10 mm., length 16 mm. 7180: height 20 mm., length 24 mm.

Localities and horizons. This species has been collected from E₁ and E₂ beds. It has its maximum abundance in E₂. The high E₂a beds at L21(13)4, L21(5)11, and at L21(5)10 are rich in examples associated with the subspecies of *E. bisulcatum*, and *Cravenoceras* cf. *C. gairense*, &c. It occurs in abundance in the highest faunal band on Slieve Anierin, which is considered to be in the *Ct. nitidus* zone, E₂b3, and here the species is associated with *E. rostratum* sp. nov., *Ct. nititoides*, and *Ct.* cf. *Ct. nitidus*.

The species has been collected in E₁ beds from all the prominent faunal bands above the *C. leion* zone (at this lower level it has not been collected, but *Chaenocardiola bisati* sp. nov. occurs).

Discussion. It is apparent from a study of many specimens of this form that the shape is rather variable, ranging from young individuals in which the height of the valve is about half the length to larger specimens in which height and length are approximately equal. (Slab 7177 has young and adult specimens.) The dimensions originally given by Baily (1860, p. 19), when converted into millimetres give a height of about 20 mm. and a length of about 28 mm. This would be considered large for most of the Slieve Anierin specimens, but 7180 approximates to these measurements, while a few rare incomplete individuals (which if complete would be larger still) have been found. The area beneath the umbo often appears to be broken and since it carries about five ribs results in deficient rib counts. Although Baily's original figure for the ribs is twenty-five, they vary up to about thirty, but twenty-five appears to be the average. The internal moulds show a distinct ribbing around the ventral margin, becoming less strong towards the umbo. Plasticine impressions of these internal moulds show that the ribs on the inside of the shell were very broad and flat-topped at the extreme ventral edge, becoming narrower as they fade towards the umbo. At the extreme ventral edge very short furrows can sometimes be seen on the flattened summits of these internal ribs. On the original specimens these short furrows appear as short intercalated ribs between the larger ribs. In internal ribbing, at least, they resemble members of the Cardiidae, for example *Prosodaena* sp. (Morley Davies 1935, p. 153, fig. 201), which is a member of the Adacnidae, an aberrant Miocene offshoot of the Cardiidae. The resemblance between the superficial morphology of this form and the Carboniferous *Chaenocardiola* is close. More detailed knowledge of the hinge and ligament area in *Chaenocardiola*, however, is needed before its true affinities can be determined.

This species is mentioned in several faunal lists from beds of E₁ and E₂ age from the north of England and most of these are included by Demanet in the synonymy of the species (1941, p. 67). Stephens *et al.* (1942, p. 348; also 1953, p. 94) state that *E. bisulcatum* and *Chaenocardiola footii* are the two most abundant forms in the Edge

Marine Band in the Rombalds Moor area in Yorkshire. This band may be on the same horizon as that seen at L21(5)11 and at L21(13)4. Hudson and Cotton (1943, p. 167) record the species at two levels within E_1 which can also be broadly correlated with the Slieve Anierin horizons containing the species. In Ireland the form has been recorded in North Co. Dublin by Smyth (1950, p. 320) in E_2 beds. Moseley (1954) records it in the Lancaster Fells in the Tarnbrook Wyre Marine Beds of E_{2a} age. The species is widespread at this low E_2 level, although it occurs both lower and higher in the succession. The first E_1 fauna to be described in Ireland (Nevill 1957, pp. 297–8) does not include this species nor is it mentioned in E_2 (pp. 298–300). Baily's original specimens were from Rosscliff, Co. Clare, and he mentions material from Westown, Co. Dublin; from near Drogheda, Co. Meath; and from Cahernanalt, Kendue, Co. Roscommon.

Chaenocardiola cf. *C. haliotoidea* (Roemer)

Plate 61, fig. 3

Cardita? *haliotoidea* Roemer 1850, p. 49, pl. 8, fig. 5.

Chaenocardiola haliotoidea (Roemer); Holzapfel 1889, pp. 62–63, pl. 7, figs. 5, 6.

Chaenocardiola haliotoidea (Roemer); Demanet 1941, pp. 68–69, pl. 1, fig. 7; *non* fig. 6.

Description. The shape is long and low and not very convex. The ribs are very narrow and number about forty.

Dimensions. 7183a, b: two specimens, one complete, length 10 mm., height 4 mm. (Pl. 61, fig. 3).

Locality and horizon. Valleys 4 and 2, L21(9)23 and 25 respectively; *Ct. nitoides* band, E_2b3 .

Discussion. In his description Roemer mentions forty to forty-five ribs, but there are less than this in his figure, which has a count nearer *C. footii*. Demanet describes this form as differing from *C. footii* in its smallness and its large number of ribs. Of his two figures I would refer pl. 1, fig. 6 to *C. footii*, but fig. 7 appears to be specifically distinct and to resemble 7183a and b. On Slieve Anierin this form has only been found in the *Ct. nitidus* zone. Demanet reports it also from E_1 horizons. Specimens referred to this species by H. Schmidt (1934, p. 446, fig. 7) show only twenty-one ribs and may possibly be incomplete examples of *C. footii*; they occur in E_1 beds. *Chaenocardiola* sp. is referred to but not figured in the *nitidus* zone.

Hudson and Cotton (1943, p. 167) record *C. footii* (Baily) (or *C. haliotoidea* (Roemer)) in E_{1d} and E_{1c} . The writer is uncertain exactly what is meant by this form of identification unless they intend to suggest that the two species are probably the same. The original plate given by Roemer certainly closely resembles *C. footii* but the definition of forty to fifty ribs is precise in the text. The highest band on Slieve Anierin contains a few rare specimens which accord with this definition and Roemer's specific name has therefore been retained for them.

Chaenocardiola bisati sp. nov.

Plate 61, fig. 2

Description. The general outline of this species is as already described for *Chaenocardiola footii*. All the Slieve Anierin specimens discovered so far are small, but not smaller than the smallest individuals of *C. footii*. The valves are more convex than *C. footii* in the

younger stages and bear a smaller number of strong ribs, which are separated by wide flat-bottomed furrows in which, at larger dimensions, intermediate finer ribs are present. There are about fifteen to seventeen ribs. There is a small distinctly concave area beneath the umbo.

Holotype. 7184: external mould, length 8 mm., height 5 mm. (Pl. 61, fig. 1). *Paratype*. 7185 (counterpart 7237): internal mould, length 7 mm., height 4 mm. (Pl. 61, fig. 2).

Type locality and horizon. L24(1)1. This form is very rare and occurs in the lowest *Cravenoceras leion* band, E₁a, associated with *C. leion*. Specimens have also been collected at L23(4)19 in P₂ beds, associated with *Goniatites granosus*; they are compared with this species although they are not so well preserved as the E₁ examples.

Discussion. Specimens of *Chaenocardiola footii* have their normal rib quotient at sizes comparable to those so far seen in this species (cf. 7167, which is a very small *C. footii*), and *C. bisati* is therefore to be distinguished by the smaller number of ribs (c. 17) separated by wide interspaces. In the Geological Survey Museum, two slabs (GSM Ca 1938 and 1939) collected from Holden Clough, Holden, Yorks., show incomplete large specimens of this species, and are associated with *Goniatites elegans* Bisat and are therefore of P₁c age. They show low numbers of sharp ribs (about seven but very incomplete) separated by wide interspaces. It is considered that these specimens are more adult individuals of the *C. bisati* described from Slieve Anierin. The dimensions of the two valves on Ca 1939 are: height c. 16 mm., length c. 23 mm. There are indications at these dimensions that in flat-bottomed grooves seen at smaller sizes there are three finer intermediary ribs, which are persistent from the umbo to the margins of the valve. The species is named in honour of Mr. W. S. Bisat.

Order PTYCHOPARIIDA Swinnerton 1915

Suborder ILLAENINA Jaanusson 1959

Superfamily PROETACEA Salter 1864

Family PHILLIPSIIDAE Oehlert 1886

Genus WEBERIDES Reed 1942

Weberides cf. *W. shunnerensis* (King)

Plate 62, figs. 1, 2

Griffithides shunnerensis King 1914, pp. 392–4, pl. 32, figs. 1–7.

Description. Headshield. The glabella is inflated anteriorly and pear-shaped. The occipital ring is distinctly separated from the rest of the glabella, and bears a central tubercle, with indications of others on each side of it. A pair of glabellar furrows slope back to meet the occipital furrow and define a pair of triangular-shaped basal lobes of the glabella. No other indications of glabellar furrows have been seen in front of this pair. The fixed cheeks are narrow with a well-defined palpebral lobe. The eyes are situated very close to the sides of the glabella and are distinctly reniform. In 7190 the eye is about 2.5 mm. long and is therefore about a third of the total length of the head shield. In relation to the convexity of the glabella the free cheeks are only very slightly raised. There are well-defined genal spines. In 7190 one of the spines is about 4 mm. long but without a complete specimen it is impossible to say where this spine would end

in relation to the thoracic segments. Surrounding the free cheeks there is a border which is about 1 mm. wide. In 7190, an impression, this border appears as a furrow in which there are about five striations which run parallel to the outer margin. Up to eight of these striations have been seen on several free cheeks. In the original trilobite the border must have been a convex band with a variable number of fine striations running parallel to the outer margin, There is a slight band between the anterior end of the glabella and the edge of the head shield; the border is very reduced in this region, its area having been invaded by the glabella. A constantly recurring feature on the glabella in the Slieve Anierin specimens is the presence of a pair of pits in front of the eye lobes and situated in the depression which surrounds and outlines the glabella. These pores are commented on by King (1914, p. 394). Each pore is situated about a quarter of the distance between the eye lobe and the front margin of the cranidium.

Thorax. Unfortunately, since there are no complete specimens in the collection, the original number and form of the thoracic segments is not known. Specimen 7191 shows some fragmentary thoracic segments. The axis in these segments appears to be about 2 mm. in width and more convex than the flanking pleurae. The pleurae are not visible. On the very small and distorted specimen 7067c the thoracic pleurae appear to have straight terminations with no indications of the development of pleural spines.

Pygidium. There are several good specimens of pygidia. The length varies from about 8–10 mm. The axis of the pygidium is strongly arched above the flanking pleurae, which are only moderately convex. The pygidium is surrounded by a wide border. There are about sixteen segments in the axis and about ten in the pleural region. Each axial segment has a single row of granules just in front of the posterior border. A single row of granules also occurs in a similar position on each of the pleurae. Some moulds of the pygidium show a concave area surrounding the pleurae (and not the convex border seen in other moulds) and are interpreted as moulds of the ventral surface of the pygidium showing the doublure, which has striations parallel to the margin.

Dimensions. 7190: the only complete headshield, width between the two genal angles 11 mm., length 7.5 mm. (Pl. 62, fig. 2). 7192 (counterpart 7283): pygidium, c. 6 mm. long (Pl. 62, fig. 1). 7193: cranidium, 6.5 mm. long; length of pygidium c. 7 mm., maximum width 10 mm.

Localities and horizon. Fragments of trilobites occur abundantly in the highest faunal band, E₂b3, on Slieve Anierin. The most extensive collecting from this band was carried out in Valley 3, L21(9)24. The trilobite specimens are associated with *Ct. nititoides*, *E. rostratum* sp. nov., *Chaenocardiola footii*, *Euchondria* aff. *E. levicula*, &c.

Discussion. These specimens compare very closely, allowing for differences in preservation, with *Griffithides shunnerensis*, described by King (1914), now known as *Weberides shunnerensis* (see Reed 1942, p. 653). The type specimens were collected from the Shun-

EXPLANATION OF PLATE 62

All specimens are from Slieve Anierin, Co. Leitrim, Eire.

Figs. 1, 2. *Weberides* cf. *W. shunnerensis* (King). 1, 7192, pygidium, $\times 7$. 2, 7190, cranidium, $\times 6$.

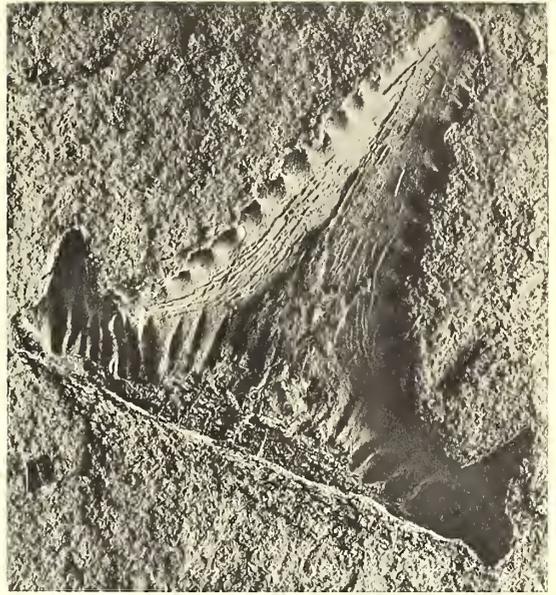
Fig. 3. *Chaenocardiola footii* (Baily). 7174, external mould, $\times 6.5$.

Fig. 4. *Edestus (Edestodus) sp.* GSM 86950, external mould, $\times 4$.

Fig. 5. *Obliquipecten costatus* sp. nov. 7169, paratype, external mould of right valve partly obscuring a right valve, probably an internal mould with external ornament partially impressed upon it, $\times 3.3$.



1 × 7



4 × 4



2 × 6



3 × 65



5 × 33



ner Fell Limestone, Great Shunner Fell, Wensleydale, north Yorkshire, a highly fossiliferous rock which yields an E_2 fauna. The Yorkshire specimens are therefore of the same general age as those from Slieve Anierin. Slight differences may exist in the number of axial segments in the pygidium, but most of the Slieve Anierin specimens are broken at the anterior end of the pygidium and the number of segments may well be more than the figures given.

There are several records of trilobites at this level in England and Ireland, but a generic name is not usually given. Scanlon (1953), Smyth (1950), and Nevill (1957) all record trilobite remains in E_2 beds in Ireland. Hudson and Cotton (1943) record a trilobite in the Alport Dale boring, Derbyshire, associated with a fauna very similar to that on Slieve Anierin. Tonks (1925) lists a trilobite in the fauna from Pace Gate Beck, Yorkshire, in beds which also yielded the type of *Ct. nititoides*. Demanet (1941, p. 154, pl. 7, figs. 4, 6) describes and figures a trilobite from E_2 near Bioul in Belgium, but it is not the same species and appears to be rather larger.

Superclass PISCES
Class CHONDRICHTHYES
Subclass ELASMOBRANCHII
Order SELACHII
Suborder HYBODONTOIDEA
Family EDESTIDAE
Genus EDESTUS Leidy 1856

Edestus (Edestodus) sp.

Plate 62, fig. 4

Description. The crown of this tooth is triangular, laterally compressed and symmetrical. Small subsidiary cusps occur at the base both anteriorly and posteriorly. The anterior and posterior edges of the tooth are serrated. There are eleven to twelve of these small denticulations along each margin but some may have been rubbed away near the apex. Each denticulation appears to be undivided. At the base of the tooth there are several raised ridges (seen as furrows in this impression).

Dimensions. Height 16 mm., width at base 18.5 mm. (Pl. 62, fig. 4).

Locality and horizon. A single specimen only has been collected (GSM 86950) from the horizon of *Ct. nititoides*, E_2b3 , in Valley 3, L21(9)24.

Discussion. Specimens of *Edestus* are extremely rare in English deposits and this is believed to be the first record from Ireland. The writer is indebted to Dr. Ramsbottom of the Geological Survey for identifying this specimen, indicating its rare nature, and also pointing out to me the paper in Russian by Obruchev (1953) on this family. The relevant generic definitions in this work (pp. 59–60) were translated with the assistance of Dr. Skiba of the Department of Geology, Imperial College. The Slieve Anierin specimen accords most nearly with the subgenus *Edestodus* Obruchev (type species *Edestodus minor* (Newberry)) in the sharply triangular outline and the small angle at the apex of the tooth which in *Edestodus* is 25–35°, and which in this specimen is approximately 29°. In the presence of the subsidiary cusps each side at the base the specimen shows

some resemblance to *Edestus heinrichsii* Newberry and Worthen (1870, pp. 350–3, pl. 1, figs. 1a, b), which is now assigned by Obruchev to the subgenus *Protopirata* Trautschold (in which the apical angle varies from 70–90°). In this species the denticles are few in number and the basal ones at the anterior and posterior margins are enlarged almost to form subsidiary cusps. The type species of the subgenus *Lestroodus* Obruchev is *L. newtoni* (Woodward) and in the original description by Woodward (1916, pp. 1–6, pl. 1) was described as possessing vertical plications or flutings at the base of the crown. These are also seen on the Slieve Anierin specimen but are more regular and more marked than in the specimens of *L. newtoni*; in this genus the apical angle varies from 40–45°.

CORRELATIONS WITH OTHER AREAS

P₁–P₂ Beds

The fossils preserved in beds of P_1 – P_2 age are too poorly preserved to allow close correlation with beds of the same age elsewhere. Hudson and Cotton (1945a, pp. 273–8), working on the Alport borehole, established a correlation with Germany. The sequence of faunas within P_1 was correlated with that from Edertal on the eastern side of the Rhenish Schiefergebirges (Pickel 1937) and the P_2 succession was compared with that in the northern Sauerland (Ruprecht 1937). There is less similarity between the P_2 faunas than those of P_1 but this, in the opinion of Hudson and Cotton (op. cit., p. 275), is mostly due to the poor definition of the diagnostic features of the species and the resulting difficulty in identification. The material of this age from Slieve Anierin adds nothing to the detailed subzoning and correlation established by Hudson and Cotton.

Basal E₁ to Middle E₂

1. Ireland

North Co. Dublin. Smyth (1950, pp. 297–304) showed that Pendleian deposits are absent in North Co. Dublin and that Arnsbergian beds succeed beds of P_2 age and overlap onto the Lower Palaeozoic. This absence of E_1 and overlap of E_2 is due to the Sudetian orogeny. As a result of faulting the succession is not so simply interpreted as the Slieve Anierin succession, nor do the described faunas appear to be so abundant.

A fauna is described (op. cit., p. 298) which is in part reminiscent of the highest *Ct. nititoides* fauna on Slieve Anierin, a notable similarity being the occurrence in both of *Productus hibernicus* and a Phillipsiid trilobite (*Weberides* cf. *W. shunnerensis* on Slieve Anierin). Unfortunately this band was not found in direct relationship to any of the other described sections; Smyth (p. 302) believes that the Rowans Brook and Walshestown sections cover the *E. bisulcatum* s.s. and *Ct. nitidus* zones, and that the *P. hibernicus* fauna is higher than any part of these two sections. On Slieve Anierin the fauna with *P. hibernicus* is included in the *Ct. nitidus* subzone. In the Rowans Brook section, which is the most complete, there are about 400 feet of beds, predominantly shale, of which about 60 feet at the base are in the Balrickard Sandstone; at other localities it is estimated that this sandstone must be considerably over 100 feet in thickness. North Co. Dublin and Slieve Anierin are alike, therefore, in the presence of a considerable thickness of arenaceous rocks within the lower part of E_2 . The first *E. bisulcatum* to be found above

this grit has not been figured but has been described by Stubblefield (*in* Smyth 1950, pp. 318–19) as intermediate between *E. bisulcatum grassingtonense* and examples of *E. bisulcatum* from the Edge Marine Band at Cononley Beck, Yorkshire. It is probable that these forms represent a higher horizon than those on Slieve Anierin since within 20 feet they are succeeded by *Ct. cf. Ct. stellarum*, a species which has not been found on Slieve Anierin. No account is given of any faunas between the grit and this band with *E. bisulcatum*.

E_2 deposits from near Garristown were described by Scanlon (1953, pp. 145–57). The faunas are too poor for close comparison and there is no record of *E. bisulcatum* itself but of *Ct. stellarum* and *Cravenoceras sp.*

Co. Meath. Nevill (1957, pp. 297–300) recorded both Pendleian and Arnsbergian stages in the Summerhill Basin, but lack of detailed information on the faunas and incomplete exposure of parts of the succession precludes any close correlation. The combined E_1 – E_2 stages are about 2,000 feet thick and the precise position of the boundary between the two stages has not been established. A basal E_1 goniatite fauna which has much in common with the fauna at L23(4)7 on Slieve Anierin is described, but the rest of the Pendleian is not exposed and the lowest exposed E_2 horizon is of E_2b age, consisting of beds with *Ct. edalense*. Two hundred feet of the succession are not exposed, and this would account for the absence of all the horizons which are present above *Ct. edalense* on Slieve Anierin. *Ct. stellarum* was collected about 300 feet above *Ct. edalense*.

In two isolated exposures in the Summerhill Basin which have not been related to the main succession (described from a drainage dyke at Mullagh) *E. bisulcatum* is associated with a *Cravenoceras*, an *Anthracoceras*, and a rich brachiopod fauna including *P. hibernicus*, a trilobite, *Dumbarella sp.*, *Posidoniella sp.*, *P. sulcata* (Hind), a coiled nautiloid and crinoid ossicles. Nevill believes that these beds are closely followed by Sabdenian strata and therefore higher than the succession described from the Mullagh dyke. On Slieve Anierin *P. hibernicus* is associated with *E. rostratum sp. nov.*, *Ct. nititoides*, and *Weberides cf. W. slummerensis* and is at a lower horizon than *Ct. stellarum*, which does not occur on Slieve Anierin. If Smyth and Nevill are correct in attributing their isolated faunas to high E_2 then a somewhat similar band must also occur at the lower level within the *Ct. nitidus* subzone. Neither author has described or figured the *E. bisulcatum* which occurs at this level but both refer to *Cravenoceras sp.* On Slieve Anierin the associated goniatite is undoubtedly *Cravenoceratooides*. The Slieve Anierin fauna includes several other forms which one would have expected to see in the faunal lists of these authors if they were describing the same horizon, e.g. *Chaenocardiola* and *Euchondria*, both abundant in the *Ct. nititoides* band.

Nevill (1957, p. 296) also mentions the abundance in P_2 and low E_1 horizons of a large compressed goniatite referred to as *Anthracoceras?* (pl. 22, figs. 6, 7). Similar forms have been collected on Slieve Anierin at these levels and identified as *Kazakhoceras sp.*

Both Smyth and Nevill therefore provide information on what is probably the highest subzone of the *Ct. nitidus* zone (i.e. the *Ct. stellarum* subzone), but do not shed any light on the lower parts of E_2 or E_1 , except for the basal beds of the latter in the Summerhill Basin. A considerable sandstone episode within E_2 also occurs in North Co. Dublin, as in Leitrim. The greywacke facies described by Nevill at the base of E_1 has not been observed in Leitrim.

Cuilcagh, borders of Co. Cavan and Co. Fermanagh. Padget (1953, pp. 17–26) described the geology of Cuilcagh (2,188 feet), which is only 10 miles from Slieve Anierin and is included in the same area of Upper Carboniferous rocks. He recorded only E_1 fossils (apart from the P_2 and P_1 forms) and found no evidence of E_2 . The fauna from a low E_1 horizon included *E. stubblefieldi* and *C. leion*; no higher goniatite-bearing beds were found *in situ*, but *C. cf. C. malhamense* was collected from some loose blocks.

Padget makes no suggestion as to the age of the succeeding shales or the grit which forms the escarpment. The latter is identical with that on Slieve Anierin, which has been proved to lie within E_2 . On Benbrack (1,648 feet), to the south of Cuilcagh, the writer has collected *Eumorphoceras cf. E. bisulcatum grassingtonense* (GSM 95317) and believes it occurs at the same level as at localities L21(5)8 and 9, and at L21(13)5 and 6. It is therefore probable that the same faunas exist on Cuilcagh, though possibly not so well exposed as on Slieve Anierin.

Palaeogeography. Hodson (1959, pp. 134–50) has discussed the palaeogeography of western Europe in *Homoceras* times and has shown (pl. 1) an embayment of the sea into the North Atlantic Continent in the north-western area of Ireland, which includes Slieve Anierin, where the Namurian beds succeed the Viséan conformably. The position of the southern margin of this embayment is based on evidence provided by the (unpublished) work of Hodson and Kelk, and there is apparently overlap to the south-west so that E_2 shales lie on Carboniferous Limestone in the south-western part of the Slieve Carna outlier north of Balla in Co. Mayo.

South of the North Atlantic Continent lay a Central Trough of sedimentation. Hodson (1954a) demonstrated the effects of the Sudetian earth-movements in north-west Co. Clare by the discovery there of *Homoceras* beds succeeding the Carboniferous Limestone; all the beds exposed on Slieve Anierin together with the *N. nuculum* beds (not present on the mountain) are absent and there is therefore a large non-sequence. The effects of the orogeny become less evident southwards across this trough and Hodson (1959, p. 140) describes a thick E_1 succession overlying the Carboniferous Limestone on the north bank of the River Shannon. Still further south the Lower Namurian beds are again overstepped, and the southern edge of the trough (against the westerly continuation of St. George's Land) is apparently near Ballagh, west of Newcastle West, Co. Limerick, where, as in Co. Clare, *Homoceras* is found resting on Carboniferous Limestone.

The Sudetian earth-movements have also been detected by Smyth (1950, pp. 295–326) in North Co. Dublin, where the whole of the Pendleian is absent. Farther south, in the Summerhill Basin, Co. Meath, Nevill (1957) found E_1 and E_2 beds succeeding P_2 , and in this area some of the higher beds of H and R_1 are also preserved. The Summerhill Basin is farther away from the shoreline of the Central Trough than North Co. Dublin and the Arnsbergian deposits are correspondingly thicker. The relationship of the Summerhill succession to the North Co. Dublin succession is very like that of the Slieve Anierin succession to that south of the embayment at Slieve Carna. On Slieve Anierin the higher zones which are preserved in the Summerhill Basin have presumably been removed by erosion leaving only the beds of *Eumorphoceras* age.

Hodson (1959, p. 139) postulated a marine connexion between the Central Trough and the north-western Ireland embayment on the basis of the faunal and lithological

similarity of the two areas. The close correlation which it is possible to establish between the Slieve Anierin succession and those of areas in the Central Trough in E₁ and E₂ times amply testify the accuracy of this statement.

2. Southern and Mid-Pennines, England

The only complete record of the Arnsbergian succession is that given by Hudson and Cotton (1943, pp. 160–72) from the Alport Dale borehole in Derbyshire. A large number of the other known occurrences of certain faunas do not allow an accurate determination of their order of superposition. The Pendleian succession is also included in the Alport borehole. Three zones were defined within the Pendleian by Hudson and Mitchell (1936, p. 26) in the Skipton Anticline in Yorkshire:

E ₁ c	Subzone of <i>Cravenoceras malhamense</i>
E ₁ b	„ „ <i>Eumorphoceras pseudobilingue</i> s.s. and <i>Cravenoceras</i> sp.
E ₁ a	„ „ <i>Cravenoceras leion</i> and <i>Eumorphoceras pseudobilingue</i> (early form)

Hudson and Cotton recognized these subzones in the Alport borehole section, but treated them as zones, and added E₁d, the *Eumorphoceras* aff. *E. pseudobilingue* zone. In the Slaidburn district of Yorkshire Parkinson (1936, pp. 318–20, pl. 24) recognized:

Upper E ₁	<i>Cravenoceras malhamense</i>	—————	<i>Chaenocardiola footii</i>
	<i>Eumorphoceras pseudobilingue</i>		C
Lower E ₁	„	„	B
	{ „	„	A
	<i>Cravenoceras leion</i>		

In this area the *C. malhamense* beds are succeeded by the Pendle Top Grit. There is obviously a close correlation between the Slieve Anierin and Pennine successions, though the grit which succeeds the *C. malhamense* beds in the Slaidburn area is not present until later in the succession in Co. Leitrim.

(a) *Cravenoceras leion* zone. Apart from the plates in Nevill (1957, pl. 22, figs. 1–3) and Bisat (1950, pl. 1, figs. 1, 2) *E. pseudobilingue* A has never been described by Bisat although he contrasted it with *E. pseudocoronula* (1950, p. 19). The former is placed by Bisat (p. 24) somewhat above the base of the *C. leion* zone with *E. pseudocoronula*, *C. leion*, *E. stubblefieldi*, &c. On Slieve Anierin the maximum abundance of this species occurs with *C. leion* slightly above beds in which *E. pseudocoronula* is more abundant and it is associated with *E. rota*.

On specimen GSM 84690 from Little Mearley Clough, *E. pseudocoronula* is associated with a fragment identified as *E. rota*. At the top of the zone or nearly so on Slieve Anierin *E. medusa* occurs, and slightly higher *E. medusa sinuosum*. Both these forms are believed to be related to the stratigraphically lower *E. pseudocoronula*. Specimen GSM Ca4782, previously identified as *Eumorphoceras* aff. *E. hudsoni* Gill, is thought to belong to *E. medusa*; it was collected about 40 feet above the lowest *C. leion* beds in Bateson Wood, 550 yards north-east of Crag House, Yorkshire. Bisat, who originally identified this specimen, noting that it might be undescribed, agrees (*in litt.*, 1960) with this identification.

E. hudsoni has not been collected in this zone nor in the succeeding one; Bisat (1950,

p. 24) includes it within E_{1a}, although Gill (1947, p. 64) is uncertain whether the band is in E_{1a} or E_{1b}. *E. stubblefieldi* has not been seen either, although included by Bisat at the level of *E. pseudocoronula* and *E. pseudobilingue A*.

The lamellibranchs at this level seem to have been neglected. Hudson and Cotton (1943, p. 169) record *Pseudamusium* in the Alport borehole, and also *Posidonia membranacea* (now *Caneyella membranacea*) and *Posidonia* cf. *P. corrugata*. *Obliquipecten* is not included though it is an abundant element in very low E₁ beds in Leitrim, associated with *C. leion*, whereas *Pseudamusium* is more abundant at the top of the zone with *E. medusa*.

Several specimens from the Alport borehole material are referred to in Book 30 at the Geological Survey Museum as *Posidonia* sp. These have been examined and found to be the same as Slieve Anierin forms referred to *P. trapezoedra*, which is extremely abundant towards the upper part of the zone. GSM Zh2000 is a slab showing *Dimorphoceras* sp. and *P. trapezoedra*, and was collected from a depth of 1065–6 feet (GSM, Book 30, p. 281). This is valuable confirmatory evidence of the burst in development of this species at about this level. From a depth of 1060–1 feet, which is 6 feet below the top of the zone, GSM Zh1973 has been identified as *Girtyoceras* sp. but may be compared with *E. medusa sinuosum* which occurs at the top of the zone in Leitrim.

Bisat (1950, p. 14) refers to the occurrence of *Eumorphoceras* aff. *E. hudsoni* at 1064 feet in the Alport material. GSM Zh1993 collected at this depth, and similarly identified, is very like the Bateson Wood specimen GSM Ca4782 and is now believed to be *E. medusa*. At lower depths in the borehole (1072–3 feet) GSM Zh2026, *E. pseudobilingue A*, is very close to the specimens collected from locality L23(4)7 where this species and *C. leion* are about equally abundant.

Hudson and Cotton refer to a *Dimorphoceras* phase in E_{1a} and these specimens have been examined and compared with Slieve Anierin specimens referred to *Kazakhoceras* sp., which are abundant at about the level at which *P. trapezoedra* first becomes so noticeable. The Alport specimens are all poor and apart from the fact that like the Slieve Anierin examples they are all very narrow compressed forms, little more can be established.

In the lower part of the succession in the Alport borehole *Eumorphoceras* sp. form A Moore is apparently more common than *E. pseudocoronula*. The former has only been imperfectly seen on Slieve Anierin at a level at which *C. leion* is dominant, with *Obliquipecten costatus*; either this horizon or the level of *E. pseudocoronula* and *E. rota* could be the one with the oldest E_{1a} fauna, though the writer believes that the latter band is lower. There is, however, close correspondence between the successions at Alport Dale and Slieve Anierin in the larger part of the zone and the lack of precise correspondence in the lower part is partly due to the poorness of the Alport borehole material.

(b) *Eumorphoceras pseudobilingue* zone. Hudson and Cotton (1943, p. 168) state that *Cravenoceras* is not common in this zone in the Alport borehole, and on Slieve Anierin it has not been collected from beds assigned to this zone. *P. trapezoedra* continues from the *C. leion* zone and in the Alport material poor specimens referred to as *Posidonia* cf. *P. costata* are believed to be the same as such specimens as GSM Zh2000 (*P. trapezoedra*) from the lower zone, so that the species apparently continues in both areas.

Eumorphoceras cf. *E. angustum* is a very abundant species at this level on Slieve

Anierin. Though it had not been defined at the time of identification of the Alport material, it nevertheless does not seem to be present. Moore (1946, p. 439) places the species in the *E. pseudobilingue* zone and states (p. 440) that the two species are not necessarily on the same horizon. On Slieve Anierin this species directly underlies *E. pseudobilingue* s.s. and is associated with *P. trapezoedra* and *Kazakhoceras* sp. showing a strongly beaded, sharp venter. The presence of notching on the sharp mid-venter is also believed to be present in the later stages of *E. pseudobilingue* s.s. which succeeds *E.* cf. *E. angustum*. Stephens *et al.* (1953, p. 92) further confirm the presence of *P. trapezoedra* in the *E. pseudobilingue* zone.

In the same memoir (loc. cit.) a goniatite referred to as *Eumorphoceras* aff. *E. pseudobilingue* is described from Ramshaw Beck in older beds than *E. pseudobilingue* s.s.; it has poorly developed ribs, a more prominent sulcus, faint spiral ornament, and a beaded keel in old age. No species which exactly fits this description has been found on Slieve Anierin. The venter has not been seen to be beaded at the diameter usually found in *Eumorphoceras* cf. *E. angustum* and the shoulder ridge is a very faintly developed feature, although in some of the specimens the faint plications of the surface which replace the earlier strong ribs ridge the surface of the faint shoulder ridge where they cross it and make the latter slightly more obvious. The beaded venter has been most obviously seen in the large compressed *Kazakhoceras* sp.

The succeeding specimens of *E. pseudobilingue* s.s. accord very well with GSM 72927 from Little Mearley Clough, near Clitheroe, and is presumably the form intended by Bisat (1928, pl. 6) as *E. pseudobilingue* B. On Slieve Anierin a few forms succeed *E. pseudobilingue* B; they have been figured and described as *E. pseudobilingue* C. Although they have some resemblance to *E. pseudobilingue* s.s. they show an earlier fading of the ribs, which are less wavy than the ribs in *E. pseudobilingue* s.s. and with a prominent groove in the shoulder region.

Parkinson (1936, pl. 24) referred to *E. pseudobilingue* C occurring below *Cravenoceras malhamense*. Bisat (*in litt.*, 1960) agrees that a shoulder groove is a marked feature of this form. Specimens collected by Parkinson from Studforth Gill have been presented by Bisat to the Geological Survey Museum (GSM Zl 5773-6) and have been examined, but only one specimen resembles the Slieve Anierin examples. It seems likely therefore that those specimens occurring below *C. malhamense* should be referred to this form, but as Bisat has never defined or figured it, there is no holotype for comparison; however, Bisat (*in litt.*, 1960) has agreed with the identification.

The species *E. pseudobilingue* s.l., as seen on Slieve Anierin, shows a reduction in the number of ribs; in *E. pseudobilingue* s.s. they are fewer and with wider interspaces than in *E. pseudobilingue* A; in *E. pseudobilingue* C the ribs fade earlier and are narrow and sharp as in the lower *E. pseudobilingue* s.s., but less tenuous in their passage across the flank than in that species. The shoulder ridge is lost and a groove more reminiscent of the later *E. bisulcatum* appears.

On Slieve Anierin at this level *Chaenocardiola footii* occurs. It is noted by Parkinson (1936, pl. 24) as appearing at the level of *C. malhamense* but on Slieve Anierin is definitely associated with *E. pseudobilingue* C, together with small *P. corrugata* but not *P. trapezoedra*.

(c) *Cravenoceras malhamense* zone. Hudson and Cotton (1953, p. 167) list *C. mal-*

hamense, *Neodimorphoceras scaliger* (Schmidt) and *Chaenocardiola footii* as the characteristic fossils of the *C. malhamense* zone in the Alport borehole, providing a striking correlation with the beds of the same age seen at localities L21(13)7 and L21(5)5 on Slieve Anierin. *Caneyella membranacea* is also abundant on Slieve Anierin, and is included in Hudson and Cotton's faunal list. On Slieve Anierin this is the highest level at which *C. membranacea* has been collected, and at this level most of the forms are referred to *C. membranacea* s.s., its subspecies *horizontalis* being less abundant.

No specimens of *Eumorphoceras* are known from Derbyshire or Slieve Anierin at this level, so that there is close correlation between the two areas on this point. In the Bradford and Skipton Memoir (Stephens *et al.* 1953, p. 92) *Cravenoceras* aff. *C. malhamense* is reported from Howgill Beck, associated with *C. membranacea* and *E. pseudo-bilingue*; this association contrasts with their separation in Leitrim and in Alport Dale.

(d) *E₁d zone or E₂a faunas*. The next fossiliferous level on Slieve Anierin is thought to correspond to the *E₁d* zone of Hudson and Cotton (1953, pp. 166–7). The most abundant species at this level is *C. cowlingense*. A comparison of these specimens with those collected from the Mirk Fell Beds of Tan Hill in Yorkshire by Hudson (1941, pp. 279–83) leads to the conclusion that they belong to the same species. The Mirk Fell beds are referred to *E₂* by Hudson, and *Anthracoceras* aff. *A. paucilobum* occurs with *C. cowlingense*. Stubblefield (Hudson and Stubblefield 1945, p. 136) also believes that the horizon of *C. cowlingense* is low *E₂* not *E₁d*.

On Slieve Anierin *C. cowlingense* is associated with a rather poor fauna, but including a few specimens of *E. bisulcatum grassingtonense*, *P. corrugata*, *P. lamellosa*, and *Chaenocardiola footii*. The Tan Hill fauna is rather different from the goniatite-lamellibranch fauna on Slieve Anierin since it includes nuculids and small gastropods but no examples of *Posidonia* or *Posidoniella*; there is also an apparent absence of fossil wood debris, which is quite common at the level of *C. cowlingense* on Slieve Anierin.

The lucky preservation of a suture in one of the Slieve Anierin specimens of *C. cowlingense* confirms the accuracy of the identification. Hudson (1941, p. 281) has figured the suture-line of GSM 62813 from Mirk Fell Beck and of GSM 62824, a meta-type of the species from an erratic in Keighley Churchyard, and a comparison of these with the Slieve Anierin specimen leaves no doubt of their being the same form. A comparison of specimens GSM CS571–4, 582, and 584 collected from the Cockhill Marine Band in Gillfields Adit, also established this identification; a very large specimen, GSM Zh2908, is from the same horizon at the Cockhill Adit.

These examples of *C. cowlingense* are particularly interesting since the Cockhill Limestone is the horizon from which Dunham and Stubblefield (1944, pp. 237–9) described *E. bisulcatum grassingtonense* and which they place in *E₂*. *Cravenoceras* is dominant in the Cockhill Limestone and since there is only one specimen of *grassingtonense* at the Geological Survey Museum it would appear that specimens of *Eumorphoceras* are as rare as they are at this level on Slieve Anierin. Dunham and Stubblefield suggest a correlation of this level with the Edge Marine Band, described by Stephens *et al.* (1942, p. 348) but in a footnote (p. 238) they also consider that it may be slightly later than this band.

The Slieve Anierin succession shows two decided levels within beds referred to *E₂a*, the lower dominated by *C. cowlingense* and with rare examples of rather variable

Eumorphoceras, some of which are definitely *E. bisulcatum*, and which have been compared with *grassingtonense*; and the upper level with *E. bisulcatum erinense* subsp. nov. and *E. bisulcatum ferrimontanum* subsp. nov. dominant, with *Chaenocardiola footii* the most abundant lamellibranch, and with no *C. cowlingsense*. The upper level is believed to be that of the Edge Marine Band.

The E₁d fauna described by Hudson and Cotton in the Alport borehole is correlated with the lower E₂a faunal band on Slieve Anierin. The *Eumorphoceras* specimens from

<i>Slieve Anierin</i> (this paper)	<i>Greenhow Mining Area</i> (Dunham and Stubblefield 1944)	<i>Bradford and Skipton Area</i> (Stephens et al. 1953)	<i>Lancaster Fells</i> (Moseley 1954)	<i>Alport Dale</i> (Hudson and Cotton 1943)
Grit	Red Scar Grit	Marchup Grit	Roeburndale Grit Group	
Barren shales	Shales and Sandstone Bands	Shales and Sandstones, &c.	Brennand Grits	
<i>High E₂a</i> <i>E. bisulcatum ferrimontanum</i> <i>Chaenocardiola footii</i>	not known in the area	Edge Marine Band	Brennand Band	E ₂ a 399-408 ft.
<i>E. bisulcatum erinense</i> <i>Chaenocardiola footii</i>		Weston Marine Band		
Barren shales	Shales and Sandstone Bands	Skipton Moor Grits	Weston Grit	
<i>Lowest E₂a</i> Dominant <i>C. cowlingsense</i> and rare <i>E. bisulcatum grassingtonense</i>	Cockhill Limestone		Tarnbrook Valley Band	E ₁ d 453-63 ft.

TABLE 3. Suggested correlations between the fossiliferous bands in E₂a on Slieve Anierin and some bands of similar age in northern England.

this level in the borehole section are poor and have been variously referred to as *Eumorphoceras* cf. *E. pseudobilingue* and *E. aff. E. pseudobilingue*, but Hudson and Cotton (1943, p. 167) state that many of the latter are indistinguishable from *E. bisulcatum*. The writer compares GSM Zh1164 with forms collected from the lowest E₂a faunal band on Slieve Anierin. The evidence suggests that the forms of *Eumorphoceras* at this level are rather variable, and Hudson and Cotton's view that the fauna has more in common with the Pendleian than the Arnsbergian may be justifiable in some respects, but the writer prefers to assign these beds to E₂ because of the presence of *E. bisulcatum*.

In the Lancaster Fells, Moseley (1954, pp. 428-30) suggests that beds with *C. cowlingsense* and *E. bisulcatum* should be correlated with the Edge Marine Band and included in the Arnsbergian, and not the Pendleian as in Hudson (1945, p. 3) and Hudson and Cotton (1943, p. 166). It is now suggested that the band with *C. cowlingsense* and *E. bisulcatum grassingtonense* should be correlated with the Cockhill Limestone and Hudson's E₁d level at Alport Dale. The writer correlates the Edge Marine Band of

Rombalds Moor with the higher band in E_{2a} on Slieve Anierin in which *E. bisulcatum* is the most abundant form; the whole fauna is a richer one than at the lower level in E_{2a}.

Moseley (1954, pp. 429–30) states that the Tarnbrook Wyre Marine Beds (E_{2a}) are made up of two horizons, but as they are exposed in different localities he is uncertain of their relative positions; he believes that the Brennand outcrops in which *E. bisulcatum* is the dominant form is the lower band. The other fauna in the upper Tarnbrook Valley contains an association of *C. cowlingsense* and *E. bisulcatum*. The Slieve Anierin succession shows that the Tarnbrook Valley material is lower and the Brennand outcrops probably equivalent to the second E_{2a} level on Slieve Anierin. Specimens of *E. bisulcatum* from some Brennand material kindly provided by Bisat appear to be close to those from the second faunal band in E_{2a} which are referred to as *E. bisulcatum erinense* subsp. nov.

Stephens *et al.* (1942, p. 348) describe the Edge Marine Band, and state that *E. bisulcatum* and *Chaenocardiola footii* are the most abundant forms. This is reminiscent of the second faunal band in E_{2a} on Slieve Anierin and contrasts strongly with the fauna of the lower E_{2a} band. The specimens of *E. bisulcatum* at this level on Slieve Anierin are believed to be very close indeed to *E. bisulcatum* s.s. but there are two subspecies present within this band, the lower being *erinense* and the higher *ferrimontanum*. Good specimens from the Edge Marine Band appear to be very rare and Bisat (*in litt.*, 1960) does not recall seeing any good specimens. The material mentioned in the Bradford and Skipton memoir (Stephens *et al.* 1953, p. 25) has been examined, but is extremely poor and inconclusive. Dunham and Stubblefield (1944, p. 260) refer to specimen GSM GM3675 (see pl. 3, fig. 3) and suggest a resemblance to *grassingtonense*. The writer suggests rather a resemblance to *E. bisulcatum ferrimontanum* subsp. nov. from localities L21(5)11 and L21(13)4. GSM GM3675 was collected from Cononley Beck and is about the best specimen in the material mentioned by Stephens *et al.* (1953, p. 25). There is an additional line of evidence by means of which the second faunal band in E_{2a} on Slieve Anierin can be correlated with beds elsewhere, since in Ireland two very easily determined goniatites, viz. *Kazakhoceras scaliger* and *Cravenoceras* cf. *C. gairense*, are associated rather less abundantly with *E. bisulcatum*. *K. scaliger* is an abundant member of the fauna attributed by Hudson and Cotton (1943, pp. 162–3) to E_{2a}. The fauna from 399–408 feet in the Alport borehole has been examined and although the specimens of *E. bisulcatum* are not easily compared, since many of them seem to be gerontic individuals, the examples of *K. scaliger* are easily determined even from very small fragments. Crinoid ossicles also appear to be common at this level, as on Slieve Anierin in the second E_{2a} faunal band. It is therefore suggested that the second faunal band on Slieve Anierin should be correlated with this level in Alport Dale.

A fauna is described in the Bradford and Skipton memoir (Stephens *et al.* 1953, p. 28) from the left bank of Holbeck, near Otley, Yorks. It is stated to be difficult to place in the succession on account of drift obscured country and faulting. The writer suggests that it should be correlated with the second E_{2a} faunal band in Leitrim and not with the Marchup Marine Beds as suggested in the memoir. Hudson (1944, p. 234) correlates this fauna with the E_{2a} horizon in Alport Dale. There is an abundance of *K. scaliger* as in Hudson's E_{2a} horizon at Alport, also *Pseudamusium* and crinoidal debris. Most of the specimens of *Cravenoceras* are too fragmentary to be of value and those of *E. bisulcatum* from this locality are not good. The specimens identified as *Posidonia* cf. *P. membranacea* are the forms now referred to as *P. corrugata elongata* subsp. nov.,

which is abundant on Slieve Anierin in the second E₂a band. *Chaenocardiola footii* is also present in both places.

A similar fauna is described in the Bradford and Skipton memoir (Stephens *et al.* 1953, p. 29) from the Washburn Valley near Leathley, Yorks., and is also correlated with the Marchup Marine Beds, but the writer would correlate it with the second faunal band in E₂a in Leitrim.

A large slab from 280 yards W. 8° S. of St. Oswald's Church, Leathley, Yorks., shows *K. scaliger* which is indistinguishable from specimens in the second faunal band in E₂a on Slieve Anierin and Hudson and Cotton's E₂a horizon at Alport. Hudson (1944, p. 234) correlates this fauna with E₂a in Alport Dale, and Stubblefield (*in* Stephens *et al.* 1953, p. 94) agrees that it may be lower than the Marchup Marine Beds. A discussion between Hudson and Stubblefield (1945, pp. 135–7) over the possible correlation of the Cockhill Limestone with the Weston Marine Beds in the Washburn Valley can be considered at this point in the light of the Slieve Anierin succession. *E. bisulcatum* from the Weston Marine Band at Leathley (GSM WE947) is compared with *E. bisulcatum erinense* from the second faunal band in E₂a on Slieve Anierin, and the *E. bisulcatum* from the Cononley Beck Edge Marine Band with *E. bisulcatum ferrimoutanum* from the same band on Slieve Anierin. Both subspecies occur within one continuous fossiliferous band and it is therefore suggested that this second faunal band in E₂a should be correlated with the Weston and the Edge Marine Bands.

The Warley Wise marine band material has not been seen, but the lamellibranch fauna listed by Bray (1927, p. 53) appears to be similar to that found in the second band in E₂a. Hudson believes, on faunal and stratigraphical evidence, that this band is below the Weston Marine Band. It may be that the two subspecies of *E. bisulcatum* which occur within the one band on Slieve Anierin have elsewhere led to the conclusion that two very different levels were being seen.

The writer would suggest that the Warley Wise, the Edge and the Weston Marine Bands should all be correlated with the second faunal band in E₂a on Slieve Anierin and that the lower faunal band corresponds with the Cockhill Limestone. This would support Stubblefield's suggestion that the Weston Grit is earlier than the Marchup Grit and that the Grassington Grit is earlier than either.

Although the second faunal band in E₂a on Slieve Anierin does not yield as abundant examples of *Cravenoceras* as the lower band, it does yield a few which are referred to *Cravenoceras* cf. *C. gairense*. In the material at the Geological Survey Museum from Cononley Beck listed by Stephens *et al.* (1953, p. 25) is a *Cravenoceras* with an acutedged open umbilicus; however, most of the specimens have been rejected and thrown away and the few fragments now left do not show the umbilicus but only simple *Cravenoceras* ornament. Since *C.* cf. *C. gairense* is typical of the second faunal band on Slieve Anierin it would be a valuable additional line of evidence if it could be found in some of the marine bands in the Pennines which it is suggested should be correlated with this level. Some specimens have been found at the Geological Survey Museum which had been identified as *Cravenoceras* cf. *C. holmesi*, presumably because the umbilical edge appears to be raised; however, in *C. gairense* there are three spiral ridges around the umbilicus which make it unmistakable. The specimens now assigned to the latter species, e.g. GSM JS1479, 1491, and 1492, were collected from a road-cutting on the east side of the road 520 yards west-north-west of Crickton, Llanrhidian, Glam.

(Survey Book 29, p. 267). Specimens GSM JS1121 and 1117 were collected from a stream in Moorlakes Wood, 250 yards north-east of Courthouse Farm, Ilston, Glam., and are also the same species. A further link with the Slieve Anierin horizon exists in the presence of *Dunbarella* sp. (GSM JS1113) in the Glamorgan fauna; it is believed to be the same species as that on Slieve Anierin and shows a large number of ribs and no definition of the anterior ear by a furrow.

(e) *Cravenoceratoides bisati* and *Ct. edalense* fauna, lowest E_2b . The lowest E_2b subzone, that of *Ct. bisati*, contains dominant *Ct. edalense* and less common *Ct. bisati*. The most

<i>Slieve Anierin</i> (this paper)	<i>Greenhow Mining Area</i> (Dnnham and Stubblefield 1944)	<i>Simonseat Anticline near Skipton</i> (Hudson 1939)	<i>Lancaster Fells</i> (Moseley 1954)	<i>Alport Dale</i> (Hudson and Cotton 1943)
<i>Ct. nititoides</i> <i>E. rostratum</i> <i>Productus hibernicus</i> <i>Weberides</i> cf. <i>W. shunnerensis</i> <i>C. holmesi</i> <i>A. tenuispirale</i>	<i>A. tenuispirale</i>	Pace Gate Beck (Tonks 1925) <i>Ct. nititoides</i> <i>Productus</i> sp.	? <i>Ct. stellarum</i> <i>C. holmesi</i> <i>Anthracoceras</i> beds	<i>E. rostratum</i> at 300–6 ft. (referred to as the <i>Ct. nitidus</i> level by authors) few horizons with faunas worth recording
Dominant <i>E. bisulcatum leitrinense</i> ; rare <i>Ct. nitidus</i> <i>C. subplicatum</i>	Colsterdale Limestone no record of any of these species	Birk Gill Limestone <i>A. aff. A. discoides</i> <i>C. cf. C. holmesi</i>	<i>nitidus</i> Limestone <i>Cravenoceras</i> of <i>cowlingense</i> group, <i>Ct. lirifer</i> and rare <i>Ct. bisati</i>	354–60 ft. <i>Ct. edalense</i>
Dominant <i>Ct. edalense</i> , rare <i>Ct. bisati</i>		<i>C. aff. C. holmesi</i> <i>C. cf. C. subplicatum</i>		
Grit	Red Scar Grit	Red Scar Grit	Roeburndale Grit	

TABLE 4. Suggested correlations between the fauna above the grit on Slieve Anierin and ones of similar age in northern England.

common lamellibranch is *Posidonia corrugata elongata*. The succeeding beds contain very abundant but poor forms attributed to *Cravenoceras subplicatum*.

Hudson (1945, pp. 2, 4) states that there are two horizons within the *Ct. bisati* subzone, a lower faunal band with *C. subplicatum* and an upper with *Ct. bisati*. The various sections described by Hudson (1944, pp. 233–41) all appear to lead to this conclusion. On Slieve Anierin the maximum abundance of *Ct. edalense* is definitely beneath *C. subplicatum* and only unfossiliferous horizons occur beneath the former. The Marchup Marine Beds are described in the Bradford and Skipton memoir (Stephens *et al.* 1953, pp. 26–29) as characterized by *Ct. bisati*, and presumably in part at least they belong to

the *Ct. bisati* subzone and can therefore be correlated with the beds immediately above the grit on Slieve Anierin. It is to this level that the beds from Holbeck and the Washburn River, which have already been discussed, have been ascribed in the memoir. Hudson and Cotton (1945*b*, pp. 9, 10), in describing the *Ct. bisati* subzone in the Edale Valley in Derbyshire, have not been able to determine the relative positions of the two faunal bands of the subzone.

In the Lancaster Fells, Moseley (1954, pp. 432–3) has not included *C. subplicatum* in his faunal list but includes *C. cf. C. cowlingense* group and *Ct. lirifer*; these two forms are associated together in four bands within the subzone with no distinction into lower and upper. There can be no doubt of the order of succession in these beds on Slieve Anierin.

(*f*) *Cravenoceratoides nitidus* subzone. The base of this subzone is characterized by a small *E. bisulcatum* which has constrictions and is described as *E. bisulcatum leitrinense* subsp. nov. It does not conform with *E. bisulcatum varicata* Schmidt (1934, p. 449, fig. 29 and p. 445). At this level only fragments of *Cravenoceratoides* ornament have been found, which show clearly the forking and the asymmetrical nature of the lirae, suggesting that they represent either *Ct. nitidus* or *Ct. nititoides*. It seems probable that they are fragments of the former, but for some reason the species does not appear to have been as common in this area as elsewhere, whereas the *Eumorphoceras* is relatively abundant in the shales at this level. A few rare specimens of *C. holmesi* have been found slightly lower than *E. bisulcatum leitrinense*, but are more abundant above this level.

In Alport Dale, Derbyshire, Hudson and Cotton (1943, p. 162) record a *Ct. nitidus* band from a depth of 300–6 feet and a *Ct. edalense* horizon at 354–60 feet. Between these two depths there were few horizons with faunas worth reporting, and there is no record of anything comparable with *E. bisulcatum leitrinense*. The material collected by the same authors (1945*b*, pp. 9, 10) in Edale has also been examined at the Geological Survey Museum but is extremely poor and there is no indication of this horizon.

At the Geological Survey Museum there are a few imperfect specimens which are believed to be the same subspecies; GSM Da1593, 1594, and 1599 were collected in a section on the left bank of the stream, 150 yards to the south-east of Low Stubbing and 820 yards N. 11° W. of Holy Trinity Church, Cowling, Yorks. Stubblefield has commented in Geological Survey Book 28, p. 20, that Da 1599 shows constrictions with two to three ribs between them and that the ribs resemble short stubby plications as are seen in some of the Scottish examples of *E. bisulcatum*.

Dunham and Stubblefield (1944, pp. 239–41) describe the Colsterdale Limestone as abounding in *Ct. nitidus* at the level of the Colsterdale Marine Beds in the Greenhow mining area, and with *E. bisulcatum* rare in the shales at this level. The latter is described as the variety with short stout ribs which elsewhere characterizes this horizon. GSM CS853 and CS859 (Survey Book 35, p. 51) from locality 25 of Dunham and Stubblefield have been examined, but are too poor and fragmentary to compare satisfactorily with *E. bisulcatum leitrinense*.

However, one very interesting connexion that can be established is that GSM CS891, identified as *Cravenoceras cf. C. holmesi*, from the Colsterdale Marine Band in a stream section 300 yards west of Ivin Waite, west of Pateley Bridge, Yorks., is now attributed to *Anthracoceras tenuispirale*, and this species first appears on Slieve Anierin at the level

of *E. bisulcatum leitricense* and soon becomes the dominant species. It is suggested therefore that the Colsterdale Limestone corresponds to the *E. bisulcatum leitricense* level on Slieve Anierin.

In the Pateley Bridge area *Ct. nitidus* is only abundant in the limestone whereas *Eumorphoceras* occurs in the shales; it is therefore possible that the lack of suitable limestone-forming environments in the Slieve Anierin area at this time may be connected with the scarcity of *Ct. nitidus*. Dunham and Stubblefield (1944, p. 241) correlate the Colsterdale Marine Beds in general terms with the Marchup Marine Beds of the Bradford and Skipton area. There is, however, no record in the Greenhow area of beds with *Ct. bisati*; the Colsterdale Marine Beds succeed the Red Scar Grit and their fauna of *Ct. nitidus* has already been discussed. The limits of the Marchup Marine Beds do not appear to be exactly defined, but the Slieve Anierin succession suggests that the level of the Colsterdale Marine Beds is above the *Ct. bisati* subzone and at the lower level within the *Ct. nitidus* subzone. The *Ct. nitidus* fauna seen in the Greenhow area has not been seen in the Bradford and Skipton country.

(g) *Anthracoceras tenuispirale* fauna. *A. tenuispirale*, which was first described from the *Ct. nitidus* subzone in the Namurian of Belgium by Demanet (1941, pp. 148–9, pl. 6, fig. 18; pl. 7, figs. 1, 2), is abundant on Slieve Anierin and can now be demonstrated in beds of this age in the Pennine area. The high magnification needed to detect the spiral ornament suggests the possibility that this species may well have been overlooked in the past and may have been identified as either *A. paucilobum* or *A. glabrum*, or, like the Colsterdale specimen, as *C. holmesi*.

Moseley (1954, pp. 433–4) records *Anthracoceras* of the *paucilobum* group in the *Anthracoceras* beds above the *Ct. nitidus* limestone in the Lancaster Fells, but unfortunately, no illustrations of the fossils are given and the material does not appear to be available; it can only be suggested, therefore, that as this is the same level as that with abundant material on Slieve Anierin, Moseley's *Anthracoceras* specimens may be *A. tenuispirale*.

(h) *Cravenoceras holmesi* fauna. At this level *C. holmesi* has only been seen as external impressions in which the ridge around the umbilical edge in the adult is seen as an impressed groove. The species occurs rarely lower in the succession just below the *E. bisulcatum leitricense* horizon and a few internal moulds have been found at this lower level showing the rim around the umbilicus and fragmentary sutures. The crushed impressions which are so common above the *A. tenuispirale* horizon are inferior and mostly not very large specimens. In this species the ridge is not a decided feature until the adult stage. A larger specimen, in which the ridge must have been a very marked feature, is seen as an impression in GSM Zg1349, collected from Meerbrook, Staffs.

The position of *C. holmesi* in the succession has been the subject of some discussion. Hudson (1945, p. 4) placed the *C. holmesi* fauna beneath the *Ct. nitidus* horizon on evidence from Greenholes Beck in the Lancaster Fells. Moseley (1954, pp. 432–3) disagreed with this and believed that Hudson (1944, p. 238) did not record the fauna of the *nitidus* limestone in the Greenholes Beck succession and was led astray by the rare occurrence of *Ct. nitidus* above the level with *C. holmesi*. On Slieve Anierin it appears that if the level of *E. bisulcatum leitricense* is correctly correlated with the *Ct. nitidus* horizon elsewhere (and the evidence is distinctly in favour of this contention) then the

maximum abundance of *C. holmesii* is definitely above the horizon of *Ct. nitidus*. However, it must be pointed out that the species is already scantily present slightly lower than *E. bisulcatum leitrinense* although its period of dominance is higher in the succession.

Moseley (1954, pp. 432–5) erected the subzone of *C. holmesii* above the *Ct. nitidus* subzone and below a subzone of ?*Ct. stellarum*. The evidence for the latter does not seem to be strong, since Moseley states that badly preserved specimens of ?*Cravenoceratoides* (possibly *Ct. stellarum*) were obtained from a thick calcareous band. He also states that Hudson may have had better material and that the horizon is tentatively regarded as the base of the *Ct. stellarum* subzone.

Hudson (1945, p. 4) mentions another section in the River Noe Valley in Edale, Derbyshire, where it is possible to determine the relative positions of *Ct. nitidus* and *C. holmesii*. This section was described by Jackson (1927a) and subsequently by Hudson and Cotton (1945b, pp. 9, 10); the latter describe a higher fauna including *Ct. nitidus*, *C.* cf. *C. holmesii*, and *E. bisulcatum* var. above shales with *C. holmesii* and *C. cowlingsense*. The material available at the Geological Survey Museum, however, is all so poor and fragmentary that it was found impossible to compare it with any of the goniatites from Slieve Anierin. Specimens GSM Zi968 and 969 are, however, believed to be *Productus hibernicus*, which occurs in a rich faunal band above the *C. holmesii* beds on Slieve Anierin. GSM Zi1487 also shows a *Productus* and a trilobite pygidium. Hudson and Cotton (1945b, p. 9, footnote) state that Bisat (*in litt.*, 1945) considered that *Ct. nititoides* was an important member of this fauna, which they refer to the *Ct. nitidus* subzone.

(i) *Cravenoceratoides nititoides* fauna. Above the beds with *Ct. holmesii* on Slieve Anierin occurs the most prolific fossil band in the succession, rich in goniatites and lamelibranchs but also containing the brachiopods *P. hibernicus* and rare *Orbiculoidea nitida*, and the trilobite *Weberides* cf. *W. slummerensis*. Specimens of *Ct. nititoides* are extremely abundant and it is virtually impossible to distinguish between them and the holotype (GSM 49964) collected from Pace Gate Beck, near Blubberhouses, Yorkshire (see Bisat 1932, pl. 2, fig. 2).

Tonks (1925, pp. 251–2) originally collected from this locality and includes trilobite remains in his faunal list. *E. bisulcatum* is recorded as rare. Unfortunately it is now impossible to collect from this locality and there is little material in the Geological Survey Museum collections apart from the holotype of *Ct. nititoides* and the paratypes GSM Zi5779–86. On the evidence of *Ct. nititoides* and the trilobite remains it is suggested that this band should be correlated with the Pace Gate Beck exposure. Hudson (1945, footnote, p. 5) states that the shale exposure in Pace Gate Beck is an isolated one, that it occurs towards the top of the Birk Gill Shales, and that it is not possible at this locality to locate its position in relation to other Arnsbergian faunas. The fauna given by Hudson (1939, p. 329) for the Birk Gill Limestone appears to be nearer to that of the Colsterdale Limestone, with common *Ct. nitidus*, whereas the Pace Gate Beck fauna is obviously distinct and the inference from Hudson's remarks (1945, footnote, p. 5) is that it is higher in the Birk Gill Shales than any of the faunas described by him from these beds. It is unfortunate that these exposures are so incomplete but the succession on Slieve Anierin establishes the position of this band dominated by *Ct. nititoides* about 40 feet above the horizon with *E. bisulcatum leitrinense* and very rare *Ct. nitidus*, and below the first appearance of *N. nuculum*.

In Alport Dale Hudson and Cotton (1943, p. 162) record a fauna at a depth of 300–6 feet; this fauna has been examined and specimen GSM Zh955 is considered to belong to *E. rostratum* sp. nov., which occurs at the *Ct. nititoides* level on Slieve Anierin. It shows the same merging of the ribs into fine striae at about half-way across the flanks and the same extremely prominent lingua in the striae. At this level *Ct. nititoides* is present as well as *Ct. nitidus*, trilobite remains and *Productus* sp.; all the evidence favours the correlation of this level in the borehole with the *Ct. nititoides* band on Slieve Anierin.

An interesting occurrence at the *Ct. nititoides* level on Slieve Anierin is the presence of *Euchondria* aff. *E. levicula* Newell (1937, p. 107), previously only identified in American deposits. Newell (*in litt.*, 1960) agrees that the Slieve Anierin specimens are extremely close to the American material. The species is a very abundant member of the lamelli-branch fauna at this level. No information is available as to its stratigraphical level in the American succession in terms of the British goniatite succession, but it is an Upper Carboniferous (Pennsylvanian) species.

It is considered significant that Tonks (1925, p. 252) included *Aviculopecten* aff. *A. dissimilis* Fleming in the Pace Gate Beck faunal list. This species has a left valve with radial ornament and a right valve with concentric ornament only, suggesting that his specimens were the same as the lamelli-branchs associated with *Ct. nititoides* on Slieve Anierin. The *Euchondria levicula* specimens from Slieve Anierin are better preserved, and show the nature of the ligamental area as well as the discrepant ornament of the two valves. This is further evidence of the postulated correlation of the two horizons.

3. Germany

Arnsberg, Westphalia. The Namurian succession of the Arnsberg area in Westphalia, Germany, has been described by Schmidt (1934, pp. 440–61), and there is close correspondence with the sequence of faunas on Slieve Anierin. The *E. pseudobilingue* beds are not subdivided (*op. cit.*, pp. 445–6) and Schmidt states that the forms of this species are extremely variable and not always easy to separate from *E. bisulcatum*. The example of the former species which has been figured, however (*op. cit.*, p. 446, fig. 1), resembles *E. pseudobilingue* s.s. with rather wavy ribs as seen at localities L21(5)4 and L23(4)1 on Slieve Anierin.

Dinorhoceras scaliger Schmidt (*op. cit.*, p. 446, fig. 2), now *Kazakhoceras scaliger*, is found at this level in Ireland also, where it is associated with *Cravenoceras* aff. *C. malhamense* and first appears a little above *E. pseudobilingue* s.s.

The drawing of *Chaenocardiola haliotoides* (Roemer) (*op. cit.*, p. 446, fig. 7) shows only twenty-one ribs whereas this species is supposed to have rather large rib counts. It looks very much like an immature specimen of *Chaenocardiola footii*, which on Slieve Anierin first appears at about the level of *E. pseudobilingue* s.s. Schmidt does not believe that the German forms are the same as the British species, but his drawing does not seem to support his argument.

Patteisky (1929, p. 20, pl. 17, fig. 13) figured *Chaenocardiola haliotoidea* and the large number of ribs appears to conform with the original description of the species. It is associated, however, with *Sagittoceras discus* (Roemer), now *Girtyoceras discus* (Roemer), which in England is described from high B₂ (Moore 1946, pp. 397–8). On Slieve Anierin the only specimens which have been referred to this species have been collected from the *Ct. nititoides* level in E₂.

The figures given for *Cravenoceras* cf. *C. leion* (Schmidt 1934, p. 446, fig. 3) and for *C. cf. C. inallhauense* are too poor for comparison and according to Schmidt the genus is rarely found. He mentions fish remains about 10 mm. below the described fauna and which were attributed by Aldinger (1931, pp. 190–3) to *Coelacanthus stensioi* Aldinger (now *Rhabdoderma stensioi* (Aldinger) (Demagnet 1941, pp. 166–8)) and *Coelacanthus* sp. Similar remains have been found at L20(16)2 on Slieve Anierin, where they are known to be in E₁, and occur above L20(16)1, where a high *C. leion* zone fauna is exposed, including *E. medusa*.

The beds of E₂ age at Arnsberg allow a more detailed subdivision, and the fauna (op. cit., pp. 446–8) can broadly be correlated with the E_{2a} beds on Slieve Anierin. It is difficult to suggest any closer comparisons within E_{2a} as some of Schmidt's figures suggest features that are rather generalized. The figure of *E. bisulcatum* (op. cit., p. 447, fig. 12) shows several bifurcating ribs like *E. bisulcatum grassingtonense*; but the ribs appear to be rather geniculate and in fact like those of *E. bisulcatum erinense* subsp. nov. from the second faunal band in E_{2a} on Slieve Anierin. It would be unwise to do more than point out that the figure certainly resembles *E. bisulcatum* s.l., which occurs below the grit on Slieve Anierin.

The next horizon at Arnsberg with *C. edalense* (op. cit., p. 448) obviously represents the beds seen immediately above the grit on Slieve Anierin. The specimen illustrated in fig. 23, p. 448 would now be assigned to *Ct. bisati*, since there is repeated bifurcation of the lirae. On Slieve Anierin this form is considerably less common than *Ct. edalense*. Forms like *Cravenoceras* sp. (fig. 26, p. 448) and *C. cf. C. leion* (fig. 25, p. 448) are said to occur beneath the beds with *Ct. bisati*, but Schmidt's figures are small and poor, and it has not been found possible to compare them with forms from Slieve Anierin.

Schmidt (1934) refers fig. 28, p. 448 to *Posidoniella membrancea* (now *Caneyella membranacea*) but it is now thought to be *Posidonia corrugata elongata* subsp. nov., which is an abundant associate of *Ct. edalense* on Slieve Anierin, whereas *C. membranacea* does not extend beyond E₁.

The next horizon contains *Anthracoceras paucilobum* and *Cravenoceras nitidum* (now *Ct. nitidus*), and probably corresponds with the horizon of *E. bisulcatum leitrinense* on Slieve Anierin. The *Enmorphoceras* at this level is *E. bisulcatum varicata* Schmidt, which has similarities with *leitrinense*, but the latter has fewer ribs between the constrictions. *A. paucilobum* has not been seen with absolute certainty from this horizon on Slieve Anierin, but *A. tenuispirale* appears with *leitrinense* and soon becomes the dominant member of the fauna.

The occurrence of *Posidoniella laevis* Brown at this level in Germany corresponds with a similar appearance at a comparable level on Slieve Anierin. Such forms are now referred to *P. variabilis erecta* subsp. nov. *Ct. nitidus* is rare at this level on Slieve Anierin but the horizon of *leitrinense* is believed to be the same as that at which *Ct. nitidus* is common in other localities, e.g. the level of the Colsterdale Limestone in the Greenhow area, near Grassington in Yorkshire (Dunham and Stubblefield 1944, pp. 239–41).

The succeeding beds at Arnsberg, containing *Cravenoceras holmesii* and *C. cowlingsense* are believed to be the equivalent of the *C. holmesii* beds on Slieve Anierin, where *C. holmesii* is abundant just above the *A. tenuispirale* beds and beneath a band dominated by *Ct. nititoides*. Fig. 40, p. 449 (Schmidt 1934) is very like the evolute examples of *C. holmesii* on Slieve Anierin, where, however, it has not been found associated with any

undoubted examples of *C. cowlingsense*. *Posidoniella variabilis* also occurs at this level on Slieve Anierin.

There is no record at this point in Schmidt's succession of any band comparable with the *nititoides* horizon on Slieve Anierin. The next level described by him consists of shales with *C. stellarum* (now *Ct. stellarum*) and *C. nititoides* (now *Ct. nititoides*). He describes spiral sculpture on some of these forms, which he otherwise ascribes, on umbilical diameter, to the two species just mentioned, assigning specimens in which the umbilicus is completely closed to *Nuculoceras nuculum*, and within which zone these forms are considered to be the lowest fauna.

Spiral sculpture has not been seen in any of the Slieve Anierin specimens of *Ct. nititoides* and no specimens of *N. nuculum* or of *Ct. stellarum* have been collected. On Slieve Anierin there is therefore definite evidence for a *Ct. nititoides* band below the *N. nuculum* zone which is considered by Hudson (1945, p. 2) as the top of the E₂ stage, but is placed by Bisat (1928) and also by Stephens *et al.* (1953, p. 95) as the lowest division of H. On the whole, excluding small differences in identification partly due to poor material, there appears to be a close resemblance between the sequences in the geographically widely separated areas of Westphalia and Leitrim.

Edelburg. Bisat (1950, p. 14) has compared the basal E₁ succession from Edelburg, near Menden, Germany, described by Ruprecht (1937), with the succession near Wiswell, Lancashire; Carla Beck, near Skipton, Yorkshire; the Whinney Gill Reservoir, near Skipton; and the Alport Dale boring, Derbyshire. The form referred to by Ruprecht as *E. pseudobilingue* (1937, p. 272, pl. 10, fig. 7) is now assigned to *E. pseudocoronula* and does not differ from specimens in the *C. leion* zone on Slieve Anierin. *Posidonia trapezoedra* (op. cit., pp. 272-3, pl. 10, figs. 9, 10) is very abundant near the top of E₁ on Slieve Anierin but was first described by Ruprecht from lower P₂ beds with *Goniatites granosus*. *E. tornquisti* (Wolterstorff), which Bisat (1950, p. 20) considers may be the same as *Eumorphoceras sp.* form *A* Moore, and which was originally described from Magdeburg (Wolterstorff 1899, pp. 34-36, pl. 2, figs. 12-14), is a very rare form on Slieve Anierin. Here again there appears to be close similarity between the Irish and German faunas.

4. Poland and Czechoslovakia

Schwarzbach (1936, pp. 442-3) described several species and varieties of *Phillipsia* from Silesia. Most of the specimens came from Horizons Ia-d, II, and III at the top of the Ostrauer Schichten. Patteisky (1936, p. 4) has tabulated the main marine bands in these beds and described some of the goniatites. He correlates (op. cit., pp. 24-26) these younger bands with the *Ct. nitidus* beds in England. He figures *Cravenoceras* (cf.?) *C. nititoides* Bisat (op. cit., pl. 1, figs. 7a, b) but the plates are too poor to allow comparison with specimens of *Ct. nititoides* from Slieve Anierin. Even Patteisky describes this form as *Cravenoceras sp.* (p. 14) and the identification would thus appear to be far from certain. His specimen, however, is from Horizon IVb and most of Schwarzbach's trilobite records are from the younger marine horizons. It seems probable that these discrepancies are due to rather varying interpretations by different authors of some of the English species, and also to the poor material available.

Susta (1928, p. 421) records *Phillipsia mucronata* M'Coy, *P. eichwaldi* Fischer, *P.*

mladeki Smetana, and *Griffithides acuminatus* Roemer from the Gaebler Horizon, the youngest band in the Ostrauer Schichten. He also records *Eumorphoceras* sp. at this level but does not figure the species. On Slieve Anierin *Weberides* cf. *W. shumnerensis* is associated with *Ct. nitoides*, which occurs about 40 feet above the level of *E. bisulcatum leitricense*; the latter is believed to represent the level of *Ct. nitidus* elsewhere and is taken as the base of the *Ct. nitidus* subzone. It therefore appears that the Silesian trilobites occur at closely similar horizons to the Slieve Anierin specimens. Schwarzbach (1936, p. 427) also records trilobites from Horizon X in the Ostrauer Schichten, which is placed by Patteisky (1936, pp. 21–23) in IV/1S. He records *Sudeticeras ostraviensis* from this horizon. Moore (1950, p. 33) has commented that so little appears to be known about this species that comparison with others is valueless. No suture is known and Patteisky admits that it can be confused with *A. paucilobum*. The other goniatites recorded at this level are *Cravenoceras* sp., *C. (?Sudeticeras) latecostatum* Patteisky (op. cit., p. 13, pl. 1, fig. 11), *Dimorphoceras* sp., and ?*A. paucilobum*. It is difficult to place this fauna in terms of the Slieve Anierin succession, but it must lie near the P_2/E_1 boundary. It is interesting that the only other trilobites found on Slieve Anierin occur at this level, which is devoid of goniatites, but must lie either just below or just above the base of E_1 . Patteisky (1933, p. 44, pl. 2, fig. 30) also describes *Phillipsia acuminatus* Roemer from this level in the Sudetenland. Trilobites thus appear to have been widespread elements in the faunas at certain levels in the lower Namurian.

5. Belgium

Basal Namurian faunas from the area around Namur are described by Demanet (1941; map, p. 53). The *E. pseudobilingue* beds are divided into a lower and an upper division, the former about 10 metres thick and fossiliferous, the latter about 125 metres thick and practically without fossils.

The fauna of the lower division given by Demanet (1941, p. 22) is a rich one, but rather surprisingly includes only three goniatite species. Only one form of *E. pseudobilingue* is described and figured (op. cit., pp. 135–6, pl. 5, figs. 11–14) and it does not resemble any of the forms of that species collected on Slieve Anierin, but has features much more reminiscent of the specimens of *E. bisulcatum* which occur below the grit. *C. leion* (op. cit., pp. 140–1, pl. 5, figs. 21–23) is stated to be associated with *E. pseudobilingue*; the third goniatite is *Anthracoceras* sp. There is in addition a large nautiloid and lamellibranch fauna, together with a few brachiopods, conodonts, and fish remains.

Apart from *C. leion* there are no records of any of the abundant goniatites of E_1a found on Slieve Anierin. Crushed specimens of *Cravenoceras* are notoriously difficult to deal with and, judging from the photographs, it would be difficult to be certain of the specific determination of these specimens. An illustration of the suture-line, which is only described by Demanet (op. cit., p. 141), would be desirable for comparison with that figured by Bisat (1930, p. 29). The sharply acute edge to the umbilicus, which can usually be seen on the specimens of *C. leion* from Slieve Anierin, does not appear to be a feature of the Belgian material. The photographs of *Eumorphoceras* appear to be far more conclusive and do not resemble any of the E_1 species on Slieve Anierin.

Demanet includes *Posidonomya (Posidonia) membranacea*, now *Caneyella membranacea*, in his faunal list, and on Slieve Anierin this form does not extend beyond E_1 deposits. Unfortunately the material is not figured, but Demanet has figured the species

in a previous publication (1938, pl. 10, figs. 5–11) from P_2 deposits and his conception of the species obviously concurs with that of the writer. He remarks (1941, p. 80), however, on the variation in obliquity of the species within E_1 . This is interesting since the writer believes that there is a more oblique form of the species than that which Demanet figured from P_2 levels, and it occurs particularly abundantly on Slieve Anierin at the level of *Cravenoceras* aff. *C. malhamense*. However, in E_2 beds there is an elongated variety of *Posidonia corrugata* which appears often to have been mistaken in faunal lists for *C. membranacea*. Without figures it is impossible to tell to which of these two forms Demanet's material should be assigned. I believe the lower form to be *C. membranacea* and since it is associated with *C.* aff. *C. malhamense* it is an E_1 form. I refer the higher forms to *P. corrugata elongata* subsp. nov. and this is most abundant in E_{2a} deposits and in E_{2b} , but I have not seen undoubted examples at lower levels. The evidence for the E_1 age of these beds does not therefore appear to be conclusive, and indeed Demanet's illustrations of *Eumorphoceras* suggest otherwise.

Demanet apparently believed that the *E. bisulcatum* which he found with *Ct. edalense* in the lower Nmlb beds was *E. bisulcatum* s.s., and he does not distinguish beds in which *E. bisulcatum* is the dominant goniatite beneath the *Ct. edalense* beds. All the available evidence from successions described elsewhere, notably Arnsberg (Schmidt 1934, pp. 446–7), Alport Dale (Hudson and Cotton 1943, pp. 162–3), and the Edale Anticline, Derbyshire (Hudson and Cotton 1945, p. 10), indicate that this zone of *E. bisulcatum* s.s. exists below the zone of *Ct. nitidus* (the basal subzone of the latter is correlated with Demanet's *Ct. edalense* beds).

Demanet does not suggest that his succession is possibly incomplete. This apparent gap in the Belgian succession appears to the writer to support the view that the beds assigned to E_1 , certainly from the level at which the figured specimens of *E. pseudobilingue* were collected, are probably more correctly assigned to E_2 .

Dorlodot and Delépine (1930, p. 58, pl. 8, fig. 4) described and figured *E. pseudobilingue* from Bioul in Belgium. They apparently only had one specimen, which was extremely crushed and distorted. It appears from the figure to be too poor and inconclusive to be compared with the Slieve Anierin material.

The *E. pseudobilingue* beds (Zone de Bioul, Nmla) of Belgium are succeeded by the Zone de Malonne, Nmlb, which is divided into lower, middle, and upper. The lower division (Nmlb inférieur) is characterized by *C. edalense* and is apparently present at all the Nmlb localities tabulated by Demanet (1941, p. 56). The description of this species given by Demanet (op. cit., pp. 141–2) mentions only one bifurcation of the lirae at the umbilical edge, which indicates that it is not *Ct. bisati*. Demanet's plates (op. cit., pl. 6, figs. 1–3), although a little indistinct, appear to be very like *Ct. edalense* as collected above the grit on Slieve Anierin. At this level on Slieve Anierin *E. bisulcatum* does not occur, but Demanet (1941, p. 56) lists this species at four of the Nmlb localities. However, the single figure (pl. 5, fig. 15) of the form from this level is so poor that it is impossible to compare it with any of the Slieve Anierin specimens.

Posidonia aff. *P. wapamuckensis* is also recorded from many of the localities by Demanet, but is not figured from this level; it has previously been figured from P_2 beds (Demanet 1938, pp. 117–18, pl. 10, figs. 14–18). Demanet (1941, p. 81) comments that the specimens in Nmlb are far larger than the American ones and frequently difficult to distinguish from *P. corrugata*. This suggests that these specimens are the same as the

forms from this level on Slieve Anierin described as *P. corrugata gigantea* subsp. nov. and *P. corrugata elongata* subsp. nov., and associated there with *Ct. edalense*.

Ramsbottom (1959, p. 405) believes that *Caneyella wapamuckensis* (Girty) from the Caney Shale of Oklahoma includes at least two species. In his opinion Girty's figure 9 (1909, pl. 3) is very like *Posidoniella variabilis*, and figs. 6, 7, and 11 (on the same plate) are all reminiscent of *Posidonia corrugata*. This tends to support the present contention that Demanet's specimens are probably incorrectly ascribed to *P. aff. wapamuckensis*.

Demanet (1941, p. 29) includes *A. tenuispirale* in his fauna but not in the lower Nmlb faunal and locality chart (pp. 55–56) and it is therefore presumed not to be a very prominent member of this fauna. This coincides with the evidence on Slieve Anierin where the species is seen only rarely beneath *E. bisulcatum leirimense*, but becomes more abundant later.

Dimorphoceras sp. and *A. paucilobum* complete Demanet's goniatite fauna for this level. The latter has not been seen at this horizon on Slieve Anierin; specimens attributable to *Anthracoceras* are present but it is difficult to be sure of the species. *D. looneyi* occurs on Slieve Anierin at a horizon a little above the beds with *Ct. edalense*. The nautiloid and lamellibranch faunas given by Demanet are far larger than those on Slieve Anierin.

The fauna of the succeeding middle Nmlb or *C. nitidum* beds (of Demanet, but now *Ct. nitidus*) comes from 6–10 metres of fossiliferous beds at the base, which are succeeded by unfossiliferous strata. The fossils from the entire thickness are treated as one fauna so that it is impossible to make exact correlations with Slieve Anierin. *Ct. nitidus* is rare on Slieve Anierin, but the level at which it is abundant elsewhere is believed to be represented by *E. bisulcatum leirimense*. From what is regarded as the same level in Germany Schmidt has described *E. bisulcatum varicata*, and Demanet has likewise described and figured this subspecies in Belgium (1941, pp. 138–9, pl. 5, figs. 16, 17). He describes it as having strong constrictions, about six in a whorl, and with seven ribs between them. This is obviously different from *leirimense*, although the general aspect of Demanet's figures is rather like some of the less clearly preserved Slieve Anierin material.

Griffithides serotinus Demanet is recorded at locality Bioul 23, but appears to be distinct from *Weberides cf. W. shumnerensis* which occurs on Slieve Anierin. The trilobite level in Belgium is associated with *Ct. nitidus* and *E. bisulcatum varicata* and appears to be lower than the horizon on Slieve Anierin, which yields abundant *Ct. nititoides* and *E. rostratum sp. nov.* There is apparently no record of a *C. holmesi* fauna in Belgium nor have *C. cowlingsense* or *C. subplicatum* been recorded.

Posidoniella variabilis is abundant in Belgium as on Slieve Anierin and the form included in Demanet's lists as *P. laevis* Brown is thought to be the same as *P. variabilis erecta* subsp. nov. *Posidonia corrugata* is not included in the lists given by Demanet but is very abundant on Slieve Anierin. *Posidonomya aff. P. wapamuckensis* is included, however (as in the lower Nmlb fauna), and the more correct designation of this form has already been discussed.

A. tenuispirale is abundant both in Belgium and on Slieve Anierin. It is very abundant just above *E. bisulcatum leirimense* on Slieve Anierin, but higher in the succession it is replaced by *C. holmesi*. In Belgium it presumably occupies a similar position since it occurs with *Ct. nitidus*. Since there is no record of the succeeding *C. holmesi* fauna or the *Ct. nititoides*—*E. rostratum* band, it may be that the unfossiliferous beds which succeed the latter on Slieve Anierin are present at a lower level in Belgium.

The succeeding 'Nmlb supérieur' is characterized by *Nuculoceras nuculum* and is therefore higher in the sequence than any of the beds exposed on Slieve Anierin, but corresponds with the successions at other localities.

Dorlodot and Delépine (1930, pp. 57–58, pl. 1, figs. 1–5) figured specimens of *E. bisulcatum* from the Namur area; they are not like any of the Slieve Anierin forms, but as they are said to be associated with *N. nuculum*, *A. glabrum*, and *Ct. nitidus* (*Homoceras nitidum* of these authors) it seems likely that more than one form is included in this specific determination; also, since *N. nuculum* is referred to, some at least must occur at higher levels than any which are exposed on Slieve Anierin.

6. North America

There is evidence that there was open communication between the seas of western Europe and North America at least during uppermost Viséan and Lower Namurian times. Several American formations contain goniatite species that are very similar to those known in western Europe.

Miller and Youngquist (1948, p. 656) and Youngquist (1949, pp. 282–3) have claimed that faunal elements which are distinct in the European succession are found associated together in the Barnett Shale of Texas, the Caney Shale of Oklahoma, and the White Pine Shale of Nevada. Youngquist (op. cit., p. 282) states that *Eumorphoceras*, *Girtyoceras*, and *Goniatites* s.s. occur in direct association in the White Pine Shale. Gordon (1957) described goniatites from northern and eastern Alaska, and for the first time in North America recorded the genus *Sudeticeras* (*S. alaskae* Gordon). *G. crenistria* Phillips, *G.* cf. *G. granosus* Portlock and *Cravenoceras* sp. are also recorded but Gordon has no evidence to suggest an overlap of the ranges of *Goniatites* and *Cravenoceras*. The more obvious similarities between some of the species in the Slieve Anierin succession and those in American formations will be briefly outlined, but it seems impossible at present to establish accurate correlations based on the succession of faunas.

The fauna of the Caney Shale of Oklahoma (over 1,000 feet thick) was described by Girty (1909), and is important as it includes the type material of *E. bisulcatum* Girty (1909, pp. 68–70, pl. 11, figs. 15–19a). The subspecies *erinense* and *ferrimontanum* from Slieve Anierin are both believed to be very close to *E. bisulcatum* s.s. In Ireland, England, Belgium, and Germany such forms appear to be typical of the lowest zone in E₂, that of *E. bisulcatum* s.s. The resemblance of *Caneyella wapamuckensis* (Girty) (1909, pp. 34–35, pl. 3, figs. 6–11) to at least two species, namely *Posidoniella variabilis* and *Posidonia corrugata*, has already been referred to. The former has been observed on Slieve Anierin throughout E₁ and E₂ deposits and in the lower P₂ beds, and the latter becomes abundant at about the middle of E₂. The genus *Caneyella* was erected on the abundant specimens of this lamellibranch in the shales, and species like *C. nasuta* (p. 37, pl. 3, figs. 12–14) appear to be very like *C. membranacea*, particularly fig. 14.

Adelphoceras meslerianum Girty was originally described from the Caney Shale but is now attributed to *Girtyoceras meslerianum*. This genus is not known to occur in the rather poor P₁–P₂ faunas of Slieve Anierin. Moore (1946, pp. 405–6, pl. 23, fig. 6) described GSM 72716 from a P_{1a} level in the Bowland Shales of the River Ribble, Dinckley, Lancashire, and was satisfied that there was no valid distinction between this specimen and GSM For.1867 (op. cit., pl. 23, fig. 3) collected from the Caney Shale.

Goniatites newsomi Smith from the Caney Shale (Girty 1909, pp. 62–63, pl. 12, figs. 11, 11a) also occurs on Slieve Anierin very near the top of P₂, and has been recorded by Moore (1936, p. 185, pl. 2, figs. 6, 12) from the Bowland Shales. The species was referred to the genus *Lyrogoniatites* by Miller and Furnish (1940, pp. 368–9), who erected a subspecies *L. newsomi georgiensis*, which differs from the typical *L. newsomi* in that the whorls are lower and broad and therefore the conch more nearly globular. In crushed shale material it is difficult to detect such a difference, but the close similarity of Moore's plates of the English material, the Slieve Anierin material, and the figures of the American form, whether *newsomi* or *georgiensis*, is convincing evidence of the close relationships of all these forms.

Padgett (1953, pp. 22, 23) listed *Neoglyphioceras subcircularis* from the *G. granosus* zone of P₂. On Slieve Anierin only undoubted *G. granosus* has been collected but the former genus is known from America also and is listed by Miller and Furnish (1940, p. 361) as a form known from Oklahoma, Arkansas, Texas, P₂ of England, Ireland, Belgium, France, Germany, and also Morocco and northern Algeria. *Gastrioceras caneyanum* Girty is the genotype of *Paragoniatites* and is considered by Bisat (1955, p. 16) to be very close to *Neoglyphioceras*. There are therefore several forms from the Caney Shale which are known at specific levels in the succession of faunas established elsewhere.

The type specimens of *Leiorhynchus carboniferus polypleurus* come from the Moorefield Shale of Arkansas (Girty 1911) and are indistinguishable from those collected on Slieve Anierin about 3 feet below *G. granosus* at the base of P₂, and also forms figured and described by Demanet (1938, pp. 83–87, pl. 8, figs. 9–14). Demanet's figured specimens are from upper V3c, which is equivalent to P₂ in age. However, he records this species from the *E. pseudobilingue* zone, in which it has not been found on Slieve Anierin.

Girty (1911, pp. 103–4, pl. 14, fig. 4) identified one specimen from the Moorefield Shale as *E. bisulcatum*; only a single specimen, described as senile, was available. The identification was later amended to *Girtyoceras limatum* (Miller and Faber) by Miller and Furnish (1940, pp. 364–6, pl. 47, figs. 6–12). This form appears to be similar to *E. medusa* which occurs near the top of the *C. leion* zone on Slieve Anierin and above *E. pseudocoronula*, to which it is believed to be related.

Miller and Youngquist (1948, pp. 662–5) described examples of *E. bisulcatum* from the Barnett formation in central Texas. They also figured a new species, *E. plummeri* (op. cit., pp. 665–7, pl. 100, figs. 1–4, 20, 21), and compared it with the specimen (GSM 72603) figured by Moore (1946, pl. 22, fig. 3), which was associated with *N. nuculum* and collected from Samlesbury Bottoms, River Darwen, Lancs. There is no evidence for the *N. nuculum* zone on Slieve Anierin and no specimens of *Eumorphoceras* from the mountain appear to conform with *E. plummeri*, although *E. rostratum* sp. nov. displays certain points of similarity. *Girtyoceras meslerianum* (Girty) is also described from the Barnett formation, which, in terms of the European succession, apparently has species as widely separated as the base of P₁ and the *N. nuculum* zone, assuming that *E. plummeri* is correctly compared with the Samlesbury Bottoms material.

Gordon (1960, pp. 140–3) described a new genus, *Paracravenoceras*, from the Barnett Shale of Texas, and which also occurs rarely in the Caney Shale of Oklahoma. *P. ozarkense* is abundant in the Fayetteville Shale of Arkansas and *P. barnettense* is common in the Chainman Shale of Utah. The genus is said to be common in, and restricted to, the Lower *Eumorphoceras* zone. It has sinuous transverse growth lamellae

in the young and a distinctive form of ventral lobe in the suture. Nothing resembling this genus has been seen on Slieve Anierin.

Another form which so far appears to be peculiar to America is *E. girtyi* Elias. It was attributed by Elias (1956, pp. 130–2, pl. 6, fig. 7) to an E_1 age, and described as possessing an intra-ventral carina and a reticulate pattern of striae on the ventro-lateral area. Nothing comparable occurs in E_1 on Slieve Anierin. However, the type is said to be associated with *E. plummeri*, which was originally likened by Miller and Youngquist (1948, pp. 665–7) to the forms associated with *N. nuculum* collected by Moore from Sablesbury Bottoms, Lancs. It is therefore difficult to know at which level any similar species might occur in the Slieve Anierin or other western European succession. Only a cross-section illustrates the original description by Elias, but material from the Redoak Hollow Formation of southern Oklahoma has been figured by Elias (1958, p. 32, pl. 3, figs. 10–13); unfortunately these figures do not shed any light on the problem.

One interesting connexion with American lamellibranch species has been established with the discovery of *Euchondria* aff. *E. levicula* in the highest faunal band on Slieve Anierin. Newell (*in litt.*, 1960) has confirmed the close similarity between the Slieve Anierin specimens and the described material from the Hushpuckney Shale of Iowa and the Labette Shale of Missouri.

7. Morocco

Delépine (1941) described some Namurian goniatites from Morocco, including (p. 79) a very small specimen (unfortunately not figured) which he tentatively assigned to *E. bisulcatum*. He also described and figured (*op. cit.*, p. 77, pl. 6, figs. 4–7) *C. nitidum* (Phillips); the specimen illustrated in fig. 4 was collected with *N. nuculum* and *A. glabrum*. Judging from the plate the ornament appears to be rather fine and hairlike, and not like the normal asymmetrical lirae of typical *Ct. nitidus*. Figs. 5–7 are too poor for comparative purposes.

C. africanum Delépine (*op. cit.*, pp. 75–76, pl. 6, figs. 1–3) appears to be a form which in its somewhat evolute aspect suggests *C. holmesi*. Hudson (1941, p. 282) has commented on the wide distribution of the *Cravenoceras* group to which this species belongs in the *Eumorphoceras* beds of Europe, North Africa, and North America, and also that some of the species described from America may in fact be synonyms of the European species. Delépine also refers to the resemblance of *C. africanum* to *C. holmesi* and *C. cowlingense*. There is certainly a resemblance to the specimens of *C. holmesi* from Slieve Anierin and to those figured from Arnsberg by Schmidt (1934, p. 449, fig. 40).

Conclusion

As more evidence becomes available a remarkable picture of the extent of the Namurian goniatite faunas emerges and the great similarity of specimens from locations geographically far removed from each other is striking. Local geographical variants obviously occur. *E. bisulcatum*, for example, both from E_{2a} levels on Slieve Anierin and from similar levels in England, is very close to *E. bisulcatum* s.s. from the Caney Shale, and yet these forms are not quite the same. Similarly, amongst the lamellibranchs, *Euchondria* aff. *E. levicula* is very close to the American forms, but is not quite the same.

These differences, however, are fine ones and the overall picture is of a basic population which is remarkably uniform over a very wide area. The appearance of trilobites at

specific levels in the succession both in western Ireland, England (Pace Gate Beck, the Alport boring, and in the Edale Valley), and in Silesia, is also striking proof of the widespread nature of certain horizons. The geographical extent and remarkable abundance of the *Posidonia corrugata* group is also a feature of this part of the succession. *P. becheri* was often extremely abundant in P_1 times but the success and vigour of the *corrugata* group surpassed it both in time range and range of variation. In E_1 only *Caneyella* approached it in abundance but above E_1 this genus is no longer seen.

This widespread uniformity of the goniatite-lamellibranch faunas is not confined to the narrow time range with which this work has been concerned. The foundations of all such studies were firmly laid by Bisat (1928, pl. 6) for the whole of the Namurian and now the correlations established by him are being endorsed and amplified in greater detail both vertically and horizontally.

As methods of illustrating specimens improve, it becomes increasingly obvious that although language and other national difficulties may often obscure the true features of the specimens and lead to varying interpretations, often of the same species, good well-reproduced photographs smooth out such difficulties and bear silent witness to the widespread nature of these goniatite and lamellibranch species, and may truly be a more accurate substitute for the actual specimens than words alone.

APPENDIX

1. Fossiliferous localities on Slieve Anierin

a. West of Slieve Anierin

LEITRIM 20(16) (text-fig. 3)

1. North bank of stream 500 yds. west of Glen Bridge; best material 3–4 ft. above stream level. *Eumorphoceras medusa*, *Pseudamusium praetenuis*. E_{1a} .
2. South bank of stream 450 yds. east of Glen Bridge. 10 ft. section of friable shales. *Coelacanthus sp.* E_{1a} .

LEITRIM 20(12) (text-fig. 3)

1. At un-named bridge on Dowra track 1,600 yds. north of Glen Bridge; calcareous mudstone at stream level; *Sudeticeras* cf. *S. newtonense*. Basal 3 ft. of the overlying 10-ft. section of papery shales yield *Caneyella membranacea*, *C. membranacea horizontalis* subsp. nov. High P_2 .
2. 15 ft. shale section in stream, with prominent hard band. High P_2 .

b. North of Slieve Anierin; Stony River

LEITRIM 20(8) (text-fig. 2)

1. 25-ft. shale section 100 yds. upstream from point where 500-ft. contour crosses the Stony River; at base *Obliquipecten costatus* sp. nov., *C. leion*, *Eumorphoceras* cf. *E. sp.* form *A* Moore. E_{1a} .
2. 40-ft. section 100 yds. east of 1; shales at base yield *Pseudamusium praetenuis*, *E. medusa*, *Kazakhoceras sp.* E_{1a} .
3. 50-ft. section of friable dark-grey shales on south bank near point where 600-ft. contour crosses Stony River; fauna collected on scree includes *Posidonia corrugata*, *P. trapezoedra*, *Pseudamusium sp.*, *Kazakhoceras sp.* Similar fauna collected *in situ* on opposite side in gully higher up hillside. E_{1a} .

LEITRIM 21(5) (text-fig. 2)

1. Right bank 250 yds. upstream from confluence of 1st tributary; 25-ft. section; lower reaches barren, but fallen shales yield *P. corrugata*, *P. trapezoedra*, *Kazakhoceras sp.* Low E_{1b} .

2. Few yds. upstream from 1; band *in situ*; solid beds at base yield *P. corrugata*, *P. trapezoedra*, *Kazakhoceras* sp., *Eumorphoceras* cf. *E. angustum*. Low E₁b.
3. 200 yds. downstream from confluence of 2nd tributary; hard black shales 3 ft. above stream. *P. corrugata*, *P. trapezoedra*, *Kazakhoceras* sp. Low E₁b.
4. 150 yds. downstream from confluence of 2nd tributary; 20-ft. section; lowest 2–4 ft. yield *E. pseudobilingue* s.s., *P. corrugata*, *P. trapezoedra*, *Chaenocardiola footii*; succeeding 6 in. yield different fauna, *E. pseudobilingue* C, *C. footii*, *P. corrugata*. Low E₁b. Opposite this section fallen blocks from upper part of section yield *C. membranacea*, *K. scaliger*, *Cravenoceras* aff. *C. malhamense*. E₁c.
5. First north bank section upstream from confluence of 2nd tributary; 3 ft. of papery shales above a hard calcareous mudstone yield *C. membranacea*, *K. scaliger*, *C.* aff. *C. malhamense*. E₁c.
6. 150 yds. upstream from 5 on left bank; 10-ft. section. *Cravenoceras* sp., *Chaenocardiola footii*. E₁c.
7. 100 yds. upstream from 6; hard shales at base. *Posidonia lamellosa*. E₂a.
8. North bank 175 yds. downstream from confluence of 3rd tributary; 15–20 ft. of thicker bedded shales (overlying friable unfossiliferous black shales), forming high continuous sections on either side of valley until 3rd tributary. *P. lamellosa*, *P. corrugata*, *C. footii*, *Cravenoceras cowlingense*, *E. bisulcatum grassingtonense*. E₂a.
9. At confluence of 3rd tributary; same beds and fauna as at 8, but at stream level.
10. Right bank of 3rd tributary 220 yds. upstream from confluence; 4 ft. 6 in. of fossiliferous shales exposed at top of section. *E. bisulcatum erinense* subsp. nov., *E. bisulcatum ferrimontanum* subsp. nov. (much less common), *K. scaliger*, *Anthracoceras glabrum*, *Cravenoceras* cf. *C. gairense*, *P. corrugata*, *P. corrugata elongata* subsp. nov., *C. footii*, *Dunbarella* aff. *D. elegans*, *Pseudamusium* sp., *Stroboceras subsulcatum*, crinoidal debris. High E₂a.
11. Right bank of Stony River 300 yds. upstream from confluence of 3rd tributary and along the river to the grit escarpment; 4 ft. of shales at stream level with *E. bisulcatum ferrimontanum* subsp. nov., *K. scaliger*, *Cravenoceras* cf. *C. gairense*, *C. footii*, *P. corrugata*, *P. corrugata elongata* subsp. nov., *Dunbarella* aff. *D. elegans*, *Dunbarella* sp., *Pseudamusium* sp., *Stroboceras subsulcatum*, crinoidal debris. High E₂a.

c. *South-east of Slieve Anierin*

LEITRIM 21(14) (text-fig. 3)

Dolerty Stream East

1. In western tributary 10 yds. west of 2; 5 ft. of sandy shales. *Chaenocardiola footii*. High E₁b.
2. In western tributary above fork at 3; *P. corrugata*, *P. trapezoedra*. Low E₁b.
3. Bed of stream at fork, and in both banks of eastern tributary for about 5 ft. from stream bed. *Eumorphoceras* cf. *E. angustum*, *Kazakhoceras* sp., *P. corrugata*, *P. trapezoedra*. Low E₁b.
4. In eastern tributary above fork; 20 ft. of shales; at base *C. footii*, *P. corrugata*. Low E₁b.
5. North bank a few yds. before fork; 2 ft. of shales exposed 6–8 ft. above stream. Fauna as at 3. Low E₁b.
6. North-east bank; 30 ft. high section of shales, top 10 ft. inaccessible. At about 20 ft. from base, *E. medusa*, *Pseudamusium praetenuis*, *P. trapezoedra*, *Kazakhoceras* sp. At about 10 ft. from base, *P. trapezoedra*, *P. corrugata*, *Kazakhoceras* sp. E₁a.
7. South-west bank 20 yds. upstream from 6; 4–6 ft. of shales. *E. medusa*, *Pseudamusium praetenuis*, ? *Stroboceras* sp. E₁a.
8. South-west bank 100 yds. upstream from 9, and a few yards beyond the last field boundary; 6-ft. section; soft mudstone 3–4 ft. above stream with *E. pseudocoronula*, *E. rota*, *C. leion*, *Kazakhoceras* sp. E₁a.
9. North-east bank about 380 yds. upstream from BM 931·0; 8 ft. of thinly leaved black shales. *Caneyella membranacea*, *C. membranacea horizontalis* subsp. nov., *Sudeticeras* sp. High P₂.
10. South-west bank about 300 yds. upstream from BM 931·0. P₁.
11. South-west bank at bend in stream 120 yds. upstream from 12; sandstones with occasional thin sandy shales. *Chonetes* sp., *Dunbarella* sp., *Leiorhynchus* sp., obscure *Goniatites* sp. P₁.
12. Section upstream from BM 931·0; upstream from massive calcareous horizon on lip of upper waterfall, a few yds. above waterfall at 13; alternations of friable shales and calcareous mudstones; 3 ft. of mudstones on north-east bank yield *P. becheri*, obscure *Goniatites* cf. *G. striatus* group, *Orbiculoidea* sp., ? worm burrows, *Mourlonia striata*. P₁.

13. To north of bridge (BM 931-0), 250 yds. along track to north-east from road to old coal level from the Ballinamore road; 2 ft. of calcareous mudstone overlying 3 ft. massive limestone yields *P. becheri*, *Goniatites* cf. *G. striatus* group, ? worm tubes, indet. brachiopods. P₁.
14. Stream section 40 yds. south-east of bridge; 6 in. mudstone underlying 3 ft. black limestone forming a small waterfall yields *Goniatites* cf. *G. striatus* group, crinoidal debris, abundant worm burrows. P₁.
15. Stream section 75 yds. south-east of bridge; mudstone band near base of 6-ft. section. *Goniatites* cf. *G. striatus* group, indet. gastropods. P₁.

Doherty Stream West

16. Long overgrown exposure under right bank of tributary 350 yds. south of BM 1249-8; *C. leion*. E_{1a}.
17. 20 yds. upstream from 18; 1 ft. of shales with *Dunbarella* sp. and *P. becheri* overlying 9 in. mudstone with *P. becheri*. P₁.
18. Few yds. upstream from 19; hard band at 19 near base of section. *P. becheri*. P₁.
19. Few yds. upstream from 20; 4-5 ft. of mudstone with *P. becheri*; in middle of section is harder horizon with *Productus* sp. P₁.
20. Stream sections at bridge where track south-west from BM 986-1 crosses stream near ruined cottages on 900-ft. contour; below bridge, 40 ft. of black bituminous limestone; above bridge, 4 ft. of mudstones with *P. becheri* dominant overlying 18 in. massive limestone, and then 2 ft. of mudstones with *P. becheri* and very abundant worm tubes. P₁.

d. *South of Slieve Anierin: Aghagrania River and tributaries*

LEITRIM 23(8). Aghagrania River (text-fig. 4)

1. West bank 150 yds. north-north-west of Aghagrania Bridge; black limestone with *Dunbarella* aff. *D. elegans*. P₁.
2. East bank 8 yds. upstream from 3; 1 ft. of shale. *P. becheri*, *G. striatus* s.l., *D.* aff. *D. elegans*, *Mourlonia striata*. P₁.
3. East bank at stream level 100 yds. north of Aghagrania Bridge, just beyond stepping-stones; shales yield *Goniatites* aff. *G. falcatus*, *P. becheri*, *D.* aff. *D. elegans*. P₁.
4. East bank at stream level 30 yds. upstream from 5, and separated from latter by calcareous mudstone horizon; 1-2 ft. of shale with *Goniatites striatus* s.l., *Archaeocidaris urii*, indet. pleurotomariid gastropod. P₁.
5. East bank at stream level just north of Aghagrania Bridge; 1 ft. of shale with *G. striatus* s.l., *Chonetes* sp. P₁.
6. West bank 60 yds. south of Aghagrania Bridge, below house on east bank; 4 ft. mudstones. *Thrincoceras* cf. *T. hibernicum*, orthoconic nautiloids, crinoidal debris, indet. pleurotomariid gastropod. P₁.
7. North-west bank 150 yds. south-west of Aghagrania Bridge; 2-3 ft. of mudstone overlying massive limestone horizon yields *Thrincoceras* cf. *T. hibernicum*, *P. becheri*, *Productus* sp., indet. brachiopods, orthoconic nautiloids. P₁.
8. South-east bank opposite 7. Same fauna. P₁.

LEITRIM 23(4) (text-fig. 4)

1. At bridge over western branch of 1st tributary, 130 yds. to north of fork; large slabs of dark grey shale. *E. pseudobilingue* s.s., *P. corrugata*. Low E_{1b}.
2. 20 ft. shale section in 1st tributary, 500 yds. upstream from confluence. *P. trapezoedra*, *E. medusa sinuosum*. E_{1a}.
3. West bank of 1st tributary, 450 yds. upstream from confluence; 15 ft. section. *P. trapezoedra*. E_{1a}.
4. 10 ft. section 50 yds. north of 5; fauna from stream level to 6 ft. *C. membranacea horizontalis* subsp. nov., *Kazakhoceras* sp. E_{1a}.
5. West bank of 1st tributary, 350 yds. upstream from confluence; 20 ft. shales; at 15 ft. from base *C. leion*, *P. corrugata*, *P. trapezoedra*, *Kazakhoceras* sp., *E. medusa*. E_{1a}.
6. East bank opposite 7, but at slightly lower horizon; highest material collected at 8 ft. above stream level, with *E. pseudobilingue* A, *C. leion*; at 5 ft. *C. leion*, *E.* cf. *E. pseudocoronula*; at 4 ft. *C. leion*. E_{1a}.

7. West bank of 1st tributary 250 yds. above confluence; 3 ft. of shales at about 10 ft. above stream bed. *E. pseudobilingue* A, *C. leion*. E₁a.
8. West bank of 1st tributary 200 yds. above confluence; 3-ft. shale section. *Obliquipecten costatus* sp. nov., *C. leion*, *E. pseudocoronula*. E₁a.
9. East bank 25 yds. downstream from 8; collection 3 ft. from top of 8-ft. high shale section overlying calcareous mudstone. *C. leion*, *O. costatus* sp. nov. E₁a.
10. Narrow ravine in 3rd tributary 150 yds. north of confluence, just south of waterfall over calcareous band; friable shales with *C. leion*, *O. costatus* sp. nov. E₁a.
11. Narrow ravine 50 yds. south of 10; shales at base with *O. costatus* sp. nov. E₁a.
12. South bank of Aghagrania River 30 yds. downstream from confluence of 3rd tributary; 2 ft. of shales with *P. corrugata*, *Pseudamusium praetenuis*. E₁a.
13. South bank 160 yds. upstream from confluence of 2nd tributary; 4 ft. shales. *P. corrugata*, *C. membranacea horizontalis* subsp. nov., *Kazakhoceras* sp. P₂.
14. South bank 40 yds. upstream from confluence of 2nd tributary; 15 ft. shales; at base *C. membranacea*, *C. membranacea horizontalis* subsp. nov., *Sudeticeras* sp.; few yds. to east a soft clay-like band a few ft. above base yielded *P. corrugata*. P₂.
15. South bank of Aghagrania River between 1st and 2nd tributaries; 20 ft. shale section; collections from 3 levels—(1) 6 ft. from base, west side, *P. corrugata*, *Kazakhoceras* sp.; (2) 10 ft. from base, *C. membranacea horizontalis* subsp. nov.; (3) 15 ft. from base, *Chonetes* sp., *Lingula* cf. *L. parallela*, *P. corrugata*, *Obliquipecten costatus* sp. nov., trilobite remains. (1) and (2) P₂, (3) probably E₁a. Scree material, not *in situ*, in front of section yielded *E. pseudocoronula*, *C. leion*. E₁a.
16. South bank between 1st and 2nd tributaries; shales 3 ft. 6 in. above stream level, *Lyrogoniatites newsomi georgiensis*, *C. membranacea*; at base calcareous mudstone with imperfect brachiopods. P₂.
17. 480 yds. north-north-west of Aghagrania Bridge, on east of track, and 40 ft. above stream; 6–8 ft. of friable shales, *Pseudamusium praetenuis*, *P. corrugata*, *Chonetes* sp., trilobite remains; soft clayey band in centre of section, *P. corrugata*, *Kazakhoceras* sp., *C. membranacea horizontalis* subsp. nov. P₂.
18. East side of stream at lower horizon than 17; 5–6 ft. of shales. *Dunbarella* aff. *D. elegans*, *Sudeticeras* sp., *Coleolus* sp. P₂.
19. 450 yds. north-west of Aghagrania Bridge; 30-ft. section in westerly loop of stream; collection from 3 levels—(1) 3 ft. from base, *Leiorhynchus carboniferus polypleurus*; (2) 6 ft. from base, *G. granosus*, *Sudeticeras* cf. *S. crenistriatum*, *Coleolus namurcensis*; (3) 20 ft. from base, *Sudeticeras* sp., *G. granosus*, *C. nanurcensis*, *Kazakhoceras* sp., *Orthoceras* cf. *O. calamus* de Koninck, *Dunbarella* aff. *D. elegans*, *C. membranacea*, *C. membranacea horizontalis* subsp. nov., *P. corrugata*, *Chaenocardiola bisati* sp. nov. P₂.
20. 350 yds. north-north-west of Aghagrania Bridge; rich goniatite band in soft mudstone. *Sudeticeras* cf. *S. crenistriatum*, *Thrinoceras* cf. *T. libernicum*, *C. nanurcensis*, *Productus* sp., *Mourlonia striata*. P₁.

LEITRIM 24(1) (text-fig. 4)

1. West bank 100 yds. north of farmhouse, near point where 800-ft. contour crosses river; 3 ft. shales about 6 ft. above stream. *E. pseudocoronula*, *E. pseudobilingue* A, *E. rota*, *C. leion*, *P. praetenuis*, *Chaenocardiola bisati* sp. nov., *C. membranacea horizontalis* subsp. nov., *Kazakhoceras* sp. E₁a.
2. Embayment on south side of river about 100 yds. north-north-east of right-angled bend in road; 6 ft. of thin-bedded decalcified sandy rocks with obscure brachiopods. P₂.
3. North bank 400 yds. west-south-west of right-angled bend in road; 6 ft. of decalcified beds; obscure brachiopod moulds only. P₂.
4. South bank 1,100 yds. upstream from confluence of 3rd tributary; thin-bedded arenaceous limestone with crinoidal remains. P₂.
5. South bank 500 yds. from confluence of 3rd tributary; upper 2 ft. limestone bed in soft black shales yields *Productus* sp. and indet. brachiopods. P₂.
6. South bank 330 yds. upstream from confluence of 3rd tributary. *G. granosus*, *Sudeticeras* cf. *S. crenistriatum*, indet. brachiopods. P₂.
7. North bank 300 yds. upstream from confluence of 3rd tributary; 3 ft. shales. *Sudeticeras* sp., *P. corrugata*, *Pseudamusium* sp. P₂.
8. North bank 250 yds. upstream from confluence of 3rd tributary; 15–20 ft. shale section on east side at 8 ft. from base yields *C. membranacea horizontalis* subsp. nov.; at base on western side *Chonetes*

- sp.*, *Sudeticeras sp.*, *Leiorhynchus sp.*, *P. corrugata*; 3 ft. above base, *Sudeticeras sp.*, *Coleolus nanurcensis*; 9 ft. above base, *Sudeticeras sp.*, *P. corrugata*. P₂.
9. South bank 230 yds. upstream from confluence of 3rd tributary; 6 ft. black shales. *G. granosus*, *Sudeticeras sp.*, *C. membranacea*, *C. membranacea horizontalis* subsp. nov., *Obliquipecten costatus* sp. nov., *Dunbarella* aff. *D. elegans*. P₂.
10. North bank 200 yds. upstream from confluence of 3rd tributary; 6 ft. shale section; near base, *P. corrugata*, *Sudeticeras sp.* P₂.

LEITRIM 21(13) (text-fig. 3)

4. East side of Aghagrania River, 780 yds. east from BM 1163·1, 100 yds. upstream from 6; 2 ft. of hard fossiliferous shales overlain by 4 ft. of friable unfossiliferous shales. *E. bisulcatum ferrimontanum* subsp. nov., *Kazakhoceras scaliger*, *Cravenoceras* cf. *C. gairense*, *P. corrugata*, *P. corrugata elongata* subsp. nov., *Chaenocardiola footii*, *Dunbarella* aff. *D. elegans*, *Stroboceras subsulcatum*, *Pseudamusium sp.*, crinoidal debris. High E₂a.
5. Western valley side 50 yds. beyond last field boundary and 650 yds. east of BM 1163·1; 6 ft. of slabby shales resting on friable unfossiliferous shales; fauna as at 6. Low E₂a.
6. East bank 750 yds. east of BM 1163·1; 16 ft. of shales (underlying 20 ft. of friable unfossiliferous shales) with *Cravenoceras cowlingense*, *E. bisulcatum grassingtonense*, *C. footii*, ?*Dimorphoceras sp.*, *Posidonia lamellosa*, *Stroboceras subsulcatum*, plant remains. Low E₂a.
7. 15-ft. shale section on west bank 950 yds. north of right-angled bend in road; lower 6 ft. with *C. membranacea*, *Chaenocardiola footii*, *Cravenoceras* aff. *C. malhamense*, *K. scaliger*, *Actinopteria persulcata*. E₁c.
8. West bank just above waterfall near point where 1,000-ft. contour crosses stream; 15 ft. of sandy shales; at base *P. corrugata*, *C. footii*, *E. pseudobilingue* C., *Cycloceras purvesi*. High E₁b.
9. West side of waterfall 850 yds. north of right-angled bend in road; 6 ft. of shales. *P. corrugata*, *P. trapezoedra*, *Eumorphoceras* cf. *E. angustum*, *Kazakhoceras sp.* Low E₁b.
10. East side of waterfall at 9, high in bank; 8 ft. of shales; same fauna. Low E₁b.

LEITRIM 20(16) (text-fig. 3)

3. Western branch of 1st tributary 360 yds. north of fork; 3-ft. shale section, upper 2 ft. sparsely fossiliferous. Probably E₁c.
4. Shale sections in both banks below house, 30 yds. south of 3. Probably E₁c.

e. Top of Slieve Anierin (above grit)

LEITRIM 21(9) (text-fig. 3)

- 1 to 14. Several small valley-like exposures, varying in height from 10 to 30 ft.; only 13 has a stream (headwaters of Stony River). Basal beds in valleys 1 to 10 are in shales with *Ct. edalense*, *P. corrugata*, *Cravenoceras* cf. *C. subplicatum*. Basal beds at 11 are at a higher level and yield *Dimorphoceras sp.*, those at 12 *P. corrugata*, and at 13 *C. holmesii* and *C. cf. C. subplicatum*. E₂b1.
15. Valley 150 yds. north-east of 16, and 400 yds. south-east of trig. stn. 1,628 ft.; lower exposure of hard shales at top of 15 ft. scree yields *Ct. cf. Ct. bisati*, *Cravenoceras sp.*, *P. corrugata*; larger 30 ft. shale exposure upstream, at base *C. cf. C. subplicatum*, *Ct. bisati*. E₂b1.
16. Small exposure of shales in hillside, 400 yds. south-south-east of trig. stn. 1,628 ft. *A. tenuispirale*. E₂b2.
17. Outcrop 300 yds. north-west of valley 1 (L21(9)26). Lower horizon with *Ct. edalense*, *C. cf. C. cowlingense*, *P. corrugata*. E₂b1. Higher horizon (at about same level as 18) with *P. corrugata*, *A. tenuispirale*. E₂b2.
18. Small shale outcrop 150 yds. north-west of Valley 1 (L21(9)26). *P. corrugata*, *Anthracoceras sp.* E₂b2.
19. 150 yds. north-east of L21(13)3; fauna at lower level *P. corrugata*, *Posidoniella variabilis*, *Dimorphoceras sp.*; at higher level *E. bisulcatum leitrinense* subsp. nov., *P. corrugata*, *Cravenoceratoides sp.* (with asymmetrical lirae). E₂b2.
20. 50 yds. north-west of bend in grit escarpment, at bottom of narrow corridor overlain by thick peat; large slabs of fossiliferous shale overlying friable unfossiliferous shales. *Ct. edalense*, *Ct. bisati*, *P. corrugata elongata* subsp. nov. E₂b1.
21. South-west side of wide valley with small stream 120 yds. north of 20; scree makes collecting difficult. *Cravenoceras holmesii* occurs sparsely below *E. bisulcatum leitrinense* subsp. nov. Also

- occurring *A. tenuispirale*, *P. variabilis*, *P. variabilis erecta* subsp. nov., *Dimorphoceras* sp., *P. corrugata*, *P. corrugata elongata* subsp. nov. E₂b2.
22. 75 yds. north-east of 21 and 200 yds. north-east of bend in grit escarpment; higher beds than at 20, but not as high as those at 21. *P. corrugata*, *Posidoniella variabilis erecta* subsp. nov. E₂b1.
23. Valley 4, the most south-easterly of four prominent valleys, and containing the most complete succession E₂b1 to 3; the lowest beds (corresponding to the first fossiliferous beds above the grit at 20) contain *Ct. edalense*, *Ct. bisati*, *P. corrugata elongata* subsp. nov., and *P. corrugata*, E₂b1. (See Table 2.)
24. Valley 3; basal beds seen are in a rich band of *E. bisulcatum leitricense* subsp. nov.; thereafter succession as in Valley 4, but collecting easier. E₂b2 to 3. (See Table 2.)
25. Valley 2; highest faunal band, with *Ct. nititoides*, *E. rostratum* sp. nov., &c., overlain by unfossiliferous shales and then flagstones. E₂b3.
26. Valley 1; *Ct. nititoides* horizon exposed about 15 ft. above stream; overlying succession as in Valleys 3 and 4. E₂b3.
27. Deep east-west valley with stream, 650 yds. south of trig. stn. 1,628 ft. Basal beds in horizon of *E. bisulcatum leitricense* subsp. nov., E₂b2. The *Ct. nititoides* horizon occurs at the eastern end, E₂b3.
28. East-west valley containing small stream 600 yds. south of trig. stn. 1,628 ft. Basal beds in *leitricense* horizon, E₂b2; exposures end before *Ct. nititoides* band.
29. Small dry east-west valley 75 yds. north of 28; 20 ft. of shales with *A. tenuispirale*, *P. corrugata*, *C. holmesi*, *P. variabilis erecta* subsp. nov.; succession starts above *leitricense* level and does not reach the *Ct. nititoides* band. E₂b2.

LEITRIM 21(13) (text-fig. 3)

1. Hillside exposure 100 yds. east of Valley 4 (L21(9)23); 2 ft. of shales with *Dimorphoceras* (*Paradimorphoceras*) cf. *D. looneyi*, *P. corrugata*. E₂b1.
2. Several small shale exposures in hillside 150 yds. east of 1; *Ct. edalense*, *P. corrugata elongata* subsp. nov. E₂b1.
3. Long valley with tiny stream $\frac{1}{4}$ mile east of Valley 4 (L21(9)23), and exposing slightly lower beds; at entrance 20 ft. of beds are overlain by 6-8 ft. of shales with *Ct. edalense*, *P. corrugata*, *P. corrugata elongata* subsp. nov.; higher 8-10 ft. of shales contain *P. corrugata*, *Cravenoceras* cf. *C. subplicatum*. E₂b1.

2. New specimen and locality numbers for Yates (1961)

	Yates (1961)	New		Yates (1961)	New
(a) <i>Specimens:</i>					
<i>E. medusa</i>	St. Ri. 2.23	7018	<i>E. medusa</i>	Agh. 8.1	7027
	St. Ri. 2.26	7019	<i>sinuosum</i>	Agh. 8.2	7028
	Doh. 6B.10	7020		Agh. 8.4	7029
		7021 counterpart		Agh. 8.10	7030
	Doh. 6B.14	7022		St. Ri. 2.22a	7031
	St. Ri. 2.24	7023	<i>E. rota</i>	Agh. 21.3	7012
		7024 counterpart		Doh. 50.1	7013
	Doh. 6B.7	7025		Agh. 21.4	7014
	St. Ri. 2.25	7026			
(b) <i>Localities:</i>					
<i>E. medusa</i>	Doh. 6	L21(14)6	<i>E. rota</i>	Agh. 21	L24(1)1
	St. Ri. 2	L20(8)2		Doh. 50	L21(14)8
<i>E. medusa</i>	Agh. 8	L23(4)2			
<i>sinuosum</i>	St. Ri. 2	L20(8)2			
(c) <i>Explanation of Plate 6:</i>					
<i>E. medusa</i>	Doh. 6B.10	7020	<i>E. medusa</i>	Agh. 8.1	7027
	St. Ri. 2.23	7018	<i>sinuosum</i>	Agh. 8.2	7028
<i>E. pseudo-</i>	Agh. 21.3	7213	<i>E. rota</i>	Agh. 21.3	7012
<i>coronula</i>				Doh. 50.1	7013

3. Notes on preservation

Goniatites. The goniatites are most commonly preserved as external moulds or impressions from which plasticine replicas showing the original external aspect of the fossils can easily be made. In a true internal mould of a goniatite there should be sutures visible as, for example, in many of the sutured internal moulds described by Currie (1954) and also in most of the material collected by Moore from various localities in England and Ireland and deposited at the Geological Survey Museum.

The specimens in shale from Slieve Anierin, however, have been preserved under far less favourable conditions and sutures are scarcely ever preserved. Frequently only the long living chamber is clearly visible, so that the internal mould does not reveal any sutures. The term internal mould is used, with the proviso that the specimens usually lack the sutures of true internal moulds. The internal moulds would show the minor features on the internal surface of the shell in reversed or negative relief. But at the same time they would also show, due to the thinness of the shell itself (and in apparent contradiction of the strict definition of the term mould), the major structural features of the shell, e.g. strong ribs, ventro-lateral ridges and furrows, in positive relief. It is also possible occasionally for some of the finer features of the test, seen in reverse in the external moulds or impressions, to be impressed to a certain extent onto the unsutured internal mould. The same phenomenon is seen also in some of the lamellibranchs.

The constrictions seen in such a species as *Eumorphoceras pseudocoronula*, although more prominent on the internal moulds, are also visible on the exterior of the test. In the external impressions the constrictions are seen in reverse as ridges. On the internal moulds they are more strongly defined and seen as strong furrows. In some goniatites, however, the constrictions are entirely due to an internal thickening of the shell and not visible externally. The specimens of *Goniatites granosus* collected from P₂ show constrictions very strongly on the internal moulds but they are not visible on the outside of the shell.

Lamellibranchs. As with goniatites external moulds or impressions are common but in several genera internal moulds are equally abundant. After death and the subsequent decay of the soft parts it would be natural for the valves to part and for internal moulds to be formed. Many specimens of the genus *Euchondria*, for example, show the multiple ligament pits along the dorsal margin and must therefore be internal moulds. There is an added complication in these specimens in that although they are basically internal moulds the external ornament of the valve has to a certain extent been impressed on to the internal mould during the compaction of the sediment. This method of preservation is not unknown, as Newell (1937, pl. 19, fig. 1) figures similarly preserved valves from America and uses the term 'subinternal mould'. The same process may also have happened occasionally in other genera; for example, the ornament in both *Pseudamusium* and *Obliquipecten* often has a curiously muted aspect, which may be due to its impression onto a presumably smooth internal mould.

Trilobites. In the case of *Weberides* from the highest faunal band, some of the pygidia are preserved as external moulds or impressions of the dorsal surface of the exoskeleton and therefore show the convex rim as a depression surrounding the pleurae, which are in reversed relief. However, other pygidia are obviously moulds of the ventral surface of the exoskeleton, since they show surrounding the pleurae (which are in apparent positive relief) a concave area which bears fine striations parallel with the margin; this is in fact a mould of the convex doublure.

REFERENCES

- ALDINGER, H. 1931. Über karbonische Fische aus Westfalen. *Paläont. Z.* **13**, 186–201.
 BAILY, W. H. 1860. Explanation to Sheet 142. *Mem. geol. Surv. Ireland*, 18–19, figs. 9a–e.
 BEUSHAUSEN, L. 1895. Die Lamellibranchiaten des rheinischen Devon mit Ausschluss der Aviculiden. *Abh. preuss. geol. Landesanst.* **17**, 364–5
 BISAT, W. S. 1924. The Carboniferous goniatites of the north of England and their zones. *Proc. Yorks. geol. Soc.* **20**, 40–124, pl. 1–10.
 ——— 1928. The Carboniferous goniatite zones of England and their continental equivalents. *Congr. Avanc. Ét. Stratigr. carbonif.* Heerlen, 1927, 117–33, pl. 6, 6a.

- BISAT, W. S. 1930. On *Cravenoceras leion* sp. nov., the basement goniatite of the Namurian, Upper Carboniferous. *Trans. Leeds geol. Ass.* (20), 28–32.
- 1932. On some Lower Sabdenian goniatites. *Ibid.* **5**, 27–37, pl. 1, 2.
- 1933. The Carboniferous goniatites of the neighbourhood of Tenby. *Proc. Geol. Ass., Lond.* **44**, 412–14.
- 1934. *Anthracoceras* from the E₂ zone of the Namurian. *Trans. Leeds geol. Ass.* **5**, 112–18.
- 1936. The faunal stratigraphy and goniatite phylogeny of the Carboniferous of western Europe with notes on the connecting links with North America. *Int. geol. Congr.*, 16th sess., U.S.A., **1**, 529–37, pl. 1.
- 1950. The junction faunas of the Viséan and Namurian. *Trans. Leeds geol. Ass.* **6**, 10–26, pl. 1, 2.
- 1955. On *Neoglyphioceras spirale* (Phillips) and allied species. *Publ. Ass. Étud. Paléont.* **21**, 13–18, pl. A.
- DUNCAN, C. and MOORE, E. W. J. 1931. On the occurrence of a British Coal Measure goniatite in Missouri, U.S.A. *Proc. Yorks. geol. Soc.* **22**, 1–8, pl. 1.
- BOATE, G. 1652. *Ireland's naturall history: being a true and ample description, etc.* London.
- BRAY, A. 1927. The Carboniferous sequence between Lothersdale and Cowling (Colne). *J. Manchr. geol. Ass.* **1**, 44–57.
- BRONN, H. 1828. *Posidonia becheri*, eine neue fossile Muschel der Übergangs-Periode. *Z. Miner.* **1**, 262–9, pl. 2.
- CALDWELL, W. G. E. 1959. The Lower Carboniferous rocks of the Carrick-on-Shannon syncline. *Quart. J. geol. Soc. Lond.* **115**, 163–87, pl. 6.
- CHARLESWORTH, J. K. 1953. *The geology of Ireland.* Edinburgh.
- COLE, G. A. J. and HALISSY, T. 1924. *Handbook of the geology of Ireland.* London.
- CRUISE, R. J. 1878. Explanatory Memoir to accompany Sheets 66 and 67. *Mem. geol. Surv. Ireland.*
- CURRIE, E. 1954. Scottish Carboniferous goniatites. *Trans. roy. Soc. Edinb.* **62** (2), 527–602, pl. 1–4.
- DAVIES, A. MORLEY. 1935. *Tertiary faunas*, **1**. London.
- DELÉPINE, G. 1941. Les Goniatites de Carbonifère du Maroc et des Confins Algéro-Marocains du sud (Dinantien-Westphalien). *Notes Serv. Min. Maroc.* **56**, 1–108, pl. 1–8.
- DEMANET, F. 1938. La faune des couches de passage du Dinantien au Namurien dans le synclinorium de Dinant. *Mém. Mus. Hist. nat. Belg.* **84**.
- 1941. Faune et stratigraphie de l'étage namurien de la Belgique. *Ibid.*, **97**.
- DORLODOT, J. S. and DELÉPINE, G. 1930. Faune marine de Terrain houiller de la Belgique. Répartition stratigraphie dans le région de Charleroi et la Basse-Sambre. *Mém. Inst. géol. Univ. Louvain*, **6**, 1–112, pl. 1–10.
- DUNHAM, K. C. and STUBBLEFIELD, C. J. 1944. The stratigraphy, structure and mineralization of the Greenhow mining area, Yorkshire. *Quart. J. geol. Soc. Lond.* **100**, 209–68, pl. 21, 22.
- ELIAS, M. K. 1956. Upper Mississippian and Lower Pennsylvanian formations of south-central Oklahoma. In *Petroleum Geology of Southern Oklahoma*. Symposium: *Amer. Ass. Petrol. Geol.* 56–134, pl. 1–6.
- 1958. Late Mississippian fauna from the Redoak Hollow Formation of southern Oklahoma. *J. Paleont.* **32**, 1–57, pl. 1–4.
- ETHERIDGE, R. Jr. 1873. Explanation to Sheet 32, Central Lanarkshire. *Mem. geol. Surv. Scotland*, 103–4.
- 1874. Notes on Carboniferous Lamellibranchiata (Monomyaria). *Geol. Mag.*, N.S., Dec. 2, **1**, 300–6, pl. 13.
- ETHERIDGE, R. 1888. *British fossils: Pt. I, Palaeozoic.* Oxford.
- FRECH, F. 1899. *Lethaea geognostica*: Pt. 1, *Lethaea palaeozoica*, **2** (2), Die Steinkohlenformation. Stuttgart.
- GILL, W. D. 1947. On the Upper Bowland Shales in Carla Beck, near Skipton, Yorks. *Proc. Leeds phil. lit. Soc.* **5**, 60–64.
- GIRTY, G. H. 1909. The fauna of the Caney Shale of Oklahoma. *Bull. U.S. geol. Surv.* **377**, 5–106, pl. 1–13.
- 1911. The fauna of the Moorefield Shale of Arkansas. *Ibid.* **439**, 1–148, pl. 1–15.
- GORDON, M. 1957. Mississippian cephalopods of northern and eastern Alaska. *Prof. Pap. U.S. geol. Surv.* **283**, 1–61, pl. 1–6.

- GRIFFITH, R. 1818. *Geological and mining survey of the Connaught coal district in Ireland*. Dublin.
- HIND, W. 1896–1905. A monograph of the British Carboniferous Lamellibranchiata. *Palaeontogr. Soc. (Monogr.)*, **1**, 1896–1900; **2**, 1901–5.
- HODSON, F. 1954a. The beds above the Carboniferous Limestone in north-west County Clare. *Quart. J. geol. Soc. Lond.* **109**, 259–83, pl. 11, 12.
- 1954b. The Carboniferous rocks of Foynes Island, Co. Limerick, Ireland. *Geol. Mag.* **91**, 153–60.
- 1959. The palaeogeography of *Homoceras* times in western Europe. *Bull. Soc. belge Géol. Pal. Hydr.* **68**, 134–50, pl. 1.
- and MOORE, E. W. J. 1959. *Goniatites striatus* and related forms from the Viséan of Ireland. *Palaeontology*, **1**, 384–96, pl. 64–69.
- HOLZAPFEL, E. 1889. Die Cephalopoden-führenden Kalke des unteren Carbon von Erdbach-Breitscheid bei Herborn. *Paläont. Abh.*, N.F., Band 1 (der ganzen Reihe Bd. 5), Heft 1, 3–77, pl. 1–8.
- HUDSON, R. G. S. 1926. On the rhythmic succession of the Yoredale Series in Wensleydale. *Proc. Yorks. geol. Soc.* **20**, 125–35.
- 1939. The Millstone Grit succession of the Simonsat anticline, Yorkshire. *Ibid.* **23**, 319–49.
- 1941. The Mirk Fell Beds (Namurian, E₂) of Tan Hill, Yorkshire. *Ibid.* **24**, 259–89.
- 1944. The faunal succession in the *Ct. nitidus* zone in the mid-Pennines. *Proc. Leeds phil. lit. Soc.* **4**, 233–42.
- 1945. The goniatite zones of the Namurian. *Geol. Mag.* **82**, 1–9.
- 1946. The Namurian goniatites *Cravenoceratoides bisati* Hudson and *Cravenoceratoides lirifer* n. sp. *Proc. Yorks. geol. Soc.* **25**, 375–86, pl. 21, 21a.
- and COTTON, G. 1943. The Namurian of Alport Dale, Derbyshire. *Ibid.* **25**, 142–73.
- — 1945a. The Lower Carboniferous in a boring at Alport, Derbyshire. *Ibid.* **25**, 254–329.
- — 1945b. The Carboniferous rocks of the Edale anticline, Derbyshire. *Quart. J. geol. Soc. Lond.* **101**, 1–36, pl. 1.
- and MITCHELL, G. H. 1937. The Carboniferous geology of the Skipton anticline. *Summ. Progr. geol. Surv., Lond.*, for 1935, (2), 1–45.
- and STUBBLEFIELD, C. J. 1945. Discussion on Dunham, K. C. and Stubblefield, C. J. 1944. The stratigraphy, structure and mineralization of the Greenhow mining area, Yorkshire. *Quart. J. geol. Soc. Lond.* **101**, 135–7.
- HULL, E. 1878. *Physical geology and geography of Ireland*. London.
- 1881. *The coalfields of Great Britain*. 4th ed. London.
- HYATT, A. 1884. Genera of fossil Cephalopoda. *Proc. Boston Soc. nat. Hist.* **22**, 273–338.
- Ireland, Dail. 1921. *Memoir. Commission of inquiry into the resources and industries of Ireland (Connacht Coalfield, 127–44)*. Dublin.
- JACKSON, J. W. 1927a. The succession below the Kinder Scout Grit in north Derbyshire. *J. Manchr. geol. Ass.* **1**, 15–32, pl. 1.
- 1927b. Geology of the Rossendale Anticline. Explanation of Sheet 76. *Mem. geol. Surv. U.K.*
- 1927c. New Carboniferous lamellibranchs and notes on other forms. *Mem. Manchr. lit. phil. Soc.* **71**, 93–122, pl. 1–3.
- KANE, Sir R. 1845. *Industrial Resources of Ireland*. 2nd ed. Dublin.
- KING, W. B. R. 1914. A new trilobite from the Millstone Grit of N. Yorkshire. *Geol. Mag.*, Dec. 6, **1**, 390–4, pl. 32.
- LEIDY, J. 1856. Indications of two new genera of extinct fishes. *Proc. Acad. nat. Sci. Philad.* **7**, 414.
- M'COY, F. 1844. *A synopsis of the characters of the Carboniferous Limestone fossils of Ireland*. Dublin.
- 1851. Descriptions of some new Mountain Limestone fossils. *Ann. Mag. nat. Hist.*, Ser. 2, **7**, 167–75, pl. 1.
- MEEK, F. B. 1874. New genus *Euchondria* Meek. *Amer. J. Sci.* **7**, 445, 488–9.
- MILLER, A. K. and FURNISH, W. M. 1940. Studies of Carboniferous Ammonoids, Pts. 1–4. *J. Paleont.* **14**, 356–77, pl. 45–49.
- — 1958. The goniatite genus *Anthracoeras*. *Ibid.* **32**, 684–6.
- and YOUNGQUIST, W. 1948. The cephalopod fauna of the Mississippian Barnett formation of central Texas. *Ibid.* **22**, 649–71, pl. 94–100.
- — and NIELSEN, M. L. 1952. Mississippian cephalopods from western Utah. *Ibid.* **26**, 148–61, pl. 25, 26.

- MOORE, E. W. J. 1936. The Bowland Shales from Pendle to Dinckley. *J. Manchr. geol. Ass.* **1** (3), 167–92, pl. 1–3.
- 1939. The goniatite genus *Dimorphoceras* and its development in the British Carboniferous. *Proc. Yorks. geol. Soc.* **24**, 103–28, pl. 15.
- 1946. The Carboniferous goniatite genera *Girtyoceras* and *Eumorphoceras*. *Ibid.* **25**, 387–445, pl. 22–27.
- 1950. The genus *Sudetoceras* and its distribution in Lancashire and Yorkshire. *J. Manchr. geol. Ass.* **2** (1), 31–50, pl. 1–3.
- 1958. Dimorphoceratidae from the Upper Viséan Shales of Co. Leitrim, Eire. *Proc. Yorks. geol. Soc.* **31**, 219–26, pl. 14.
- MOSELEY, F. 1954. The Namurian of the Lancaster Fells. *Quart. J. geol. Soc. Lond.* **109** (for 1953), 423–54, pl. 22.
- NEVILL, W. E. 1956. The Millstone Grit and Lower Coal Measures of the Leinster Coalfield. (Appendix on the non-marine fauna by R. M. C. Eagar.) *Proc. R. Irish Acad.* **58** (B), 1–16, pl. 1–5.
- 1957. The geology of the Summerhill Basin, Co. Meath, Ireland. *Ibid.* 293–303, pl. 22.
- NEWBERRY, J. S. and WORTHEN, A. H. 1870. Descriptions of fossil vertebrates. *Geol. Surv. Illinois*, **4**, 347–71, pl. 1–4.
- NEWELL, N. D. 1937. Late Palaeozoic pelecypods: Pectinacea. *Rep. geol. Surv. Kansas*, **10**.
- NOYER, G. V. DU. 1863. On the bituminous coal of the Arigna district, Counties of Roscommon and Leitrim. *Geol. Mag.*, 81–92, pl. 5, 6.
- OBRUCHEV, D. 1953. A study of Karpinsky's work on the Edestidae. *Trans. Inst. paleozool. Acad. Sci. U.R.S.S.* **45**, 1–85, pl. 1–6 (in Russian).
- PADGET, P. 1953. The stratigraphy of Cuilcagh, Ireland. *Geol. Mag.* **90**, 17–24.
- PARKINSON, D. 1926. The faunal succession in the Carboniferous Limestone and Bowland Shales at Clitheroe and Pendle Hill. *Quart. J. geol. Soc. Lond.* **87**, 188–244, pl. 12–17.
- 1936. The Carboniferous succession in the Slaidburn district, Yorkshire. *Ibid.* **92**, 294–331, pl. 24–26.
- PATTEISKY, K. 1929. *Die Geologie und Fossilführung der Mährisch-Schlesischen Dachschiefer und Grauwackenformation*. Troppau.
- 1933. Faunen- und Floren-Folge im ostsudetischen Karbon. *Berg.- u. hüttenm. Jb.* **2**, 41–52, pl. 2.
- 1936. Die obercarbonischen Goniatischen der Hultschiner und Ostrauer Schichten. *Neues Jb. Min. Geol. Paläont.* **76**, 1–30, pl. 1.
- PHILLIPS, J. 1836. *Illustrations of the geology of Yorkshire*. Pt. 2, *The mountain Limestone district*. London.
- PICKEL, W. 1937. Stratigraphie und Sedimentanalyse des Kulms an der Edertalsperre. *Z. dtsh. geol. Ges.* **89**, 233–85, pl. 11–14.
- RAMSBOTTOM, W. H. C. 1959. Distinctions between the Carboniferous lamellibranch genera *Caneyella*, *Posidonia* and *Posidoniella*. *Palaontology*, **1**, 405–6, pl. 71, figs. 8–14.
- REED, F. R. C. 1942. Some new Carboniferous trilobites. *Ann. Mag. nat. Hist.*, 11th ser., **9**, 649–72, pl. 8–11.
- ROEMER, F. A. 1854. Beiträge zur geologischen Kenntnis des nordwestlichen Harzgebirges. *Palaontographica*, **3** (1), 1–67, pl. 1–10.
- RUPRECHT, L. 1937. Die Biostratigraphie des obersten Kulm im Sauerlande. *Jb. preuss. geol. Landesanst.* **57**, 238–83, pl. 9, 10.
- RUZHENCEV, V. E. 1947. Representatives of the family Dimorphoceratidae Hyatt in the Carboniferous deposits of the Urals. *C.R. Acad. Sci. U.R.S.S.* **56**, 521–24 (in Russian).
- SCANLON, J. E. 1953. The Carboniferous rocks near Garristoun, Co. Dublin, and in the adjacent part of Co. Meath. *Sci. Proc. R. Dublin Soc.* **26**, 145–57, pl. 12.
- SCHMIDT, H. 1925. Die carbonischen Goniatischen Deutschlands. *Jb. preuss. geol. Landesanst.*, **45**, 489–609, pl. 19–26.
- 1934. Cephalopodenfaunen des älteren Namur aus der Umgegend von Arnsberg in Westfalen. *Ibid.* **54**, 440–61.
- SCHWARZBACH, M. 1936. Die Trilobiten im Oberkarbon Oberschlesiens. *Ibid.* **56**, 422–43.
- SMYTH, L. B. 1950. The Carboniferous System in N. Co. Dublin. *Quart. J. geol. Soc. Lond.* **105**, 295–326, pl. 17–19.

- SPATH, L. F. 1934. *A catalogue of the fossil Cephalopoda in the British Museum (Natural History)*. Pt. 4 The Ammonoidea of the Trias.
- STEPHENS, J. v. *et al.* 1942. The faunal divisions of the Millstone Grit Series of Rombalds Moor and neighbourhood. *Proc. Yorks. geol. Soc.* **24**, 344-72, pl. 31.
- 1953. Geology of the country between Bradford and Skipton (Sheet 69). *Mem. geol. Surv. U.K.*
- SUSTA, V. 1928. *Stratigraphie des Ostrau-Karviner Steinkohlenreviers im Lichte der Paläontologie*. Der Kohlenbergbau des Ostrau-Karviner Steinkohlenreviers, **1**, 381-484, 75 pl.
- TONKS, L. H. 1925. The Millstone Grit and Yoredale rocks of Nidderdale. *Proc. Yorks. geol. Soc.* **20**, 226-56, pl. 19.
- WEIGELT, J. 1922. Die Bedeutung der Jugendformen karbonischer Posidonomyen für ihre Systematik. *Palaeontographica*, **64**, 43-130, pl. 22-31.
- WOLTERSTORFF, H. 1899. Das Untercarbon von Magdeburg-Neustadt und seine Fauna. *Jb. preuss. geol. Landesanst.* **19**, 3-64, pl. 2, 3.
- WOODWARD, A. S. 1917. On a new species of *Edestus* from the Upper Carboniferous of Yorkshire. *Quart. J. geol. Soc. Lond.* **72**, (for 1916) 1-6, pl. 1.
- YATES, P. J. 1961. New Namurian goniatites of the genus *Eumorphoceras*. *Palaeontology*, **4**, 54-58, pl. 6.
- YOUNGQUIST, W. 1949. The fauna of the White Pine Shale of Nevada. *J. Paleont.* **23**, 276-305, pl. 56-64.

PATRICIA J. YATES
Department of Geology,
Imperial College,
London, S.W. 7

Manuscript received 22 November 1961

FURTHER STUDIES ON MICRO-ORGANISMS AND THE PRESENCE OF SYNGENETIC PYRITE

by LEONARD G. LOVE

ABSTRACT. Various microscopic pyrite forms are described from Lower Jurassic and Carboniferous argillaceous rocks and it is confirmed that solution of the pyrite reveals abundant microfossils of a limited range of morphological variety which are described and figured. Two groups are distinguished, one showing clear association with plant material and the other with animal remains. Of the latter, occurrences of later geological and Recent ages are briefly noted and figured. Both forms were probably of a saprophytic nature and are thought to have been involved in the production of hydrogen sulphide and, consequently, the precipitation of the iron sulphide with which they are now found. The environment of this activity is discussed with particular reference to the Liassic deposits studied. No stratigraphic distinction is found for the microfossils within the inclusive period from Lower Carboniferous to Lower Jurassic.

THIS paper presents the results of research in continuation of that published earlier by the author (Love 1957). While elaborating the phenomena then described, it demonstrates their extensive occurrence in other strata and throws some light on the many problems previously left unsolved. These arose from the original demonstration that microscopic pyrite grains of generally characteristic sizes and shapes, occurring in various shales and a bituminous limestone of the Scottish Lower Carboniferous sequence, exclusively embodied small objects regarded as microfossils of a hitherto unknown type. On the basis of this association, these bodies were held to be the remains of organisms which themselves were producers of hydrogen sulphide and became filled and coated with iron sulphide as a result. The smaller of the two types of micro-fossil designated, *Pyritosphaera barbaria* Love 1957, was yielded by small uncompressed spherical pyrite grains with a characteristic framboidal surface texture. In size and form these resembled the pyrite grains already noted in the geological literature by many authors (see Love 1957, pp. 429, 437) from many other beds of dark shale, coal, and indeed certain other rocks more generally associated with their yield of metal ores. At the time, however, the investigation was not carried into these fields. The larger supposed micro-organism, *Pyritella polygonalis* Love 1957, appeared also to have counterparts in such rocks.

The present paper is concerned with furthering knowledge of the palaeontology and ecology of these organisms. Attention is mainly confined to the Rhaetic and Lias of Britain and some supporting studies on Carboniferous and more recent deposits. The Rhaetic and Liassic rocks were chosen as providing accessible and well-known sequences of suitable argillaceous rocks whose general conditions of deposition have already been studied in detail by other authors.

It had already been demonstrated (Love and Zimmerman 1961) that studies of sulphide spheres might with success be applied to such ancient rocks as the Lower Proterozoic Mount Isa Shales of Queensland, Australia, in suggesting the origin of the vast quantities of primary sulphide present there. The slightly metamorphosed condition of the rock, however, added difficulty to the work attempted and precluded much additional understanding being gained of the phenomena observed. In the case of the Permian Kupfer-

schiefer of Germany, the classic ground of dispute over the origin of pyrite spheres in dark shale, it has been found possible to apply the findings of the present paper and to demonstrate much the same range of micro-organisms in a very similar environment; being concerned with ideas on ore genesis this is published elsewhere (Love 1962).

In the present work the small particle size of some of the organic material imposed a limit to the usefulness of the ordinary microscope, and it is likely that with improved methods and the use of more elaborate equipment much more information including chemical data will become available against which many of the conclusions so far reached may be tested. The subject-matter is of wide significance in the formation of an important type of sedimentary rock.

Full acknowledgement to the work of others is made in the text. Thanks are also due to all those who at various times have provided specimens for special study. The research was carried out in the Department of Geology of the University of Sheffield.

LOWER JURASSIC STUDIES

Source of material. The Westbury Beds provided the Rhaetic specimens and were principally collected from the Garden Cliff section near Westbury on Severn, Gloucestershire, and from St. Mary's Well Bay, Glamorganshire. Lower Lias rocks were taken from St. Mary's Well Bay and the Yorkshire coast at Robin Hood's Bay and near Redcar; Middle Lias specimens from the Yorkshire coast south-east of Staithes; and the Upper Lias succession of Grey Shales, Jet Rock, Alum Shale Series, and Peak Shales from shore sections around Whitby. Confirmatory specimens from boreholes near Whitby were kindly provided by Dr. J. E. Hemingway.

The South Wales and Gloucestershire sections of Rhaetic and Lias are described in detail by Richardson (1905) while the Lias of the Yorkshire coast is described by Hemingway (1934) in general terms and some of the sections in greater detail by Howarth (1955). All these authors paid close attention to faunas but only Hemingway recorded details of the finer microflora of these beds, referring (*op. cit.*, p. 257) to the presence of spore cases, microspores and macrospores in the Alum Shales and Jet Rock Series. Although few preparations to reveal this microflora have been carried out by the present author (necessarily involving a different process from that described below), enough has been seen to show much material present in most of the beds studied, and Mr. D. Wall (personal communication) confirms the presence of spores, algae, and hystrichospheres in many of the Liassic strata.

Remarkably consistent results were obtained from the Rhaetic and Liassic rocks, from which the normal dark to grey, fine or only slightly silty shale and mudstone lithologies were analysed. In subsequent sections, therefore, it has not been found necessary to specify the particular horizons from which described material was obtained.

Description of the pyrite. The Jet Rock is typical of much of the Liassic and Rhaetic strata in the occurrence of pyrite, which X-ray examination showed to be the only sulphide present. There are pyritic replacements of delicate mollusc shells and thin coatings around concretions (Hemingway, *in* Hallimond *et al.* 1950, p. 60), as well as finely disseminated pyrite in the forms with which this paper is concerned, and revealed only by the microscope (Pl. 63, fig. 15). In other beds, such as the Alum Shales, larger irregular masses of pyrite occur. In nearly all the shales encountered, however, from

highly to only slightly bituminous, or even slightly silty, the finely disseminated pyrite is abundantly present and it is clearly an important and widespread component of the rock. Although predominant as small single or compound rounded spheres, six types of occurrence are described. Some of these intergrade and precision in distinguishing them is not really possible. The significance of the forms will appear in a later section.

Pyrite type (a). Small grains up to 2–3 μ in size varying in shape between angular and spherical. The latter, at the upper end of the size range, may well intergrade with the material of type (b). In the case of the smallest grains even determination of their shape becomes difficult. All are scattered throughout the shale as may be seen either from thin sections or from mounts of a poorly disaggregated shale in which thin clots of material remain in their original state. The proportion of type (a) is undoubtedly much increased at the expense of other types, and also of concretions, nodules, and shell replacement material after crushing of the rock. The pyrite seen on spores is sometimes in tiny grains but due to their small size a relationship to the spore tissue can seldom be determined.

Pyrite type (b). Simple spheres ranging in size from 2–3 μ up to 15 μ or 20 μ . Often the framboidal texture so often associated with this form of pyrite can be observed in which the surface of the spheres is composed of numerous tiny grains or crystals of sulphide. This is a detail only clearly seen in reflected illumination from above a polished surface (see Love 1957, pl. 33, fig. 2).

Pyrite type (c). Multiglobular bodies of more complex outline. They show rounded bulges each of the same size range and texture as the individual spheres (type (b)) as if compounded of them. In individual isolated multiglobular bodies tested, the component parts are not easily prised apart with a fine needle, and certainly not without rupturing the structure. Their outlines are those of the bodies in Pl. 63, figs. 10, 12. Some of the compound bodies attain a nearly uniform equatorial outline, and only solution will reveal their nature. At the other extreme, however, some are difficult to distinguish from unconnected but touching single spheres. From the nature of the organisms released by solution of the sulphide it is unlikely that many of the instances in which spheres are seen just touching in thin sections and rather dense mounts of isolated material do in fact represent actual organic connexion rather than chance juxtaposition. It is certainly not felt safe to attribute to organic causes all the forms such as chains, rings, and even budding, that might be surmised purely from study of sections of the rock.

The surface texture of the multiglobular pyrite bodies, and also the single spheres at the larger end of their size range, may be rougher when seen in outline, and have a coarser surface texture of large pyrite grains or crystals, than is normal in the framboidal texture. They tend therefore to be reminiscent of the Kiesklümpchen (verezte Bakterien

EXPLANATION OF PLATE 63

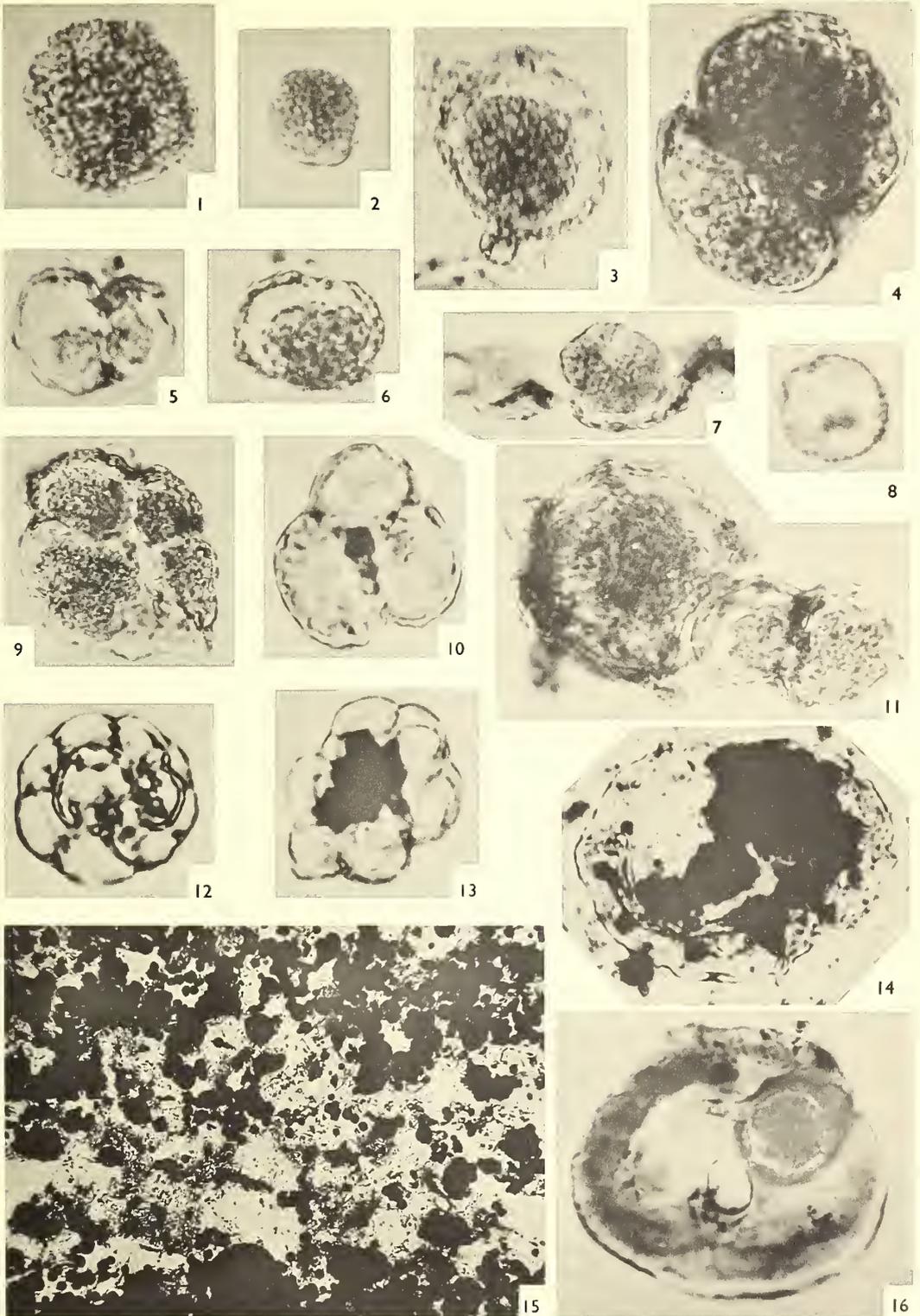
All figs., Liassic material.

Figs. 1–13. Micro-fossils released from pyrite grains in shales. 1, 2, 5–8, 10–13, $\times 2,000$ approx. 3, 9, $\times 1,000$. 4, $\times 3,000$.

Fig. 14. Spore or pollen grains with pyrite coating, $\times 500$.

Fig. 15. Thin section of *P. spinatum* zone shale normal to bedding in ordinary transmitted light; black grains are pyrite, $\times 250$ approx.

Fig. 16. Plant spore with vesicle and corebody, cleared of pyrite, $\times 1,600$.



Typ II) (mineralized bacteria) which Neuhaus (1940, p. 319, fig. 6) described from the Kupferschiefer. The material now described shows gradations between larger and smaller surface grains, possibly corresponding to some extent with the size of the bodies bearing them. Possibly, therefore, some of the Kiesklümpchen-types are a particularly coarse extreme of the Kieskügelchen, Neuhaus's normal framboidal sphere.

When seen disaggregated from the rock, a number of multiglobular pyrite grains especially from the more bituminous shales may show shreds of organic tissue attached. It is very probable that from a highly compressed shale containing fragments of plant tissue of many kinds such material may remain adhering to a pyrite grain by chance, so apart from those cases which may appear significant from the prepared oxidation mounts, such occurrences are not pressed as sources of information.

Pyrite type (d). Undoubted pyrite on recognizable spores and pollen grains and on other bodies of a similar general shape and material. These bodies (Pl. 63, fig. 14), usually from 30 μ to 100 μ in size, and clearly exceptional in character, may show single isolated grains or spheres of pyrite (types (a) and (b)) or a mass of spheres to the extent of a complete cover of pyrite. The coarse Kiesklümpchen texture of pyrite may be developed in partially covered bodies, perhaps explaining the nature of others of similar texture but completely pyritic. It is difficult to demonstrate by physical means the relationship of the pyrite to the spore or pollen grains. In some cases it is easily detached and leaves no mark or damage; in others an angular depression may be left; and again in others the pyrite may appear to be united with the wall material, for manipulation with a needle only ruptures the whole specimen.

In some of the shales studied spores, pollen grains, and similar bodies with adherent pyrite form a substantial part of that aspect of the microflora, an observation which Mr. D. Wall confirms. They are often individually of a sufficiently high aggregate specific gravity to appear in the heavy fraction of a bromoform separation. So too are many aggregates of pyrite from the shale containing fragments of organic tissue, and generally of unidentifiable origin, but to which the general description of pyrite as for spores and pollen is fully applicable.

Pyrite type (e). Larger pyrite 'microberries' up to 120 μ in size. These are found when the finer fraction from a less intensely crushed rock is examined beneath a high-power binocular microscope. The descriptive name given by Macfadyen (*in* Love 1957, p. 437) is retained. They have a generally rounded shape and are clearly composed of large numbers of smaller spheres, 20–50 μ in size, which give the characteristic appearance. The microberry as a whole is not truly framboidal, but the smaller spheres are. On crushing, the berry breaks down readily into the separate smaller spheres, and these in turn break down into material between 0.5 μ and 5 μ in size, but of this the larger parts are found to be aggregate, as yet uncrushed, of the 0.5–1.5 μ grains which are therefore basic to the whole microberry. In one specimen provided by Dr. Macfadyen calcite cement held the intermediate spheres together in the microberry; they became separated after effervescence in dilute hydrochloric acid but the intermediate spheres themselves did not react with the acid.

Pyrite type (f). Foraminiferids with pyrite infillings. The author's attention was first drawn to the occurrence of such specimens in the Lias by Dr. C. G. Adams. Through the moistened calcareous tests of various Lagenids pyrite could clearly be seen (Pl. 64,

fig. 7) and on solution of the shells of such specimens accumulations of pyrite resembling the microberries were released from the chambers, whose internal shape they sometimes retained.

Experimental methods. The observations recorded in this paper concerning the bodies from the pyrite were obtained from two lines of investigation. One consisted of the chemical treatment of small *bulk* samples of pyrite concentrated from a rock, and provided adequate quantities of the final product for proper washing and preparation as permanent mounts on microscope slides. Comparison with a mounted sample of the untreated pyrite then allowed an inference to be made of the relationship between the pyrite and the cleared bodies. For the bulk process, the laboratory methods used were essentially those described by Love (1957, p. 431) and in greater detail by Love and Zimmerman (1961, pp. 883–4). Mechanical disaggregation of the rock sample by grinding was followed by separation of the heavy mineral grains, predominantly pyrite, by centrifuging in bromoform (s.g. 4.9). Unless it was to be examined for material which might be partly calcitic, the heavy residue was then treated for some days with warm hydrofluoric acid to remove traces of adhering light minerals, and when so cleaned it was oxidized in warm or hot concentrated nitric acid or other reagent. After removal of the acid and after several washings of water, the few remaining drops of suspension yielded small micro-organisms, as described below, in proportion to the original yield of rounded pyrite grains. The chemical treatment and the preparation of slides was carried out under strict precautions to avoid contamination. Though useful, bulk solution is not usually a rigorous enough method to determine some of the relationships and in many instances it was found necessary to carry out the process in such a way as to see it actually happening under the microscope.

Virtually continuous observation of the solution of the pyrite was made possible by use of the special cell, only developed late in the course of earlier work by Love (1957, p. 432) and subsequently described in detail by Love and Zimmerman (1961, pp. 884–5). It was possible to confirm that each form of micro-organism described could in fact be obtained in that condition from a particular grain of pyrite from the sediment. An inherent difficulty in this method, however, is that it is frequently impossible to preserve the material revealed and to make a permanent mount. To achieve this it is necessary, without losing a specimen perhaps only a few microns in size, to remove the excess reagent around it and to irrigate the chamber with water to prevent later crystallization of salts produced in the reaction.

This direct observation method obviates the need for elaborate statistical support for such assertions as are made, as was attempted in earlier work (Love 1957, pp. 431–2) and the method is essential if only a limited amount of material is available, for example part of the pyritic content of a single foraminiferid. In the bulk method, large numbers of foraminiferids would be needed for a single preparation. It is also possible to observe the actual position of the sulphide, for instance whether it occurs superficially or within organic material, and to watch for evidence of other soluble minerals such as calcite originally accompanying the pyrite.

Description of the micro-organisms released from the pyrite. The micro-organisms remaining after the removal of the pyrite are varied in appearance but lie in a limited number of groups, some of which are clearly interrelated.

Group 1. Spherical bodies (Pl. 63, figs. 1, 2) 5–20 μ in diameter occurring abundantly, resembling *Pyritosphaera barbaria* Love 1957 (p. 433). They appear to be composed of a tightly packed mass of small cells, 0.5–1 μ , each one of which can be seen during solution to contain a single pyrite crystal. Occasionally, however, the aggregate of cells is looser and often the larger bodies in the size range about 20 μ show this. Polished sections of pyrite spheres in the rock confirm a uniform internal structure. The very thin skin of transparent tissue around the individual pyrite grains does not appear to affect their reflecting power and has not been observed in the sections.

Group 2. Bodies as described above (*P. barbaria*) with a partial or complete thin outer envelope of smoother tissue. If complete (Pl. 63, fig. 4) in the polar view it hardly obscures the characteristic appearance of the microspinose body, but this is no longer clear equatorially. Careful focusing of the microscope at high magnification often makes it possible to demonstrate the complete continuity of the sac below and above the core body. Other bodies (Pl. 63, fig. 2) only bear a shred of such material. The microspinose core body may be considerably smaller than the outer sac (Pl. 63, fig. 6) and less characteristically developed, in many cases appearing as a less perfectly formed mass of microgranular character (Pl. 63, fig. 5). Masses like this, if found isolated, could be included in Group 1 above. Only one core body occurs within any one sac; but the latter often occur in tightly packed compound groups, up to six together being common as well as more complex formations. Here not all the sacs necessarily contain core bodies. The tissue of the sacs is described below (Group 3) and a similar outer wall to the group, as described there, is present here.

Group 3. Hollow sacs whose general appearance is like that described for the sacs with core bodies. Less common, they are transparent to translucent and of a variable smooth to rough surface appearance. In photographs at an equatorial level of focus the walls appear as a thin line or as a rougher, thicker layer of material. The number of cells in the group may again be from one (Pl. 63, fig. 8) to many (Pl. 63, figs. 10 and 12). The outer wall as a whole often appears to be stronger and thicker than the apparently common walls separating individual sacs. Furthermore, these inner walls may not be complete and some instances giving a distinct appearance of cells in division have been noticed. This may best be described as a 'dumb-bell' shape, with a constriction but no actual wall between the cells. Sometimes such adjacent cells may be more or less equal in size but often one is smaller.

Both simple and compound sac forms have been observed while becoming cleared of pyrite. The former come from single spheres. If no well-formed core body is present the pyrite inside the sac may, in its later stages of solution, be irregular (Pl. 63, fig. 13) but is sometimes idiomorphic, though not often appearing to have impressed this shape on the sac from within. Sometimes breakdown into small dark grains can be seen. These may leave either no remnant or microgranular organic material (Pl. 63, fig. 5); it must be stressed, however, that with the empty cells it is in most cases very difficult to decide whether absolutely no grains of core material are present, as distinct from any slight granularity or roughness of the wall. The compound sac forms are released from multi-globular pyrite grains of similar outline or from apparently single spheres, the coarseness of whose outer pyrite may obscure the detailed shape. These multi-globular pyrite bodies

and the sac bodies from them appear uncompressed and usually are more or less symmetrical and free from attachment to any other material.

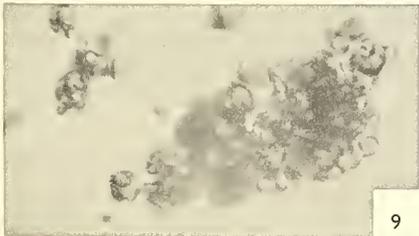
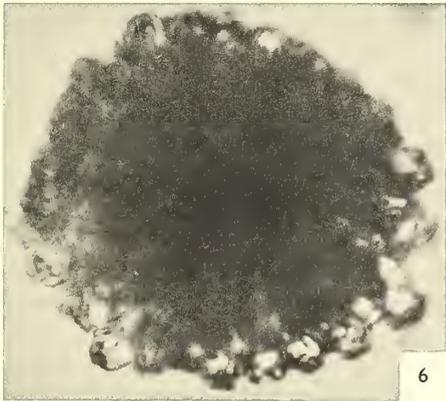
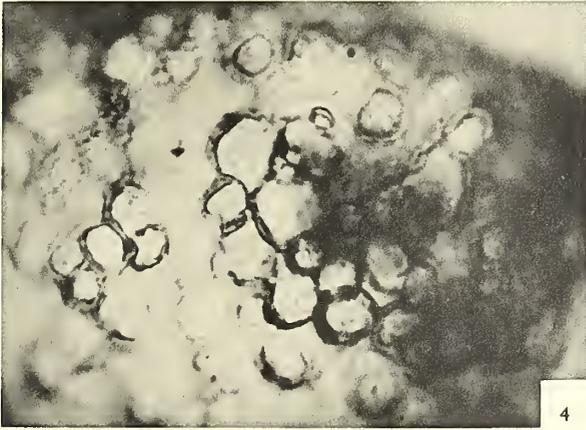
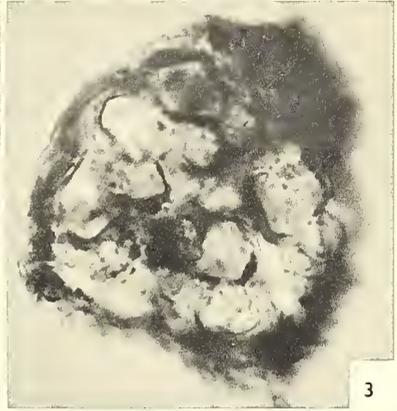
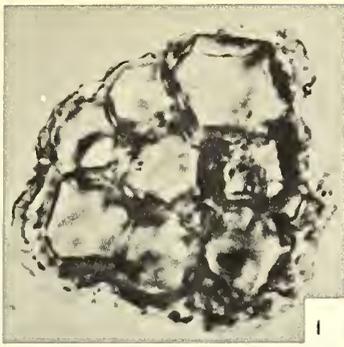
Group 4. Spores and pollen grains, recognizable at least by their general shape, showing, after solution of sulphide, patterns of irregularly developed high-relief ring markings on the surface, observed to correspond with the position of the sulphide. (This is discussed on p. 452.) In some particularly clear specimens examination at high magnification has revealed that the structures, which vary from circular to polygonal, and measure 3–10 μ are vesicle-like developments apparently within the surface layers of the exine, but often this is difficult to decide. Some markings merely appear to be the result of other components of the shale, often pyrite as spheres, pressing in during lithification. The vesicles originally contain pyrite and in some instances it has been possible to witness its disappearance from them during solution. In some of these vesicles microspinose spheres are found (Pl. 63, fig. 16) identical with the core bodies of the isolated sac-bodies, single and compound, described in Group 3 above. Other fragmental organic tissue, generally darker than the spores and of unknown origin, often also reveals round to hexagonal pits or blisters, lighter in appearance, some containing microspinose or roughly microgranular bodies.

Group 5. Small clear granules or particles 0.5–2 μ in size, yielded from the pyrite infillings of foraminiferids and from microberries (Pl. 64, fig. 8). The observation method has been used exclusively. There is no clear evidence of the presence within the pyrite of any organic structure larger than about 2 μ , which is the upper limit of the grains into which the material can be broken, and which form the profile of the intermediate round aggregates that make up the microberry as a whole. Very gentle or very rapid solution sometimes leaves them in large spherical groups, but these appear as loose clusters only and the particles readily drift apart, subject to the movement of liquid and air bubbles around them. Close observation in this freely moving condition is difficult but freshly prepared specimens appear to be small clear round cells, of a rather high refractive index and having no effect upon plane polarized light. Some are perhaps seen in a state of division but most are single, rounded to slightly elongated, and featureless.

Group 6. Many of the smallest grains of pyrite (type (a)) in the concentrates dissolve to leave small cell-bodies behind such as are described above, although others dissolve without leaving any trace as would be expected if they are derived from shell and nodule

EXPLANATION OF PLATE 64

- Figs. 1–6, Carboniferous; 7, 8, Liassic; 9, Eocene; 10, Recent material.
 Figs. 1, 3. Bodies of *P. polygonalis* type, $\times 1,400$.
 Fig. 2. Micro-fossils released from pyrite grain in shale, $\times 2,000$.
 Figs. 4, 5. Parts of surfaces of spore material showing vesicular formations and a core body. 4, $\times 2,000$.
 5, $\times 2,500$.
 Fig. 6. Partly cleared intermediate sphere from pyrite microberry, Scremerston Coal Group, $\times 3,000$.
 Fig. 7. Pyrite-infilled foraminiferid, transmitted light, $\times 30$.
 Fig. 8. Dispersed cells from solution of pyrite infilling of a foraminiferid, $\times 2,000$.
 Fig. 9. Cells from solution of a pyrite microberry, probably internal cast of a diatom, $\times 2,000$.
 Fig. 10. Cells from solution of pyrite infilling of a foraminiferid, partly or completely cleared, $\times 2,000$.



pyrite. Similar material has been observed in most bulk-prepared samples among the other organic residues but it is so small that it is not easily studied or recorded except when specially prepared. On some spores and other tissues tiny grains of pyrite have left such small cells but no particular relationship of either the pyrite or the small cells to the host material can be determined.

INTERPRETATION OF THE MORPHOLOGY OF THE MICRO-ORGANISMS

Within the variety of material released from the pyrite, the close relationships which clearly exist must now be discussed. It is convenient to consider Groups 1-4 of organic material together first, and Groups 5-6 afterwards, bringing in, where relevant, evidence obtained from sources other than the Liassic rocks.

Micro-fossils, Groups 1-4. Considering the material from isolated simple and compound pyrite spheres (pyrite types (b) and (c)) all gradations are to be found, firstly, from the single sac to the complex group and, secondly, concerning organic material within the sac, from the rough accumulation of small grains to the well-formed microspinose body of the *Pyritosphaera barbaria* type, apparently composed of similar grains. From this it is likely that representatives of two developmental series are present, the one from single to compound sacs and the other of growth of core material within the sac, this being then secondary to the appearance of the sac. It is not thought that the cores represent the residue of normal cell contents. The balance of evidence is against the original occurrence in the shale of the *Pyritosphaera barbaria* bodies free of external sacs, for even if observed solution of some spheres reveals no sacs or only shreds of attached material the grinding involved in the original preparation could have stripped off and destroyed them. Less intensely ground material showed more outer sacs. In transmitted light some isolated pyrite spheres show the presence of a very thin translucent skin at the periphery, external to the sulphide but not affecting the reflecting powers of this mineral on the upper surface of the sphere. Also suggesting the outer position of the sac, the appropriate Liassic sphere when its solution is watched does not usually show the loss of pyrite external to the sac. The tendency for the core body, when fairly well developed, to show attachment to one part of the sac wall, in an off-centre position (Pl. 63, fig. 6), is supported by the way in which many examples of *P. barbaria* have a residual polar cap or tail of attached material.

It is difficult not to regard as further manifestations of the same general phenomenon of sacs with core bodies the vesicles on Liassic spores and pollen which often contain *P. barbaria*. These formations have been shown to be equally associated with pyrite. In fact, in view of the discussion below, it may well be that the isolated saccate forms first originated in association with some plant tissue of which no other trace is now preserved.

Further interpretation and explanation will perhaps in due course be made since this aspect of the work also falls within the scope of current research and publication on the microbiological destruction of plant remains by the author's colleagues, Prof. L. R. Moore, Dr. R. Neves, and Dr. H. J. Sullivan, who are concerned with the effects of what appear to be rather similar ring or vesicle structures (present author's terminology) as one of the factors in the degradation of Carboniferous plants, spores, and pollen. The occurrence in some of these structures of core bodies recognizable as *P.*

barbaria strengthens the homology. Through the kind assistance of Dr. Neves the author was able to examine some typical Carboniferous rock material and observed that while normal maceration yielded abundant organic material of this type, when subjected to the methods described in the present paper a heavy fraction of the rock contained large partly or completely pyritized bodies whose characteristic size and shape showed them to be the same spores. Oxidation and solution of the pyrite revealed intensely vesicular exine previously not visible, with *P. barbaria* in some of the vesicles (Pl. 64, figs. 4, 5), but in the specimens actually observed during solution, while it was confirmed that pyrite occurred within the blister-like vesicles, it could not be ascertained whether any organic cores remained.

An attempt was made to determine the extent to which this pyritic condition in spores and pollen of both Carboniferous and Liassic age is to be associated with the particular secondary structure noted. The search was carried out on unoxidized material, disaggregated mechanically and by non-oxidizing mineral acids: bromine (Neves 1958, p. 3) was not used. Obviously the spores and pollen were not subjected to the usual cleaning and maceration to clarify their surface nature and observation in the detail required was therefore not easy, especially in Carboniferous material. Nothing was observed which demonstrated the existence of the vesicles in an unpyritized condition, and a close association with pyrite must be assumed.

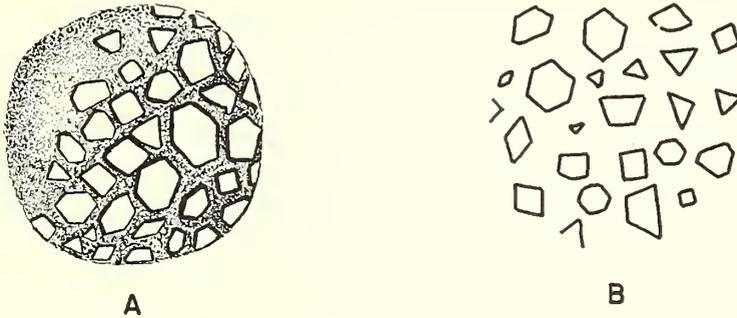
Various Carboniferous marine and non-marine shales and coals gave large yields of the same range of micro-organisms, with abundant *P. barbaria*, as described above. Free-standing compound saccate bodies were, however, distinctly more common in the Lower Jurassic rocks; obvious core bodies were rarer in the Rhaetic. The cause of these variations is not yet understood. In general chambers free of core bodies, whether isolated simple or compound bodies or on other tissue, are few in relation to the occurrence of mature and poorly formed core bodies.

Reconsideration of Pyritella polygonalis Love 1957. After study of the more complex forms of isolated saccate body described above it was found necessary to reconsider the species *Pyritella polygonalis* Love 1957 (p. 434). Although both are obtained from pyrite masses, any similarity between the type material of *P. polygonalis* and the free multisaccate bodies is not immediately apparent. A link was observed, however, through a series of preparations of rocks around the Upper Carboniferous *Gastrioceras subcrenatum* marine band first made for Dr. R. M. C. Eagar (Love 1957, p. 440). Later, more exhaustive study of material obtained from pyrite revealed a range (e.g. Pl. 64, fig. 2) similar to that obtained from the Liassic rocks and also multicellular material showing the characteristics of *P. polygonalis*. This form, in contrast to the diagnosis of the species (op. cit., p. 434), was not always as complete rounded masses but also occurred on fragments of other tissue such as spore exine in the manner of the ring structures already described. Core material occurred in some specimens of this type, some well-developed microspinose bodies of *P. barbaria* being included. On one specimen illustrated (Pl. 64, fig. 3), a margin of unaffected material surrounds the area of polygonal pattern.

Further study of slides containing *P. polygonalis* from the Burdiehouse Limestone of Scotland (the type material) confirmed this observation (Pl. 64, fig. 1) among material which was originally thought to be broken and fragmentary parts of larger bodies. The

regular form of the latter appears in all probability to be that of spores and some less-affected specimens of recognizable spores were in fact noted. The description of the cellular structure originally given, however, needs no amendment. So far, no core bodies have been found in this Burdiehouse Limestone material, although this discovery may yet be made. Their rarity here, and relative abundance elsewhere, is a factor not yet explained. The effect of these observations on the taxonomic status of *P. polygonalis* is discussed below.

The particular feature of the polygonal shape to the vesicles, well shown in Pl. 64, fig. 1, and also on the spore material in Pl. 64, fig. 4, appears to be secondary to the formation of the vesicle, derived from the idiomorphic crystal shape taken up by pyrite. The *P. polygonalis* material when pyritized has shown the remarkable Kiesklümpchen



TEXT-FIG. 1. Comparative camera lucida drawings on same scale of A, *Pyritella polygonalis*, by transmitted light; B, sulphide grains on a Kiesklümpchen body, by reflected light.

texture figured by Neuhaus (1940, p. 319, fig. 6). Here, in distinction from the small regular closely packed small pyrite crystals of the Kieskügelchen (pyrite spheres) the structure is of large, well-spaced angular crystals, up to $10\ \mu$ across. In an earlier study of the type material of *P. polygonalis*, where it abundantly occurs, comparative camera lucida drawings (text-fig. 1) were made in reflected light of pyrite crystals from a typical Kiesklümpchen body, and of the polygonal vesicles in a *P. polygonalis* body from the same rock. That the pyrite outlines were all possible random cross-sections or equatorial outlines of the pyrite cube, octahedron, or pyritohedron makes it not surprising that later it was possible, on observing actual solution, to confirm that each pyrite crystal while becoming steadily smaller, at an early stage revealed the polygonal cells in whose centre, under a covering membrane, each one was situated. At the early stage the outline of the chamber corresponded closely with the shape of the pyrite grain and the process often took place without rupture of the surface membrane. In another instance ultrasonic vibration failed to release pyrite from these bodies (or from normal framboidal spheres), again demonstrating its non-superficial position on them.

In contrast to these forms free of core bodies, the large pieces of spore material such as in Pl. 64, figs. 4 and 5 showed a mixture of pyritic forms from large angular crystals to normal framboidal areas. The latter would be expected where core bodies are present and particularly when they are large. From some present-day data (see Love 1957,

p. 434) it is probable that the pyrite is secondary to some other sulphides and its crystallization may well be governed by physical factors in its immediate environment, to give either a single large crystal in a cell or a framboidal group. Why isolated sacs tend to be filled in the latter way while the vesicles in masses of vegetable tissue tend to the single polygonal form is not understood. Even where a single grain fills a free sac the polygonal shape does not often persist, perhaps because the material is less rigid.

Conclusions concerning Groups 1-4. The two developmental series recognized for the isolated *P. barbaria* and sacs have now been extended to include the other material released from pyrite, some of it clearly secondary developments on plant debris. Of the two possible relationships between the two series the first is that the core material represents the fossilized remains of some investing parasitic or saprophytic micro-organism. In this case the sac is in the position of host. In principle such activity is common at present among lowly organisms, often with a preference for a particular host. Geologically, records are few; that noted by Kidston and Lang (1921) of supposed fungal investment of Devonian plant tissues shows no similarity to the forms under discussion here. In the present instance the host material could perhaps be small algae in the case of the simpler isolated sacs, while in the spores and pollen it could be a pre-existing secondary structure developed in the exine. The somewhat variable proportions of those forms described in different rocks is perhaps a factor in favour of the hypothesis, but the inclusion of saccate forms in which no investing material has conclusively been observed supports the contrary view. This other possibility is that the development of the sacs or vesicles is followed, in a distribution whose controls have not yet been recognized, by development of the core material to form the *P. barbaria* body, all as part of the life-cycle of a single organism.

In either case, both the limited range of the organic forms involved and the environmental evidence to be discussed later imply that a special agency was employed in the pyritization. It may be noted here that over a period of some years the characteristic form of *P. barbaria* has never been obtained by the author from unweathered rock except by the solution of sulphide. The case has already been argued (Love and Zimmerman 1961, p. 891) that the formation of the sulphide ion was part of the life activity of the organisms rather than, after their death, being of external origin or essentially based on the decomposition of their tissue. Furthermore, a distinct association with the degradation of plant material is thought to be shown, in contrast to the subject of the next section.

On morphological grounds, however, the evidence is insufficient to allow a conclusion to be reached on the nature of the organisms. It is not known even to what extent the fossilized material resembles in detail, in its microscopic appearance, its original form. Furthermore, in the combined development series favoured here on the balance of evidence but not regarded as conclusively proved, it is not clear whether the core body has a final separate existence from its sac perhaps as some form of spore. It would not be valid to suppose that it does from the observations so far made, and this would then appear to preclude the individual cells of the core body from being the starting-points of new cycles, the origin of which remains obscure. The observation that the largest forms appear to have a rather looser structure than the others is not accompanied by any evidence of breaking up and dispersing, which would indeed seem impossible

in the undisturbed muds below the interface. Alternatively many lowly organisms form resting bodies under certain, usually unfavourable, conditions. Yet these barely seem appropriate as an explanation of the enormous abundance of the material in dark shales where the activity of the organisms has been so intense.

Taxonomically, any grouping together of the microfossil forms described would involve considerable emendation of the existing genus *Pyritosphaera* and the species *P. barbaria* together with probable suppression of the genus *Pyritella* and inclusion of *P. polygonalis* in the emended species of *P. barbaria*. However, because of the complete lack of knowledge of the systematic position of the whole group, together with uncertainty about the various stages within it, and in view of the fact that current research on present-day sediments may ultimately indicate a solution to these problems, it is proposed that no taxonomic emendation should as yet be made.

Micro-fossils, Groups 5-6. Two problems arise in the interpretation of the micro-fossil material obtained from pyritic foraminiferid infillings and microberries and also from widely scattered minute sulphide grains. One concerns distinction between the former group and the pyrite which yields *P. barbaria* and associated forms. The second problem involves, in more detail, the distinction between the individual granules of organic material from the pyrite of foraminiferids and microberries and the granular material of *P. barbaria*. Two factors help to differentiate the material in the first case. The saccate condition does not seem to exist for the 20-60 μ intermediate spheres forming the pyrite masses in the foraminiferid tests and the microberries, although it commonly occurs with the spheres of the *P. barbaria* series. Furthermore, the core body of the latter, when well formed, remains unbroken after the treatment with acid, as if it were a discrete body, albeit a granular one. The opposite is the case for the spheres from the tests and microberries. It is tentatively concluded that different organisms are under consideration.

This is supported by similar evidence from Carboniferous rocks. From crushed and ground marine shale from the *Gastrioceras cancellatum* horizon of the Axe Edge locality, Derbyshire, many unopened ostracods, mostly pyritized, and also goniatite spat smaller than 100 μ in size were picked out, together with microberries. From within some of the closed shells clusters of pyrite spheres were found lying completely out of direct contact with the rest of the rock material and appearing quite different from the smooth pyrite of the shell walls, from which, in the case of the goniatites, they were separated by a delicate tissue of wall membrane. Also perfect internal moulds of goniatite spat were found composed entirely of spheres and devoid of shell. Material of all these types, and also microberries, gave on solution great quantities of 0.5-1.5 μ clear light granules (Pl. 64, fig. 6), comparable with those described from the Lias. Flattened microberries from Eocene strata, provided by Dr. J. W. Murray, and giving a similar product on solution (Pl. 64, fig. 9), were clearly the infilling of diatom tests of characteristic shape. Current work by Love and Murray demonstrates that pyrite infillings of recent foraminiferids, giving a similar product on solution (Pl. 64, fig. 10) may develop soon after death at the mud-water interface whenever de-oxygenated conditions obtain. It is believed that identification of the micro-organisms involved here may be applicable to the Liassic and Carboniferous test-infillings, so consistent is the appearance of the pyrite and the organisms within it. The origin of the spherical

microberries, of whatever age, is not yet clear. If they are internal moulds of tests well filled with pyrite, no such tests were found in the rocks examined. It is possible, however, that if the test was originally of some soft organic tissue it may have completely decayed.

The small individual granules of microfossil material (Group 6) obtained from isolated and unattached individual small pyrite grains could with equal likelihood have originated as the partly developed cores in the *P. barbaria* series, or as crushed-down material from animal tests broken or otherwise removed even within the rock, or from microberries which may also have such a source. No means is at present known of recognizing their particular origin.

It is clear that on the basis of the evidence of the pyrite material which must have developed within the tests of animals that a particular association with the degradation of animal material is attributable to the micro-fossil or present-day micro-organisms obtained from it. Again there must be some lowly organism involved and indeed the individual granules are of a size range appropriate for bacterial cocci. It might reasonably be expected that differing micro-organisms would be involved in the decay of plant and animal material. It is not proposed at present to attempt to define the taxonomic position of these micro-organisms.

It is likely that the granular organic remains found, after solution of pyrite, within the central chamber of specimens of *Tasmanites* from Liassic rocks may be assigned to this group. These large and distinctive bodies frequently contained small amounts of granular pyrite and could be picked out from the rock material for individual treatment. In all cases observed the pyrite contained organic material, and similar contents of *Tasmanites* appear to have been observed by Eisenack (1958) but no recognizable body of the *P. barbaria* type was found.

ENVIRONMENT OF FORMATION OF THE SULPHIDE

As a control on the validity of any conclusions concerning the micro-organisms drawn from geological or present-day evidence, the available geological information on the environment in which they flourished must be considered. Whatever their nature, they are very abundant, recognizable as simple pyrite spheres, and most characteristic of sedimentary rocks of the dark shale and sapropelic environment (Deans 1948, pp. 348–50). The value of applying such a simple criterion as the presence of micro-fossils to more complex rock groups has already been demonstrated (Love and Zimmerman 1961). Again, Deans has observed pyrite spheres in lesser quantity in the Northampton Sand Ironstone where Taylor (1949, p. 83) regards the limited pyrite formation as having been controlled by the temporary development of stagnancy.

It may be necessary to modify the view put forward earlier by the author (Love 1957, p. 434) that the spheres and associated forms of pyrite and micro-organisms are associated with bottom conditions entirely inimical to aerobic life. Bottom conditions in fact appear to have differed from rock to rock. In the case of the Pumpherstons Shell Bed and Oil Shale of the Scottish Lower Carboniferous sequence evidence was put forward that no aerobic benthonic life existed in the area since only free swimming or floating organisms occur as fossils. In all the beds abundant pyrite spheres were found while the very fine lamination of the sediment was undisturbed.

Related conditions are envisaged by Hemingway (*in* Hallimond *et al.* 1950, p. 68)

for the Jet Rock of the Yorkshire Lias. The beds are regarded as representing muds of slow accumulation under marine conditions in waters which at depth were deoxygenated and rich in H_2S ; as the sea extended at least to Germany the stillness must have been due to the bottom waters lying below the reach of major wave action in the open sea and therefore at some hundreds of feet in depth. The waters were fully marine, even if somewhat isolated from the main ocean. Similarity with the present state and recent history of the Black Sea is apparent.

But it must be considered whether some property of very fine sediments rich in organic matter might enable a strong resistance to deformation to be attained sooner than is generally thought to occur. Unpublished evidence from the author's collection of thin sections of Carboniferous shale sediments suggests that disturbance of a shale layer before deposition of the next may give small disarranged pellets with characters such as the cryptophyllite texture (Dunham *in* Eagar 1952, p. 358) already in their final relationship to the lamination of the pellet rather than that of the undisturbed shale. There is evidence from present-day organic-rich dark muds (J. W. Murray, personal communication) that even at the mud-water interface fine organic material binds up the clay sediment into a relative firmness. Furthermore, mucous-covered burrowers, such as *Arenicola*, which are normally prodigious ingesters of sediment, are strongly inhibited by the presence of much fine clay (Reid 1929). After deposition of the mud these factors might lead to an initially localized deoxygenation whose products would in turn lead to the beginning of the more generally foetid conditions by which other varieties of aerobic burrowers were also inhibited. It may not be necessary therefore to invoke very great depth, or alternatively, unusual climatic conditions such as the absence of all but the gentlest of winds. Some climatic factors, however, may have induced other conditions favourable to the maintenance of long-standing stagnancy over a wide area.

Hemingway regards the Jet Rock as the initial part of an Upper Lias cycle of sediments produced by the shallowing of the deep sea basins which had originated under tectonic control. At the top of the Upper Lias cycle the sands of the Blea Wyke Series yield 'frequent moulds of lamellibranchs, *Pentacrinus* debris and *Serpula* and are characterised by an abundance of worm tubes which ramify through the rock' (op. cit., p. 69). This indicates intense scavenging activity able to remove all digestible organic material from the sediment, an activity which is normal in nature when no restraint is present but which must have been absent in the muds which ultimately gave the shales at the bottom of the sequence. These shales, however, show a steady gradation upwards (op. cit., pp. 68, 69), becoming less pyritic, less well laminated, less dark, and less bituminous; they were probably formed 'in a marine environment which was becoming less stagnant and presumably less deep.' In the Alum Shale Series microscopic pyrite is still found but occasional sideritic mudstones and calcareous concretions appear. Counts of grains in thin sections of typical specimens of the Hard Shales above the Alum Shales, and the Bituminous Shales below, show that the proportion of pyrite spheres and multispheres is about half the value in the Grey Shales, Jet Rock, and Jet Rock Shale. The Alum Shale Series is compared by Hemingway with the Grey Clay of the Black Sea, laid down in an environment appreciably shallower than that of the sapropelic muds and nearer the shore.

There are two ways in which residual organic material may occur in a sediment,

giving a sapropel. Firstly, rapid deposition of organic material without much sediment at a rate in excess of that at which it can be utilized by mud-grubbing and burrowing organisms may cause some to be buried below their reach. Van Andel and Postma (1954) note that the maximum formation of sulphide in the Gulf of Paria at the present time is associated with such conditions, even where fairly strong currents renew the bottom waters. The same is recorded by Neeb (1943) from the East Indies. Secondly, toxicity in the sediment, due to the effects of stagnancy and lack of circulation, will inhibit or prevent at least aerobic organisms. This is due to the exhaustion of available oxygen for oxidation processes by organisms and the ensuing establishment of a chemically 'reducing environment'. It is believed that in the case of the shales in the Upper Lias sequence rapid deposition was not the case: nevertheless the toxicity must have been confined to the well-laminated and undisturbed sediment, for undoubtedly a bottom surface-dwelling fauna was present, however peculiarly limited in variety.

Besides free-swimming ammonites and pelagic micro-plankton living in the upper water, *Inoceramus* is prominent among thin-shelled lamellibranchs, but not common, although it increases in abundance in the Bituminous Shales 'where some horizons become oyster beds' (J. E. Hemingway, personal communication). In the Alum Shales *Nuculana ovum* is found.

In the Rhaetic beds at Garden Cliff and the corresponding ones at Lavernock, Richardson (1905) has presented clear evidence of a bottom-dwelling fauna even from the black shales, including *Pteria contorta*, *Pecten valoniensis*, *Protocardium rhaeticum*, *Gervillia praecursor*, and *Modiola minima*. Hemingway (*in* Hallimond *et al.* 1950) regards this cycle, initiated by the Westbury Beds and passing up through the Sinemurian into the Lower Pliensbachian ironstone shales, and also the Middle Lias cycle culminating in the Cleveland Ironstone Series, to be less well developed than the Upper Lias cycle. Both Hemingway (*op. cit.*, p. 70) and Raymond (1955, p. 16) regard the Rhaetic sea as having been shallower and more restricted in area than that depositing the Jet Rock.

It is probable, then, that the zone of formation of the forms of pyrite described in this paper is within the mud rather than at the mud-water interface of the sediments giving the Lower Jurassic succession. Although a 'sulphuretum', a zone charged with hydrogen sulphide and inimical to aerobic life, may have been present this need not necessarily have lain in the bottom waters if oxygenation of these was sufficient to remove that proportion of the toxic dissolved hydrogen sulphide which passed upwards out of the mud. Perhaps the limited fauna of the Jet Rock is indicative of the effect of the most extreme conditions of toxicity reached in this Series and undoubtedly conditions relaxed in the succeeding Bituminous Shales. Some parallel to this may perhaps be seen in the study by Eagar (1953, p. 341) of the non-marine lamellibranchs in shales of the Upper Carboniferous Lower Foot Mine succession of Goyt's Moss, in which much of the microscopic pyrite occurs as the small spheres under discussion in the present paper. In a series of beds of uniform grain size and composition, distinct changes of shell shape are related by Eagar, with 'probable significance', to the maximum occurrence of pyrite. Despite the latter, the benthonic population of the area appears to have continued. In fact the change downwards from aerobic to anaerobic conditions can take place at any level in the mud and in this connexion references to studies on the behaviour and effect of bacteria in muds were made in earlier papers (Love 1958, p. 435;

Love and Zimmerman 1961, p. 891). Whatever the present organisms may be, the only available records concern bacteria and for these it is clear that at depths of up to fifteen feet into fine subaqueous muds laid down in the absence of current action it is probable that sufficient circulation or migration of iron can occur to allow for much biochemical change and that the chemical system is not a closed one over the distances involved.

REFERENCES

- DEANS, T. 1948. The Kupferschiefer and the associated Lead-Zinc mineralisation in the Permian of Silesia, Germany, and England. *Rep. Int. geol. Congr., 18th sess., Gt. Britain*, Part VII, 340–52.
- EAGAR, R. M. C. 1952. Growth and variation in the non-marine lamellibranch fauna above the Sand Rock Mine of the Lancashire Millstone Grit. *Quart. J. Geol. Soc. Lond.* **107**, 339–73.
- 1953. Additions to the non-marine fauna of the Lower Coal Measures of the North-Midlands Coalfields. *J. Liv. Manchr. geol. Soc.* **1**, 328–69.
- EISENACK, A. 1958. *Tasmanites* Newton 1875 und *Leiosphaeridia* n.g. als Gattungen der Hystrichosphaeridea. *Palaeontographica*, **110**, 1–19.
- HALLIMOND, A. F. *et al.* 1950. The constitution and origin of sedimentary iron ores. *Proc. Yorks. Geol. Soc.* **28**, 61–101.
- HEMINGWAY, J. E. 1934. The Lias of the Yorkshire coast. *Proc. Geol. Assoc.* **45**, 250–60.
- HOWARTH, M. K. 1955. Domerian of the Yorkshire coast. *Proc. Yorks. Geol. Soc.* **30**, 147–75.
- KIDSTON, R. and LANG, W. H. 1921. On Old Red Sandstone Plants showing structure, from the Rhynie Chert Bed, Aberdeenshire. Part V. The Thallophyta occurring in the Peat-Bed; the succession of plants throughout a vertical section of the bed, and the conditions of accumulation and preservation of the deposit. *Trans. roy. Soc. Edinb.* **52**, 855–902.
- LOVE, L. G. 1958. Micro-organisms and the presence of syngenetic pyrite. *Quart. J. Geol. Soc. Lond.* **113** (for 1957), 429–40.
- 1962. Biogenic primary sulfide of the Kupferschiefer and Marl Slate. *Econ. Geol.* **56**, 350–66.
- and MURRAY, J. W. 1963. Biogenic pyrite in recent sediments of Christchurch Harbour, England. *Amer. J. Sci.* In the press.
- and ZIMMERMAN, D. O. 1961. Bedded pyrite and micro-organisms from Mount Isa Shale. *Econ. Geol.* **56**, 873–96.
- NEEB, I. G. A. 1943. The composition and distribution of the samples. *The Snellius Expedition*, **5**, Pt. 3, Sect. II. Leiden.
- NEUHAUS, A. 1940. Über die Erzführung des Kupfermergels der Hasseler und Gröditzter Mulde in Schlesien. *Z. angew. Miner.* **2**, 304–43.
- NEVES, R. 1948. Upper Carboniferous plant spore assemblages from the *Gastrioceras subrenatum* horizon, North Staffordshire. *Geol. Mag.* **95**, 1–18.
- RAYMOND, L. R. 1955. The Rhaetic beds and Tea Green Marl of North Yorkshire. *Proc. Yorks. Geol. Soc.* **30**, 5–23.
- REID, D. M. 1929. On some factors inhibiting the habitat of *Arenicola marina*. *J. Mar. biol. Ass. U.K.* **16**, 109–16.
- RICHARDSON, L. 1905. The Rhaetic and contiguous deposits of Glamorganshire. *Quart. J. Geol. Soc. Lond.* **61**, 385–424.
- TAYLOR, J. H. 1949. Petrology of the Northampton Sand and Ironstone Formation. *Mem. geol. Surv. U.K.*
- VAN ANDEL, T. and POSTMA, H. 1954. Recent sediments of the Gulf of Paria. *Verh. Konink. Ned. Akad. van Wet. afd. Natuurkunde*, **20**, (5).

LEONARD G. LOVE
Department of Geology,
University of Sheffield,
St. George's Square, Sheffield 1

THE SILURIAN TRILOBITE *ENCRINURUS PUNCTATUS* (WAHLENBERG) AND ALLIED SPECIES

by R. P. TRIPP

ABSTRACT. The lectotype pygidium of *Encrinurus punctatus* (Wahlenberg), the type species, is from the Wenlock Series of the Island of Gotland, in which two allied species of *Encrinurus* are present; pygidia are not diagnostic but the size of the lectotype indicates that it should be attributed to the species with larger-sized individuals. An *E. punctatus* species-group is defined; conformity with the basic arrangement of tubercles on cranium and pygidium is a necessary, but not sufficient, criterion of inclusion. The group includes also the following species: *E. macrourus* Schmidt, the smaller species from Gotland; *E. tuberculatus* (Buckland), a name revived for the British Wenlock form commonly referred to *E. punctatus*; *E. stubblefieldi* sp. nov. from the Ludlow Series of Shropshire; *E. onniensis* Whittard from the Upper Llandovery of Shropshire, and *E. deomenos* sp. nov. from the Jupiter Formation of Anticosti Island.

THE terminology used is unaltered from that of my earlier paper (1957, p. 60) except that the term fossula is used for the anterior pit in the longitudinal furrow. Hamada (1959, p. 83) considers the area between the preglabellar furrow and the facial sutures to be a true preglabellar field, but as Temple (1956, p. 424) points out 'a true preglabellar field does not bear the axial part of the facial suture and is not typically separated by furrows from the cheeks'. I agree with Temple in considering this area homologous with part of the anterior border of the cranium in other members of the Cheiruracea.

Previous research. *Entomostracites punctatus* Wahlenberg 1821 has been established as the type species of the genus *Encrinurus* Emrich (1844, p. 16), and the pygidium from the Island of Gotland which Wahlenberg figured has been selected as lectotype (Opinion 537 of the International Commission on Zoological Nomenclature). Rosenstein (1941) has published an excellent account of the Estonian form of the species, but unfortunately her paper is not widely available; she recognized the regularity of arrangement of certain cranial tubercles, and demonstrated that there is a correlation between the positions of the axial and pleural tubercles on the pygidium.

Definition of the E. punctatus species-group. Glabella widening markedly forward. Basal lateral lobes almost obsolete, middle and anterior lateral lobes represented by nodular tubercles; similar lateral tubercles on frontal lobe and false preglabellar field. Pairs of large tubercles placed opposite middle and anterior lateral lobes; two or three main rows on frontal lobe. False preglabellar field ill defined, bearing a single row of large tubercles. Fixigenal spines well developed. A column of median, or occasionally submedian, tubercles on axis of pygidium; typically eight pairs of pleurae each with a tubercle.

The following species are here referred to the group: *E. macrourus* Schmidt, *E. tuberculatus* (Buckland), *E. stubblefieldi* sp. nov., *E. onniensis* Whittard, *E. deomenos* sp. nov. None of the specimens from Scotland attributed to *E. punctatus* fall within the group. No specimens from the mainland of North America have been studied.

System of notation applied to glabellar tubercles. In the present work the system of notation applied to glabellar tubercles by the author in 1957 is adopted (text-fig. 1). The transverse rows of tubercles are numbered I to VI starting from the back; tubercles which occur between the transverse rows are symbolized by the small roman numeral of the row in front; pairs of tubercles are numbered in arabic numerals distally from the centre line. One refinement is necessary: many Silurian species have two tubercles placed one behind the other, between the proximal and lateral tubercles in row III; these tubercles, which may occur singly, are distinguished as III-2* and III-2*. Similarly, the two median tubercles sometimes present between rows III and IV are indicated as iv-0*. The four tubercles in row II are the most consistent in occurrence, but even these are not invariably present (Pl. 66, fig. 8), and adventitious tubercles sometimes occur between them (Pl. 65, fig. 7). Tubercles which occur on over 90 per cent. of the specimens are regarded as regular, while those on 10 per cent.–90 per cent. are recorded in parentheses in the tubercle formula. The regularity of arrangement of the tubercles on the frontal lobe becomes obscured in heavily tuberculated specimens. The presence or absence of tubercles is not dependent on size of individual (text-fig. 2); for example, tubercles iii-0 and III-2 are present on even the smallest British specimens but lacking on some of the larger specimens.

Acknowledgements. This study has been based entirely on museum specimens, and I am greatly indebted to the following institutions and individuals who have taken great trouble in supplying me with material. Mr. A. G. Brighton, Sedgwick Museum, Cambridge; Dr. W. T. Dean, British Museum (Natural History), London (BM); Dr. G. Y. Craig, Edinburgh University (EU); Dr. M. L. K. Curtis, City Museum, Bristol; Professor Carl O. Dunbar, Yale University, New Haven, Connecticut (YU); Mr. J. M. Edmonds, University Museum, Oxford (OUM); Professor T. N. George and Dr. E. D. Currie, Hunterian Museum, Glasgow (HM); Dr. J. Ernhold Hede, Paleontologiska Institutionen, Universitet, Lund; Dr. G. Henningsmoen, Paleontological Museum, Oslo (PIO); Dr. V. Jaanusson, Palaeontological Institute, Uppsala University (PIU); Dr. H. Mutvei, Palaeozoological Dept., Swedish Museum of Natural History, Stockholm (RS); Professor K. Orviku and Dr. R. Männil, Geological Institute, Tallinn, Estonia (PIT); Professor C. Poulsen, Mineralogical & Geological Museum, Copenhagen, Denmark; Mr. J. D. D. Smith, Geological Survey and Museum, London (GSM); Dr. Isles Strachan, Birmingham University (BU); Dr. C. D. Waterston, Royal Scottish Museum, Edinburgh; Dr. J. Ernhold Hede and Dr. V. Jaanusson have kindly read the manuscript and have most willingly provided much useful information and advice. My special thanks are due to Dr. John Temple, who has assisted at every stage in the work.

SYSTEMATIC DESCRIPTIONS

Encrinurus punctatus (Wahlenberg)

Plate 65, figs. 9–11, 13–14; Plate 66, figs. 2–3; Plate 67, figs. 5–8; Plate 68, figs. 7, 8, 10

Entomostracites punctatus Wahlenberg 1821, p. 32, pl. 2, fig. 1* (*non* fig. 1).

Encrinurus punctatus Emmrich 1844, p. 16.

Encrinurus punctatus Nieszkowski 1857, p. 604, pl. 3, figs. 6, 7.

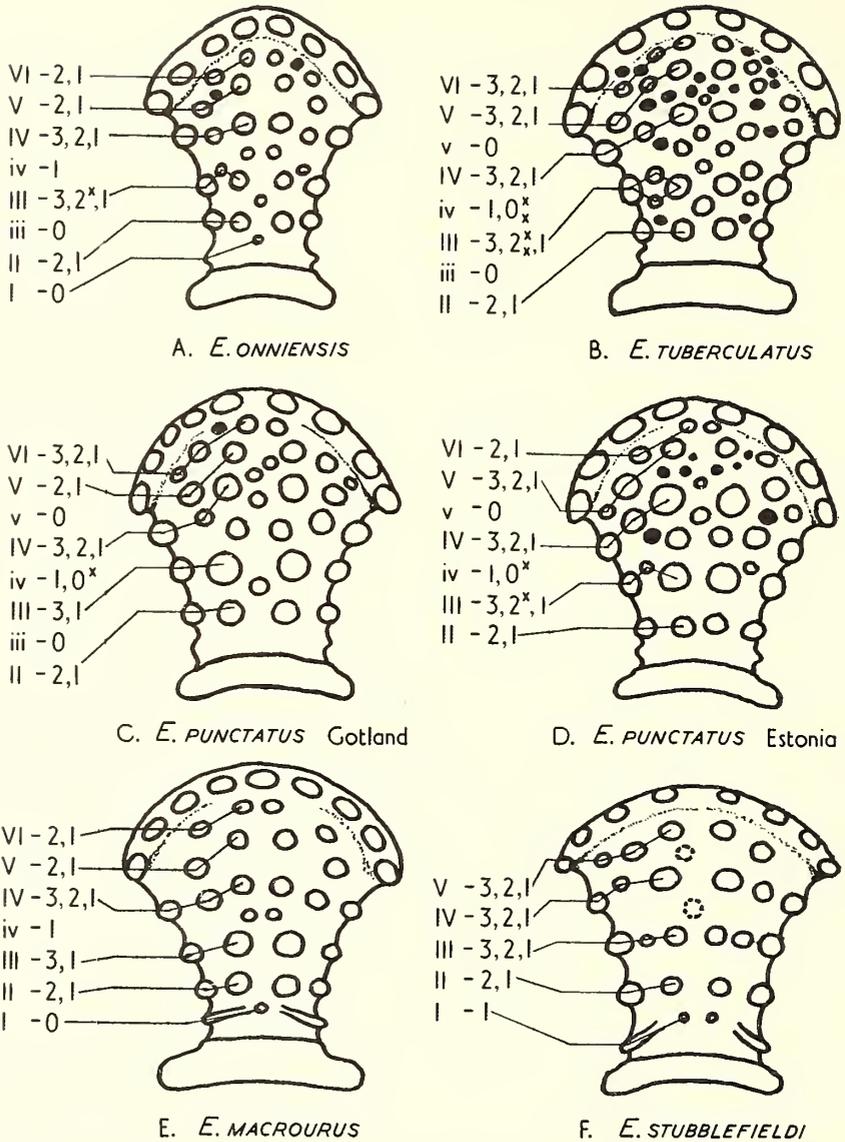
Encrinurus punctatus Schmidt 1881, p. 225, pl. 14, figs. 11–13, pl. 15, fig. 18.

Encrinurus punctatus Lindström 1901, p. 56, pl. 4, figs. 4–9, 12, 13.

Encrinurus punctatus Öpik 1937, p. 118, pl. 25, fig. 5.

Encrinurus punctatus Rosenstein 1941, p. 49, pl. 1, figs. 1–11; pl. 2, figs. 1–3, 5, *non* 4–4b; pl. 3, figs. 1–10.

Diagnosis. Glabella strongly convex, standing well above cheeks; cheeks narrow.



TEXT-FIG. 1. Arrangement of glabellar tubercles in certain species of the *E. punctatus* group. A, *E. onniensis* Whittard, Shropshire, after the syntype OUM C1 (Pl. 65, fig. 16). B, *E. tuberculatus* (Buckland), Worcestershire, after BM In. 48007 (Pl. 65, fig. 7). C, *E. punctatus* (Wahlenberg), Gotland, after RS Ar. 20320 (Pl. 65, fig. 9). D, *E. punctatus* (Wahlenberg), Estonia, after PIT Tr 1921 (Pl. 65, fig. 14). E, *E. macrourus* Schmidt, Gotland, after RS Ar. 30445 (Pl. 65, fig. 4). F, *E. stubblefieldi* s. nov., Shropshire, after GSM 36846 (Pl. 65, fig. 12). Tubercles regarded as adventitious are shaded.

Axial furrows deep and narrow. False preglabellar field rarely with a median tubercle. Central body of hypostome strongly convex anteriorly, with median lobe not projecting beyond anterior border.

Lectotype. PIU 1200 (pygidium figured Wahlenberg 1821, pl. 2, fig. 1*). Selected and figured by Tripp and Whittard 1956, p. 259, pl. 3, figs. 1, 2. Gotland.

Dimensions:

Length of pygidium (excluding articulating half-ring) 13·6 mm.

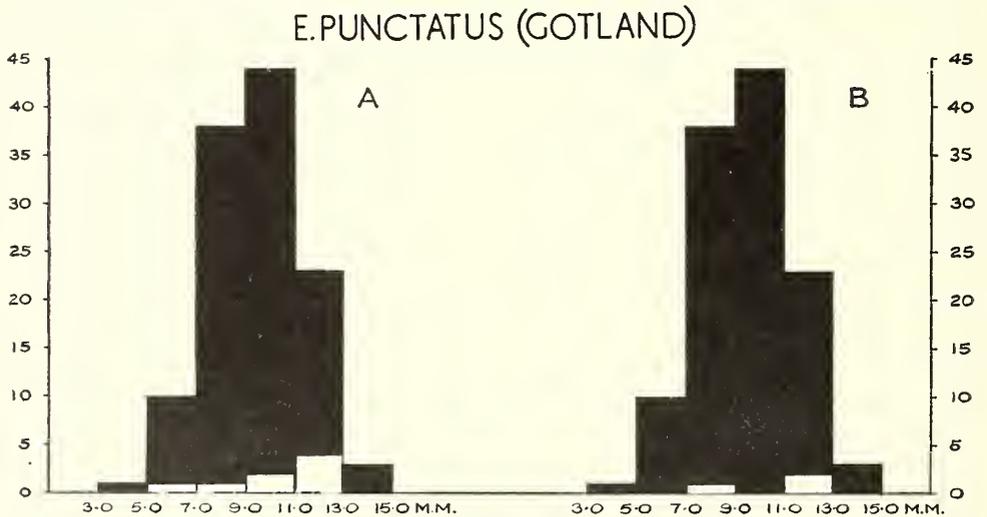
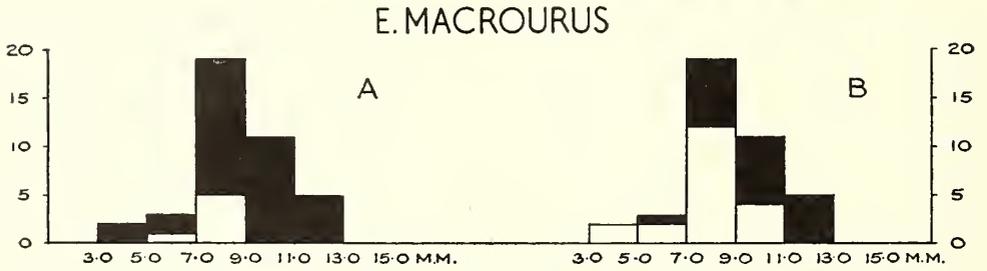
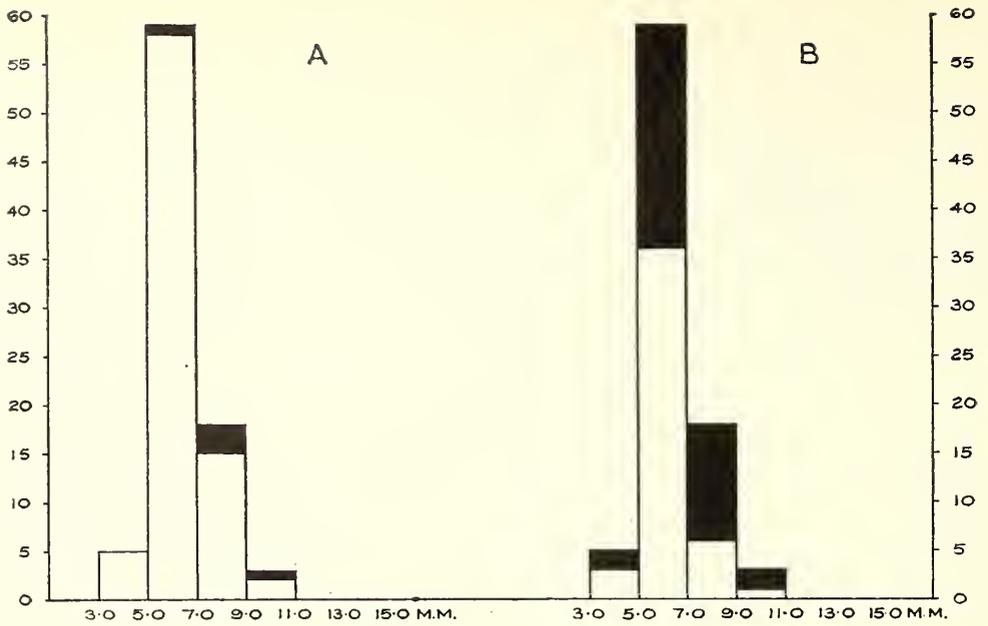
Width of pygidium 14·5 mm.

Width of axis at front 4·5 mm.

Occurrence. In Gotland as follows: Upper Visby Marl (Upper Llandoverly), Visby. Högklint Group (Wenlockian), Visby; Lansä, Fårö. Slite Group (Wenlockian), Barabacke; Biskops; Eskelhem; Fardume; Follingbo; Klintsvärn; Lergravsviken; Medebys; Myrsjö; Omkr; Slite; Stave; Stormyr; Tjelders; Tofta; Underifrån; Utbunge; Västerhejde; Västergarn; Wallstena. In Estonia as follows: Jaani Marl (J₁), Island of Saaremaa. In Norway as follows: Stage 8d (*Monograptus riccartonensis* Zone), Malmøya.

Description. Cephalon elliptical in outline, strongly convex. Glabella strongly rounded in outline anteriorly, narrowing steadily and strongly backwards to about two-thirds its anterior width; moderately convex longitudinally, strongly convex transversely. Glabella rises well above cheeks at back. Basal glabellar lobe consists of low lateral ridges and an occasional small median tubercle. Middle and anterior lateral lobes represented by nodular tubercles; similar lateral tubercles occur on frontal lobe and on false preglabellar field. These four pairs of tubercles overhang axial furrows. Middle and anterior furrows mere depressions between tubercles. Frontal lobe long. False preglabellar field continuous with glabella in convexity; preglabellar furrow broad and shallow laterally, dying out mesially. Occipital ring moderately arched transversely, considerably broader than posterior part of glabella, somewhat flattened longitudinally; occipital furrow shallow, bowed gently forwards mesially. Axial furrows deep and narrow, deepening abruptly opposite preglabellar furrow and continuing at full depth on to free cheeks; small fossulae at about own diameter behind facial sutures. Apodemes near extremities of lateral glabellar and occipital furrows, immediately inside junctions with axial furrows; occipital pair transversely elongate, basal pair a short distance in front; middle and anterior pairs smaller. A pair of small pits in corresponding positions in preglabellar furrow. Tubercles are usually hemispherical, and sometimes granular; tubercles usually perforate; a single perforation at summit of glabellar tubercles, several perforations may be present on other tubercles. Glabellar tubercle formula: (1-0); II-1, 2; (iii-0); III-1, (2*), 3; iv-(0*), 1; IV-1, 2, 3; v-(0); V-1, 2, (3); VI-1, (2, 3). Tubercle 1-0 is small, placed close behind row II. Eight, nine (never with one central), or ten tubercles on false preglabellar field; small additional tubercles occasionally present.

Fixed cheeks strongly convex, sloping steeply outwards. Palpebral lobes lingulate, almost vertical, rising higher than glabella, situated close to glabella, mid-length opposite middle lateral furrows; palpebral furrows broad and shallow. Posterior borders short (sag.) and transverse proximally, expanding steadily beyond mid-width and curving backwards; a small articulating ledge at back. Posterior border furrows broadest near



TEXT-FIG. 2. Histograms illustrating occurrence of certain tubercles in *E. tuberculatus*, *E. punctatus*, and *E. macrourus*.

Ordinate—number of specimens. A, shaded—with tubercle iii-0; A, unshaded—without tubercle iii-0. B, shaded—with any of the four III-2* tubercles; B, unshaded—without any of the four III-2* tubercles.

Abscissa—length of cranium in mm.

mid-width of cheeks. Lateral borders moderately wide, uniting with posterior borders to form slender fixigenal spines, which are directed backwards and slightly outwards and extend to the fifth thoracic segment. Doublure narrow, widening at genal angles. Anterior branches of facial sutures curve forwards and inwards, crossing axial furrows and separating false prelabellar field from pseudoglabellar areas of free cheeks; posterior branches curve outwards and backwards, crossing lateral borders opposite occipital furrow. Fixed cheeks tuberculate and shallowly pitted (particularly laterally); a column of four large tubercles overhanging axial furrow. Base of palpebral lobe faintly tuberculate. Posterior borders usually smooth, occasionally with a row of low tubercles; a few tubercles near bases of fixigenal spines.

Eyes pedunculate, large, visual surface occupies upper half of lobe. Free cheeks large, sloping almost vertically downwards. Pseudoglabellar areas moderately long (exs.) and gently convex. Axial furrows deep, continuous with border furrows. Borders widen gradually forward to axial furrows, and narrow out rapidly in front of pseudoglabellar areas. Lateral border furrows broad and shallow. Broad depressions run inwards and forwards from axial furrows, separating pseudoglabellar areas from borders. Doublure convex, narrowing forwards and backwards from axial furrows, equal to border in width and sharply upturned proximally. Shallow lateral vincular grooves for accommodation of extremities of posterior thoracic segments when enrolled extend back from mid-length of cheeks. Inner areas of cheeks shallowly pitted, with an irregular arc of four or five tubercles near eyes and one or more tubercles laterally. Tubercles scattered two-deep on pseudoglabellar areas. Lateral borders with a main row of seven tubercles increasing in size forwards, and a smaller, less regular, outer row. Borders and border tubercles more coarsely granular than rest of cephalon.

Rostral plate cuneiform, but very variable in shape, narrow, held in an almost vertical position between free cheeks, projecting downwards together with adjacent parts of free cheeks; truncated by rostral suture, occasionally bearing small tubercle; swollen and granular forwards, inturned and narrowing out between doublures of free cheeks at forefront.

Hypostome diamond-shaped, four-fifths as wide as long, broadly rounded anteriorly. Central body oval, three-quarters length of hypostome, moderately convex in both directions; longitudinal median lobe projecting and reaching to anterior border, widening slightly and fading out towards back. Maculae strongly swollen, smooth. Anterior border short (exs.), thickened and flexed ventrally downwards at median lobe; border furrow broad laterally, narrowing mesially. Anterior wings large, sloping obliquely upwards, backwards, and outwards, truncate laterally; a rounded wing process near margin. Postero-lateral extensions of wings strongly upturned. Lateral borders narrow, subparallel for a short distance, converging and increasing steadily in width posteriorly, produced into an ogive-shaped tongue. Lateral doublure widens anteriorly to form posterior wings, and posteriorly beneath tongue. Surface of central body and tongue finely granular.

Thorax about one and a third times length of cephalon, composed of eleven segments. Axis one-third anterior width of thorax, gently arched transversely, narrowing comparatively little towards back. Axial rings weakly convex from front to back, bowed forwards mesially, with faint lateral nodes. Articulating half-rings and furrows strongly developed; stout apodemes near extremities of articulating furrows. Indications of a

broken spine, or a tubercle, on tenth ring. Axial furrows shallow and narrow. Pleurae straight and horizontal to mid-width, directed more or less strongly backwards and downwards laterally. Posterior pleurae bent more strongly downwards and less strongly backwards at fulcrum, which is placed nearer axis. Inner parts of pleurae composed of a broad, gently convex, posterior band, separated by a sharp furrow from a narrow (exs.), depressed anterior band; a ledge at back of posterior band narrows out before fulcrum, and serves to articulate with anterior band of adjacent segment along a slightly sinuous suture line. Laterally, posterior band broadens, pleural furrow narrows, and bevelled articulating facets develop between band and furrow, anterior band forming a narrow border. Lateral margins of posterior bands rounded, lateral margins of articulating facets oblique. (Appearance of internal moulds differs considerably from that of testate specimens in that pleural furrows and ledges are broader, due to differential thickness of shell.) A low tubercle usually placed near fulcrum, successive pleurae sometimes with tubercles placed alternately nearer and farther from axis; additional tubercles sometimes occur.

Pygidium excluding mucro longer than cephalon, triangular, approximately as long as wide. Axis weakly arched transversely, narrowing steadily backwards, ill defined posteriorly. First ring the most strongly developed, confluent with first pair of pleurae on external, but not on internal, surface; first ring furrow continuous, but shallower mesially than laterally. Subsequent ring furrows more or less discontinuous mesially, becoming successively shorter and fainter towards back, hindmost obscure; between twenty and thirty rings can usually be counted. Articulating half-ring and furrow almost as long as first ring. Axial furrows moderately deep posterior to first pleurae, dying out posteriorly. Pleural lobes comparatively wide and moderately convex, sloping downwards with variable steepness, which increases towards back. Eight pairs of raised ribs which widen slightly laterally; ribs broad and flattened on external surface, narrow on internal moulds. First seven pairs of ribs terminate bluntly on lateral margins, eighth die out just beyond apex of axis. Interpleural furrows deep and moderately broad proximally, becoming shallower and narrower laterally; seventh pair do not reach lateral margins. Comparative width of ribs and furrows not consistent between specimens. Mucro of moderate length sometimes developed. Anterior half-pleurae short (exs.), marked off by sharp furrows. Bevelled articulating facets develop laterally between half-pleurae and first ribs, as on thoracic segments. Doublure widens towards back; inner margins converge less strongly in posterior one-fourth of their length and meet at an acute angle opposite apex of axis. Doublure granular; a row of five or more perforations pierce test horizontally at extremities of pleurae and along mucro (Rosenstein 1941, pl. 2, fig. 5). Axis of pygidium bears a row of six or seven median tubercles, spaced out at backwardly decreasing intervals. Pleurae bear a tubercle either close to axial furrow, or placed laterally, occasionally in both or intermediate positions. Size of pleural tubercles varies greatly between specimens. Smallest pygidium (2.3 mm. in length) has a short slender mucro; only seven pairs of pleurae present.

Remarks. Dr. J. Ernhold Hede has kindly studied the lectotype pygidium. He states that it is from beds which are certainly younger than the Upper Visby Marl and older than the Klinteberg Group; that its age is without doubt Wenlockian, and that it is most probably from the Höglint Group (for stratigraphical table see Hede 1960, pp. 47-52).

Two species of *Encrinurus* of the *punctatus* type occur in the Wenlock Series of Gotland, and unfortunately the pygidia cannot be distinguished morphologically. The most common is a comparatively large form, with 2σ limits for length of cranidium of 4.8–12.5 mm., compared with 4.0–8.4 mm. for the smaller species. The lectotype is a large non-mucronate pygidium measuring 13.6 mm. in length; comparison with entire specimens shows that the length of the cranidium is 15–20 per cent. less than that of the pygidium, indicating a cranial length of 10.8–11.6 mm. for the type.

It is reasonably certain, therefore, that the type pygidium is conspecific with the larger cranidia. Such morphological evidence as is available—the greater convexity for instance—supports this view. The smaller form is referred to *E. macrourus* (see below), a species which becomes common in the Ludlow series.

Specimens of *E. punctatus* from the Högklint Group, the Slite Group and Estonia differ in size and there are considerable variations in the arrangement of glabellar and preglabellar tubercles (see Table 1). The posterior tongue of the hypostome from Estonia, figured Pl. 67, fig. 5, is short, though slightly abraded.

Encrinurus tuberculatus (Buckland)

Plate 65, figs. 5–8; Plate 66, figs. 4–11; Plate 67, figs. 9–10; Plate 68, figs. 4–6

Calymène variolaire Brongniart 1822, pl. 1, fig. 3a (non fig. 3b).

Asplus tuberculatus Buckland 1836, vol. 2, p. 74, pl. 46, fig. 6. (=pl. 1 fig. 3a in Brongniart 1822).

Cybele punctata Fletcher 1850, p. 158, pl. 32, figs. 1–5.

Encrinurus punctatus Salter 1853, p. 6, pl. 4, figs. 15, 16 (non fig. 14).

Diagnosis. Glabella strongly convex, standing well above cheeks. Axial furrows deep and narrow. Glabella strongly tuberculate. Rostral plate protuberant. Central body of hypostome weakly convex anteriorly with median lobe ‘waisted’, not projecting beyond anterior border.

Holotype. Specimen figured by Buckland 1836, pl. 46, fig. 6 (dorsal shield). Present whereabouts unknown. Wenlock Limestone, Dudley, Worcestershire.

Occurrence. In Britain as follows: Woolhope Limestone, Malvern Tunnel, Worcestershire. Wenlock Limestone and Shale, Dudley, Worcestershire; Much Wenlock, Shropshire; Colwall and Malvern, Herefordshire; Walsall, Staffordshire; Pen-y-lan, near Cardiff, Glamorgan.

Description. Cheeks broader compared with glabella than in type form. Glabellar tubercle formula (I-0); II-1, 2; iii-0; III-1, 2*, 3; iv-0*, 1; IV-1, 2, 3; v-0; V-VI-1, 2, 3. Adventitious tubercles commonly occur particularly on the frontal lobe. Typically with eight tubercles on false preglabellar field. Eye lobes more slender and higher, and situated further forward—opposite anterior lateral glabellar lobes—and farther from glabella. A conspicuous row of tubercles at base of palpebral lobe. Pseudoglabellar areas of free cheeks longer (exs.), tubercles sometimes three-deep. Front part of the appropriately named rostral plate, together with adjacent parts of cheeks, projects forwards and downwards like a beak. Hypostome more strongly rounded in anterior outline; longitudinal convexity weak anteriorly. Median lobe not projecting beyond anterior border, more strongly arched transversely, longer and distinctly ‘waisted’ near mid-length. Anterior border of hypostome flexed more strongly mesially. Posterior tongue longer. Central

body and tongue more coarsely granular; numerous smooth, transverse depressions on central body may be areas of muscle attachment.

Axis of thorax less than one-third width of thorax anteriorly. Indications of a median broad-based axial spine almost always present on tenth thoracic ring, sometimes also on seventh, ninth, or eleventh rings. When preserved spine curves backwards and extends for about one and a half times width of ring. Mucro of pygidium usually of moderate length, sometimes upcurved, never absent.

Remarks. Buckland's explanation of his pl. 46, fig. 6 is as follows: 'Asaphus tuberculatus; a highly ornamented species from the Transition lime-stone of Dudley; in the collection of Mr. Johnson, of Bristol. The back alone is composed of flexible plates.' (Curtis.) Parts of Mr. Jas. R. Johnson's Collection are in the City Museum, Bristol, and in the British Museum (Natural History), but there is no trace of this specimen.

Many specimens of *E. tuberculatus* and *E. macrourus* are preserved with the hypostome in position. The hypostome fits exactly against the doublure of the cephalon along the sinuous hypostomal suture, the rostral plate and adjacent parts of the free cheeks

EXPLANATION OF PLATE 65

All photographs are of testate specimens unless otherwise stated. The specimens were coated with ammonium chloride before being photographed.

Figs. 1-4. *Encrinurus macrourus* Schmidt. 1, Klinteberg Group (Lower Ludlovian), Eksta, Gotland. RS Ar. 30206, $\times 4$. The median preglabellar tubercle off-centre. 2, Högkint Group (Wenlockian), Kappelshamn, Gotland. PIU, $\times 5$. The median preglabellar tubercle off-centre. 3, Klinteberg Group (Lower Ludlovian), Eksta, Gotland. RS Ar. 30673, $\times 6$. 4, Hemse Group (Lower Ludlovian), Petesviken, parish of Hablingbo, Gotland. RS Ar. 30445, $\times 6$. No inter-row tubercles present; eight preglabellar tubercles.

Figs. 5-8. *Encrinurus tuberculatus* (Buckland). 5, Wenlock Limestone, Dudley, Worcestershire. OUM C368, $\times 4$. Sparsely tuberculated specimen. 6, Wenlock Shale, Malvern, Herefordshire. GSM Z.4103, $\times 3$. A typical specimen; inter-row tubercles iv-0*, 1 present. 7, Wenlock Shale, Malvern, Herefordshire. BM In. 48007, $\times 4$. Heavily tuberculated specimen, with adventitious tubercles in row II. 8, Wenlock Limestone, Dudley, Worcestershire. GSM 36304, $\times 3\frac{1}{2}$. Five preglabellar tubercles on the right side.

Figs. 9-11. *Encrinurus punctatus* (Wahlenberg). 9, Slite Group (Wenlockian), Eskelhem, Gotland. RS Ar. 20320, $\times 3$. Five preglabellar tubercles on the left side. 10, Slite Group (Wenlockian), Follingbo, Gotland. RS Ar. 47293, $\times 4$. Heavily tuberculated specimen; probably ten preglabellar tubercles. 11, Högkint Group (Wenlockian), 'Vattenfallet' (the 'Waterfall'), Visby, Gotland. RS Ar. 30479, $\times 3$.

Fig. 12. *Encrinurus stubblefieldi* sp. nov., 'Upper Ludlow Shales,' Whitcliff, Shropshire, GSM 36846 (the holotype), $\times 6$. Internal mould.

Figs. 13-14. *Encrinurus punctatus* (Wahlenberg). Jaani Marl, Jaani, Saaremaa, Estonia. 13, PIT Nr 1920, tubercle iii-0 lacking. 14, PIT Tr 1882 (Bölauf Collection), $\times 3$. Exceptionally large specimen; figured by Rosenstein 1941, pl. 1, figs. 1-4.

Fig. 15. *Encrinurus* sp. Damery Beds, Woodford, near Tortworth, Gloucestershire. BM In. 54000, $\times 4$. Internal mould.

Fig. 16. *Encrinurus omniensis* Whittard. Purple Shales (Upper Valentian), Onny River Section, near Cheney Longville, Shropshire. OUM C1, $\times 4$. Internal mould.

Figs. 17-20. *Encrinurus variolaris* (Brongniart). 17, Wenlock Limestone, Dudley, Worcestershire. BU 723 (Holcroft Collection), $\times 4$. Note coalescence of a pair of tubercles in row I. 18, Wenlock Shale, Malvern, Herefordshire. OUM C372, $\times 5$. 19, Wenlock Limestone, Dudley, Worcestershire. BU 724 (Holcroft Collection), $\times 8$. 20, Wenlock Limestone, Dudley, Worcestershire. BU 725 (Holcroft Collection), $\times 4$. A median tubercle in row I.



1



2



3



4



5



6



7



8



9



10



11



12



13



14



15



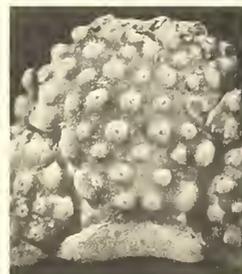
16



17



18



19



20

projecting downwards in conformity with the median flexure of the anterior border of the hypostome. When held in this position the wing processes appear to be in contact with the fossulae (Pl. 67, fig. 2) and the tip of the tongue lies opposite the posterior margin of the occipital ring and comparatively close to it (Pl. 66, fig. 4b). The proximity of the projecting rostral plate to the median lobe of the hypostome would prevent any appreciable rocking action, so practically no movement can have been possible. The same condition applies in the case of *E. variolaris* (Brongniart); Temple (1954, p. 317) writes: 'The cephalon and hypostome of *E. variolaris* seem to have formed together a rigid whole, for it is unlikely that any movement could have taken place during life along the curved hypostomal suture or the facial sutures, although there may have been sufficient elasticity in the integument to allow a very small amount of bending to occur.'

Rosenstein (1941, p. 60) demonstrated that in Estonian *Encrinurus* pygidia there is a correlation between the positions of the axial and pleural tubercles; 94 per cent. of specimens with the first tubercle on the first ring have the tubercle on the second pleurae farther from axis than the others; 75 per cent. of specimens with the first tubercle on the second ring have the tubercle on the third pleurae the farthest from the axis. The percentage of specimens which demonstrate this correlation is much larger in *E. punctatus* than in *E. tuberculatus*, even when specimens which show a slight displacement, or a displacement on one side only, are included (see Table 1).

The synonymy of *E. punctatus calcareus* Salter (1853, p. 6) cannot be established at present. Woolhope is the principal, if not the only, locality mentioned by Salter, but there are no specimens from the Woolhope Inlier in the collections studied.

Encrinurus macrourus Schmidt

Plate 65, figs. 1-4; Plate 66, figs. 1a-c; Plate 67, figs. 1-4; Plate 68, figs. 1-3, 9

Encrinurus punctatus var. *macrourus* Schmidt 1859, p. 438.

Encrinurus punctatus Rosenstein 1941, pl. 2, figs. 4-4b.

Diagnosis. Glabella widening strongly towards front, weakly convex, rarely rising above cheeks at back. Axial furrows broad. Usually nine tubercles on false preglabellar field, one medial. Central body of hypostome weakly convex anteriorly, with median lobe projecting beyond anterior border.

Lectotype. PIT Tr 1905 (thorax and pygidium). Pl. III, figs. 4a, b. Hemse Group (*Lower Ludlovian*), Petesviken, parish of Hablingbo, Gotland. Selected hereby.

Dimensions:

Length of pygidium (extremity broken)	9.0 mm.
Width of pygidium	7.8 mm.
Anterior width of axis	2.9 mm.

Occurrence. In Gotland as follows: Lower Visby Marl (Upper Llandovery)?; Norderstrand. Upper Visby Marl (Upper Llandovery), Lummelunda; Visby. Högklint Group (Wenlockian), Kapelshamn; Visby. Slite Group (Wenlockian), Klintsgvarn; Slite. Mulde Marle (Wenlockian), Fröjel. Klinteberg Group (*Lower Ludlovian*), Eksta. Hemse Group (*Lower Ludlovian*), Garsby; Kvinngårde; Linde; Petesviken; Sandarve; Visne Myr.

Description. Differs from *E. punctatus* in the following features. Dorsal shield less vaulted. Glabella widens more strongly anteriorly and is less convex rarely rising above

height of cheeks at back. The four pairs of lateral tubercles tend to be smaller. Fewer tubercles on glabella; tubercles conical or hemispherical. Glabellar tubercle formula: (1-0); II-1, 2; III-1, (2*), 3; iv-(0*, 1); IV-1, 2, 3; (v-0); V-1, 2, (3); VI-1, (2, 3). Basal lateral ridges more distinct. Typically with nine tubercles on false preglabellar field, one medial. Axial furrows broader, curving more strongly inwards. Fixed cheeks less convex sloping gently inwards to axial furrows; proximal tubercles smaller than others, not overhanging axial furrows. Eye lobes more slender placed farther apart. Pseudoglabellar areas of free cheeks shorter, bearing fewer tubercles, marked off from borders by fainter depressions. Rostral plate broader and shorter, subpentagonal, usually with a tubercle proximally; swollen forwardly. Central body of hypostome less convex anteriorly; median lobe broader, with less independent convexity and projecting forwards beyond anterior border; maculae less inflated. Median part of anterior border of hypostome less thickened and less flexed; anterior border furrow narrow, faint medially. Central body and tongue more coarsely granular. Usually with a tubercle, rarely a spine, on tenth thoracic ring, sometimes on seventh or on both. Spaces between pleural ribs of pygidium sometimes exceptionally broad with low, faintly granular ridges running parallel to the ribs.

Exoskeleton tends to be preserved enrolled, with hypostome in place. In this position the pygidium lies neatly against the doublures of the free cheeks, the projecting rostral plate fitting into the narrow V formed by the inner margins of the pygidial doublure (Pl. 66, fig. 1).

Remarks. Pygidia of *E. punctatus* and *E. macrourus* show so great a range of variation in convexity, length of mucro, strength of axial and interpleural furrows, size, number, and position of tubercles that specific differentiation is impossible. Whittard (1938, p. 119) has already drawn attention to the value of the hypostome and rostral plate in distinguishing species of *Encrinurus*.

The low ridges described above as running parallel to the ribs in the pygidia (Pl. 67,

EXPLANATION OF PLATE 66

- Figs. 1a-c. *Encrinurus macrourus* Schmidt. Klinteberg Group (Lower Ludlovian), Eksta, Gotland. RS Ar. 30206, $\times 3$. Enrolled dorsal shield. Dorsal, lateral, and frontal views; see Pl. 65, fig. 1.
- Figs. 2-3. *Encrinurus punctatus* (Wahlenberg). 2a, b, Slite Group (Wenlockian), Follingbo, Gotland. RS Ar. 30221, $\times 3$. Enrolled dorsal shield. Dorsal and lateral views. Fig. 3. Slite Group (Wenlockian) Eskelhem, Gotland. RS Ar. 20320, $\times 2\frac{1}{2}$. Dorsal shield. Frontal view: see Pl. 65, fig. 9.
- Figs. 4-11. *Encrinurus tuberculatus* (Buckland). 4a-c, Wenlock Shale, Malvern Tunnel, Herefordshire. OUM C318 (Grindrod Collection), $\times 4$. Cephalon. Dorsal, lateral and anterior views. 5, Wenlock Shale, Dudley, Worcestershire. BM I 2160, $\times 2$. Cephalon and thoracic segments. 6, Woolhope Shale, Malvern, Herefordshire. BU 727 (Ketley Collection), $\times 3\frac{1}{2}$. Incomplete dorsal shield. Lateral view showing impression of axial spine on tenth thoracic ring and upturned pygidial mucro. 7, Wenlock Limestone, Dudley, Worcestershire. EU A 133, $\times 2$. Cranidium with basal lateral ridges well developed; palpebral lobe strongly tuberculate. 8, Wenlock Limestone, Malvern Tunnel, Herefordshire. BM In. 42623, $\times 3\frac{1}{2}$. Specimen with three instead of the usual four tubercles in row II of the glabella. 9, Wenlock Limestone, Dudley, Worcestershire. BU 728 (Ketley Collection), $\times 2$. Pygidium. Lateral view, showing articulating facet. 10, Wenlock Shale, Malvern, Herefordshire. OUM C160 (Grindrod Collection), $\times 2$. Elongate dorsal shield. 11, Woolhope Shale, Malvern, Herefordshire. BU 729 (Ketley Collection), $\times 2$. Thorax and pygidium. Axial spine on tenth thoracic ring.



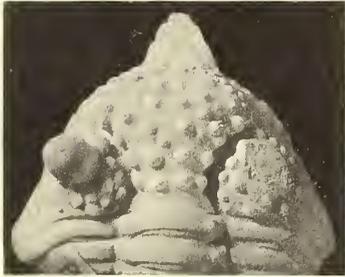
1a



1b



1c



2a



2b



3



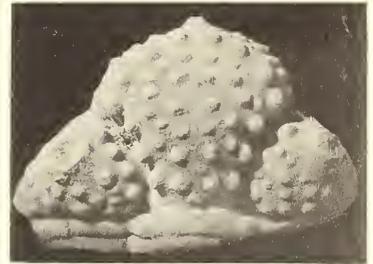
4c



5



4b



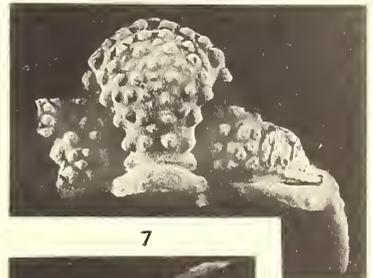
4a



6



10



7



8



9



11

fig. 3) are considered homologous with the anterior bands of pleurae in cybelid pygidia, indicating that the ribs are equivalent to the posterior bands only, not to the fused posterior band of one pleura and the anterior band of the next, the generally accepted view first promulgated by Barrande (1852, pp. 216-17).

Encrinurus stubblefieldi sp. nov.

Plate 65, fig. 12; Plate 67, figs. 14-15; Plate 68, fig. 11

Diagnosis. Cranium broad, weakly convex. Basal lateral ridges of glabella well developed; only two rows of tubercles on frontal lobe. Eight tubercles on false preglabellar field. Seven pairs of pleurae in pygidium.

Holotype. GSM 36846 (internal mould of cranium). Pl. 65, fig. 12; Pl. 67, fig. 15. 'Upper Ludlow Shales', Whitcliff, Shropshire.

Dimensions:

Median length of cranium	5.6 mm.
Width of cranium (est.)	22.5 mm.
Width across false preglabellar field	5.2 mm.
Width of glabella across basal lobes	3.2 mm.

Paratype. GSM 36844 (internal mould of cranium, thoracic segments, and pygidium). Pl. 67, fig. 14. 'Upper Ludlow Shales', N. E. Pilliard's Barn, Shropshire.

Occurrence. 'Lower Ludlow Shales'. Leintwardine, Shropshire. 'Upper Ludlow Shales', Whitcliff and N.E. Pilliard's Barn, Shropshire.

Description. Differs from *E. punctatus* in the following features. Cranium is broad and only weakly convex. Glabella widens less towards front. Glabellar tubercle formula: I-1; II-1, 2; (iii-0); III-1, 2 (*), 3; iv-(0*, 1); IV-1, 2, 3; (v-0); V-1, 2, (3). Basal lateral ridges extend to a median pair of tubercles or a single tubercle. Axial furrows broader and shallower. Cheeks broader compared with glabella. Palpebral lobes placed farther from glabella; palpebral furrows deeper and broader. Tubercles on cheeks smaller and more numerous. Fixigenal spines and adjacent borders much broader. Posterior borders finely tuberculate. Thorax narrower than cranium and narrowing more strongly towards back. Axis less than one-third anterior width of thorax. No indication of presence of axial spines. Pleural tubercles larger, situated at varying distances from axis. Pygidium shorter, composed of about eighteen rings and seven pairs of pleurae. Three or four axial tubercles, first on third ring. Pleural tubercles faint, placed fairly close to axis. Mucro slender, about half length of axis.

Remarks. No described species appears to be closely related to *E. stubblefieldi*.

Encrinurus omniensis Whittard

Plate 65, fig. 16; Plate 67, fig. 16

Encrinurus omniensis Whittard 1938, p. 118, pl. 4, figs. 6-10 (*non* fig. 11).

Diagnosis. Glabella pyriform, narrow, less elevated than cheeks at back. Eight tubercles on false preglabellar field. Eye lobes small.

Syntypes. GSM 55488 and 55489 (counterparts of an exoskeleton); OUM C1 (internal mould of a dorsal shield).

Occurrence. Purple or Hughley Shales (Upper Llandovery), Onny River Section, near Cheney Longville, Shropshire.

Remarks. The glabellar tubercle formula of the syntype OUM C1 (Pl. 65, fig. 16; Pl. 67, fig. 16) is as follows; 1-0; II-1, 2; iii-0; III-1, 2*, 3; iv-1; IV-1, 2, 3; V-VI-1, 2. A cranium from the arenaceous Purple Shales of the Bog Mine Inlier (BM In. 22533) has thirteen tubercles on the false preglabellar field, and does not belong to the species-group. Pygidia from this locality (Whittard 1938, pl. 4, fig. 11) are more triangular, more strongly vaulted and are non-mucronate.

EXPLANATION OF PLATE 67

- Figs. 1-4. *Encrinurus macrourus* Schmidt. 1, Hemse Group (Lower Ludlovian), Visne Myr, parish of Fardhem, Gotland. RS Ar. 30415, $\times 6$. Hypostome. 2, Gotland (exact locality and horizon unknown). RS Ar. 47146, $\times 8$. Left lateral view of inverted cephalon to show articulation of cranium and hypostome. Left free cheek removed, rostral plate in position; longitudinal median lobe of hypostome projects beyond anterior border. Wing process of hypostome rests against fossula near front of axial furrow; wing extends forwards close to axial furrow well beyond facial suture; posterior part of the wing is upturned, running subparallel to steeply sloping part of the axial furrow. 3, Klinteberg Group (Lower Ludlovian), Eksta, Gotland. RS Ar. 30674, $\times 6$. Pygidium. Oblique view showing ridges between ribs, considered equivalent to anterior bands of cybelids. 4a, b, Hemse Group (Lower Ludlovian), Petesviken, parish of Hablingbo, Gotland. PIT Tr 1905 (lectotype), $\times 3$. Thorax and pygidium; axial tubercles on seventh and tenth thoracic rings. Dorsal and lateral views. Photos kindly supplied by Dr. R. Männil.
- Figs. 5-8. *Encrinurus punctatus* (Wahlenberg). 5, Jaani Marl, Jaani, Saaremaa, Estonia. PIT Nr. 1922 (Luha Collection), $\times 4$. Hypostome. 6, Jaani Marl, Jaani, Saaremaa, Estonia. PIT Tr 1882. (Böläu Collection), $\times 2$. Cephalon. Oblique lateral view showing apodemal pits; see Pl. 65, fig. 14. 7, Slite Group (Wenlockian), Follingbo, Gotland. RS Ar. 47294, $\times 4$. Doublure of pygidium. 8a, b, Slite Group (Wenlockian), Vikers, parish of Boge, Gotland. RS Ar. 30223, $\times 4$. Hypostome figured by Lindström, 1901, pl. 4, figs. 5, 6, 12, 13. Plan and anterior views.
- Figs. 9-10. *Encrinurus tuberculatus* (Buckland). 9a, Wenlock Shale, Malvern, Herefordshire. BM In. 48008, $\times 3$. Hypostome. 9b, the same, $\times 2$. Ventral view of cephalon, showing underside of right axial furrow; arrow points to the facial suture, fossula lies close behind. 10, Wenlock Limestone, Malvern, Herefordshire. BM In. 48015, $\times 3$. Anterior view of inverted cephalon; rostral plate and part of left free cheek removed. Note strong median flexure of anterior border of hypostome.
- Figs. 11-13. *Encrinurus deomenos* sp. nov. 11, Jupiter Formation, The Jumpers, Anticosti Island. HM A.884, $\times 3$. Cranium. 12, Zone 4, Jupiter Formation, Sandcliff, Anticosti Island, YU 882 (holotype), $\times 8$. Anterior view of cephalon, showing free cheeks in contact and absence of rostral plate. 13, Zone 1, Jupiter Formation, East Cliff, west of Jupiter River, Anticosti Island. YU 10402, $\times 3$. Hypostome probably belonging to this species; figured by Twenhofel 1928, pl. 59, fig. 7 as *E. anticostiensis*.
- Figs. 14-15. *Encrinurus stubblefieldi* sp. nov. 14, 'Upper Ludlow Shales', N. E. Pilliards Barn, Shropshire. GSM 36844 (paratype), $\times 3$. Cranium and thorax. Internal mould. 15, 'Upper Ludlow Shales', Whitcliff, Shropshire. GSM 36846 (holotype), $\times 2$. Cranium; see Pl. 65, fig. 12. Internal mould.
- Fig. 16. *Encrinurus onniensis* Whittard. Purple Shales (Upper Valentian), Onny River Section, near Cheney Longville, Shropshire. OUM C1, $\times 2$. Dorsal shield; see Pl. 65, fig. 16. Internal mould.



1



5



8a



9a



2



7



8b



10



3



6



11



9b



13



12



4a



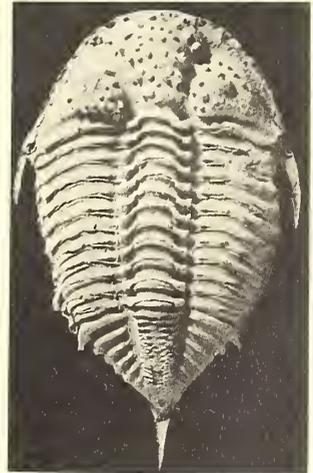
14



4b



15



16

Encrinurus sp.

Plate 65, fig. 15

Calymene ?punctata Murchison 1839, p. 661, pl. 23, fig. 8a.*Encrinurus omniensis* Curtis 1958, p. 142, pl. 29, figs. 4-5.*Occurrence.* Damery Beds and *Palaeocyclus* Band at base of Tortworth Beds (Upper Llandovery), Tortworth Inlier, Gloucestershire.*Remarks.* Cranidia from the Damery Beds differ considerably from *E. omniensis* in that the glabella is broader anteriorly, the glabella stands well above the fixed cheeks at the back, the lateral glabellar tubercles are larger, and there are ten small tubercles on the false preglabellar field. Associated free cheeks are much narrower than in *E. omniensis*, and pygidia are narrower and more strongly vaulted. Better preserved cranidia are required before the species can be described adequately.*Encrinurus deomenos* sp. nov.

Plate 67, figs. 11-13; Plate 68, fig. 12

Encrinurus anticostiensis Twenhofel 1928, pl. 59, figs. 6-8, 10 (*non* fig. 9).*Diagnosis.* Cephalon strongly arched transversely. Glabella short, rounded, inflated, standing much higher than cheeks. Glabella densely tuberculated. Rostral plate lacking.*Holotype.* YU 882 (enrolled dorsal shield). Pl. 67, fig. 12. Twenhofel, 1928, pl. 59, fig. 10. Dimensions:

Median length of cranidium	7.2 mm.
Width of cranidium	15.0 mm.
Width across false preglabellar field	6.3 mm.
Width of glabella across basal lobes	3.5 mm.

Occurrence. Jupiter Formation, Anticosti Island.*Description.* Differs from *E. punctatus* in the following features. Cephalon more strongly arched transversely. Glabella rounded, more inflated, standing high above cheeks at back. The four pairs of nodular lateral lobes considerably larger than other glabellar tubercles. Glabellar tubercle formula: (1-0); II-1, 2; iii-0; III-1, 2*, 3; iv-1; IV-1, 2, 3; (v-0); V-VI-1, 2, 3. Pseudoglabellar areas of free cheeks comparatively short, but broad, bearing eleven or twelve tubercles arranged in two irregular rows. Rostral plate lacking; a median suture separates free cheeks. Hypostome elongate; median lobe of central body short, widening towards back, not overhanging anterior border; posterior tongue long. Spine-bases occur on seventh and tenth axial rings. Pygidium strongly arched transversely; tubercles faint. Mucro slender, half length of axis.*Remarks.* The dorsal shield which Twenhofel selected as holotype of *E. anticostiensis* (1928, pl. 59, fig. 9) is quite different from the other specimens attributed to the species (figs. 6, 8, 10), all of which, including the hypostome (fig. 7), show affinities with the *E. punctatus* species-group, and are attributed to the one species. The absence of rostral plate is demonstrated both in the holotype of *E. deomenos* and in a second specimen in the Yale University Collection.

COMPARISON OF THE *E. PUNCTATUS* GROUP WITH OTHER SPECIES

The limit which has been set to the *E. punctatus* group is arbitrary. The most closely related species is one from the Hemse Group of Lau, Gotland; in this, nodular basal lateral lobes are developed, the glabellar tuberculation is more irregular and there is a tubercle in front of the lateral tubercle on the false preglabellar field. A group of species including *E. calgach* Lamont MS. is excluded because the median pair of tubercles in row II is displaced forwards, and there is a pair of equally large tubercles immediately behind them.

Several Silurian species resemble *E. punctatus* in glabellar tuberculation, although they are unrelated. Plate 65 has been arranged to illustrate similar variations which occur in *E. variolaris* (Brongniart) and in species of the *E. punctatus* group. In the first column of illustrations (figs. 1, 5, 9, 13, 17) the specimens lack tubercle III-2; in the second column this tubercle is forwardly placed (III-2*); in the third column it is paired (III-2*), and in the fourth column (excluding fig. 16) tubercles III-1, 2, 3 are in line.

E. moe from the Vormsi Stage (F_1b) of Estonia has recently been described by Männil (1958, p. 193, pl. 7, figs. 1-4, pl. 8, fig. 13). This species provides an interesting link between *E. punctatus* and the *E. multisegmentatus* (Portlock) groups, despite conspicuous differences from both. Row II consists of two pairs of tubercles, row III of three pairs, the second pair forwardly placed, as in *E. punctatus*. Nodular lateral tubercles occur. The basal glabellar lobes are strongly developed, and the false preglabellar field is divided by a median depression, as in *E. multisegmentatus*. Männil considers that the rostral plate has not been preserved, but in view of the straight connective suture between the free cheeks, it seems more probable that this species, like *E. deomenos*, lacked the rostral plate.

EXPLANATION OF PLATE 68

- Figs. 1-3, 9. *Encrinurus macrourus* Schmidt. 1, Klinteberg Group (Lower Ludlovian), Eksta, Gotland. RS Ar. 30675, $\times 5$. Pygidium with short mucro; pleural tubercles faint, all placed close to axis. 2, Hemse Group (Lower Ludlovian), Visne Myr, parish of Fardhem, Gotland. RS Ar. 30215, $\times 1.75$. Pygidium with long mucro. 3, Klinteberg Group (Lower Ludlovian), Eksta, Gotland. RS Ar. 30674, $\times 5$. Enrolled dorsal shield showing pygidium with no mucro and ridges between ribs; see Pl. 67, fig. 3. 9, Hemse Group (Lower Ludlovian), Kvinngårde, parish of Havdhem, Gotland. RS Ar. 47295, $\times 5$. Pygidium with short mucro, faint pleural tubercles, and narrow interpleural furrows.
- Figs. 4-6. *Encrinurus tuberculatus* (Buckland). 4, Wenlock Limestone, Dudley, Worcestershire. BM In. 48020, $\times 3$. Pygidium with short mucro; first axial tubercle on third ring, the faint pleural tubercles placed close to axis. 5, Wenlock Limestone, tunnel under Wren's Nest, Dudley, Worcestershire. BU 726 (Holcroft Collection), $\times 3$. Pygidium with long mucro. 6, Wenlock Limestone, tunnel under Wren's Nest, Dudley, Worcestershire. BU 805 (Holcroft Collection), $\times 5$. Pathological pygidium, showing deranged axial rings; large mucro broken off.
- Figs. 7, 8, 10. *Encrinurus punctatus* (Wahlenberg). 7, Jaani Marl, Jaani, Saaremaa, Estonia. PIT Nr. 1923, $\times 5$. Pygidium with short mucro. 8, Stage 8d, Malmoya, Norway. P10 44662, $\times 6$. Pygidium with long mucro broken off. 10, Slite Group (Wenlockian), Omkr, parish of Bunge, Gotland. RS Ar. 47296, $\times 4$. Pygidium; the fourth axial tubercle paired.
- Fig. 11. *Encrinurus stubblefieldi* sp. nov. 'Upper Ludlow Shales', Whitcliff, Shropshire. GSM 36847, $\times 3$. Pygidium. Internal mould.
- Fig. 12. *Encrinurus deomenos* sp. nov. Zone 1, Jupiter Formation, East Cliff, west of Jupiter River, Anticosti Island. YU 10397, $\times 4\frac{1}{2}$. Pygidium. Figured Twenhofel 1928, pl. 59, fig. 8, as *E. anticostiensis*.



1



2



3



4



5



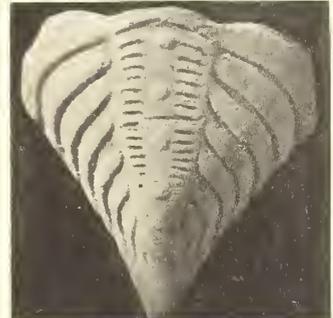
6



7



8



9



10



11



12

TABLE 1

Comparison of *E. punctatus*, *E. tuberculatus*, and *E. macrourus*

	Species	<i>punctatus</i>				<i>tuber-</i> <i>culatus</i>	<i>macrourus</i>				
	Country:	GOTLAND			ESTONIA	BRITAIN	GOTLAND				
	Horizon:	U. VISBY MARL	HÖGKLINT GROUP	SLITE GROUP	Total	JAANI MARL	WENLOCK SERIES	U. LLANDOVERY	WENLOCK SERIES	LUDLOW SERIES	Total*
Number of cranidia studied:		1	8	31	40	8	119	9	8	42	85
Length of cranium. Mean length (mm.)	10-0	10.6	8.1	8.7	6.1	9.4	6.9	6.9	6.2	6.2	6.2
Length of cranium 2σ limits (mm.)		7.8	4.7	4.8	1.6	5.6	5.1	4.1	3.8	4.0	4.0
		13.4	11.5	12.5	10.6	13.2	8.6	9.8	8.6	8.4	8.4
% of specimens with tubercle iii-0	100	100	81	85	12	93	0	25	2	6	6
% of specimens with any of the 4 III-2 ⁺ tubercles	100	100	35	50	50	97	45	38	57	46	46
% of specimens with 8 preglabellar tubercles	?	66	14	23	100	87	29	0	21	18	18
% of specimens with 9 preglabellar tubercles		0	14	12	0	5	71	80	69	73	73
% of specimens with 10 or more preglabellar tubercles		34	72	65	0	8	0	20	10	9	9
Number of pygidia studied:		1	6	7†	16	144	4	1	73	96	96
% of specimens with first tubercle on first axial ring			17	14	32	10	0	0	5	5	5
% of specimens with first tubercle on second axial ring		100	83	86	68	80	75	0	67	71	71
% of specimens with first tubercle on third axial ring		0	0	0†	0	10	25	100	28	24	24
% of specimens showing correlation of position of axial and pleural tubercles as mentioned on p. 469		0	83	72	75	43					

* Includes 26 cranidia and 18 pygidia of unknown locality.

† Only entire dorsal shields included. Certain isolated pygidia with first tubercle on third axial ring are almost certainly attributable to *E. punctatus*.

ADDENDUM

Mr. R. V. Best's interesting study of *Encrinurus ornatus* Hall & Whitfield (1961, *Journ. Paleontology*, 35, 1029-40, pl. 124) was not seen until after this paper had been submitted for publication. From his study of the number of rings between the first and second and second and third axial tubercles of the pygidium, Best was able to demonstrate the random binomial distributions of combinations of three-ring and four-ring spacing of these tubercles, suggesting that his collections came from an interbreeding population. This method of study cannot be applied to the species studied in this paper because the number of rings between the first three tubercles is more variable. The

following count of adequately preserved specimens is provided for comparison with Best's Table 1.

Species:	<i>E. tuberculatus</i>				<i>E. macrourus</i>				<i>E. spp.</i> Wenlock Series of Gotland			
	1	2	3		1	2	3		1	2	3	
First tubercles on ring no:												
Number of rings between first and third tubercles	Total				Total				Total			
10	—	1	—	1	—	—	—		—	—	1	1
9	1	42	6	49	—	10	6	16	—	10	2	12
8	5	39	8	52	1	28	9	38	5	32	10	47
7	6	26	1	33	4	17	5	26	3	23	2	28
6	2	—	—	2	—	3	—	3	5	13	1	19
Total number of specimens	14	108	15	137	5	58	20	83	13	78	16	107

REFERENCES

- BARRANDE, J. 1852. *Système silurien du centre de la Bohême: 1ère partie, Crustacés, Trilobites*, **1**, 1–935, pl. 1–51.
- BRONGNIART, A. 1822. *Histoire naturelle des Crustacés fossiles. . . Les Trilobites*. Paris.
- BUCKLAND, W. 1836. *Geology and mineralogy considered with reference to natural theology*, Bridgewater treatise, **2**, 1–128, pl. 1–69.
- CURTIS, M. L. K. 1958. The Upper Llandovery Trilobites of the Tortworth Inlier, Gloucestershire. *Palaontology*, **1**, 139–46, pl. 29.
- DALMAN, J. W. 1827. Om Palaeaderna eller de sa kallade Trilobiterna. *K. Svenska Vet. Handl.* **1**, 226–94, pl. 1–6.
- EMMRICH, H. F. 1844. *Zur Naturgeschichte der Trilobiten*. Meiningen.
- FLETCHER, T. W. 1850. Observations on Dudley Trilobites—Part 2. *Quart. J. geol. Soc. Lond.* **6**, 402–5, pl. 32.
- HAMADA, T. 1959. Gotlandian Shelly Fauna from Southwest Japan (1). *Coroncephalus kobayashii*, a new Species from the Kuraoka District, Kyūshū. *Japanese J. Geol. Geog.* **30**, 71–88, pl. 6.
- HEDE, J. ERNHOLD. 1960. *The Silurian of Gotland*. Guide to Excursion C 17, International Geological Congress, XXI session. Copenhagen.
- LINDSTRÖM, G. 1901. Researches on the visual organs of the trilobites. *Stockh. Vet. Akad. Handl.* **34**, 1–87, pl. 1–6.
- MÄNNIL, R. 1958. Trilobites of the families Cheiruridae and Encrinuridae from Estonia. (In Russian with Estonian and English summaries.) *Eesti NSV Teaduste Akad., Geol. Inst. Uurimused*, **3**, 165–212, pl. 1–8.
- MURCHISON, R. L. 1839. *The Silurian System*. London.
- NIESZKOWSKI, J. 1857. Versuch einer Monographie der in den silurischen Schichten der Ostseeprovinzen vorkommenden Trilobiten. *Archiv Naturk. Liv-, Ehst- u. Kurl.* **1**, 1–157, pl. 1–3.
- ÕPIK, A. A. 1937. Trilobiten aus Estland. *Acta Comment. Univ. Tartu. A.* **32**, 1–163, pl. 1–26.
- ROSENSTEIN, E. 1941. Die *Encrinurus*-Arten des estländischen Silurs. *Geol. Inst. Univ. Tartu.* **62**, 49–77, pl. 1–4.
- SALTER, J. W. 1853. Figures and descriptions illustrative of British organic remains. Dec. VII. *Mem. Geol. Surv.*
- SCHMIDT, F. 1859. Beitrag zur Geologie der Insel Gotland, nebst einigen Bemerkungen über die untersilurische Formation des Festlandes von Schweden und die Heimath der norddeutschen silurischen Geschiebe. *Archiv Naturk. Liv-, Ehst- u. Kurl.* **2**, 403–64.

- SCHMIDT, F. 1881. Revision der ostbaltischen silurischen Trilobiten nebst geognostischer Übersicht des ostbaltischen Silurgebiets, Abtheilung 1, Phacopiden, Cheiruriden und Encrinuriden. *Acad. Imp. des Sci. St.-Pétersbourg Mém.* (7), **30**, 1-237, pl. 1-14.
- TEMPLE, J. T. 1954. The Hypostome of *Encrinurus variolaris* and its Relation to the Cephalon. *Geol. Mag.* **91**, 315-18.
- 1956. Notes on the Cheiruracea and Phacopacea. *Ibid.* **93**, 418-30.
- TRIPP, R. P. 1957. The trilobite *Encrinurus multisegmentatus* (Portlock) and allied Middle and Upper Ordovician species. *Palaeontology*, **1**, 60-72, pl. 11, 12.
- and WHITTARD, W. F. 1956. Proposed use of the plenary powers (*a*) to designate type species in harmony with accustomed usage for the genera 'Encrinurus' Emmrich, 1844, and 'Odontochile' Hawle and Corda, 1847 and (*b*) to validate the specific name 'punctatus' Wahlenberg, 1821, as published in the combination 'Entomostracites punctatus' (Class Trilobita). *Bull. Zool. Nomencl.* **12**, 259-63, pl. 3.
- TWENHOFEL, W. H. 1928. Geology of Anticosti Island. *Geol. Surv. Canada, Mem.* **154**, 1-481, pl. 1-60.
- WAHLENBERG, G. 1821. Petrificata telluris Svecanae. *Nova Acta Soc. Sci. Upsal.* (5), **8**, 1-116, pl. 1-4.
- WHITTARD, W. F. 1938. The Upper Valentian Trilobite Fauna of Shropshire. *Ann. Mag. nat. Hist.* (11), **1**, 85-140, pl. 2-5.

R. P. TRIPP
High Wood,
Botsom Lane,
West Kingsdown,
Sevenoaks,
Kent

Manuscript received 20 September 1961

MICROPLANKTON FROM THE AMPHILL CLAY OF MELTON, SOUTH YORKSHIRE

by W. A. S. SARJEANT

ABSTRACT. Assemblages of organic-shelled microplankton from the Amphill Clay (Upper Jurassic) of South Yorkshire are described. They comprise twenty-one species of dinoflagellates, of which two are new; twenty-seven species of hystrichospheres, of which three are new; and four species of presumed microplankton *incertae sedis*. From comparison with microplankton assemblages previously described, a stratigraphic position is tentatively assigned to the horizons studied.

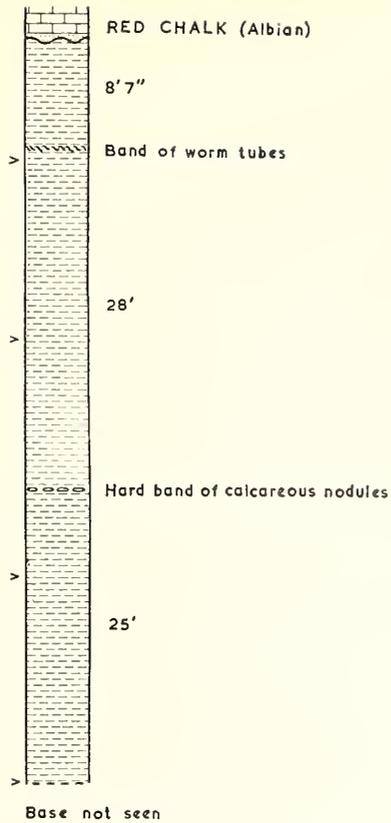
THE assemblages of fossil microplankton to be described are from four horizons within the argillaceous facies of the Oxfordian ('Amphill Clay') exposed in the clay pit of Messrs. G. and T. Earle, Ltd., at Melton, near Kingston-upon-Hull (grid reference S.E. 971268). A first visit was made to this pit during a meeting of the Yorkshire Geological Society on 13 February 1960, and a second visit in the following July, the pit having been considerably deepened between visits. At the time of the second visit, some 62 feet of grey clay were exposed below the unconformable capping of orange sands and Red Chalk (text-fig. 1). Four specimens collected were examined for microplankton, respectively from 61 ft. 7 in., 45 ft. approx., 25 ft., and 10 ft. below the overlying Cretaceous beds (henceforth referred to as the '62-foot', '45-foot', '25-foot', and '10-foot' horizons).

The samples¹ consisted of light-grey clay with yellowish flecks. Each was crushed mechanically and treated successively with hydrochloric and hydrofluoric acids: the resultant organic residue was partially oxidized with Schulze solution and washed with potassium hydroxide solution, thus further concentrating the microfossil content. The product was mounted for study in glycerine jelly.

The proportion of microfossils present proved high at all horizons, their state of preservation being generally excellent. Spores and pollen are present in abundance: at the 62-foot horizon they comprise only 40 per cent., at the 25-foot and 10-foot horizons around 50 per cent., and at the 45-foot horizon fully 70 per cent. of the total microfossil assemblage. Microplankton (dinoflagellates, hystrichospheres, and genera of presumed microplankton) form the remainder of the assemblage, foraminiferal shell linings being also present but only in extremely low numbers.

DISCUSSION OF THE ASSEMBLAGES

The relative proportions of the major microplankton groups are shown in Table 1, and especially noteworthy are the abundance of micrhystridia at the 25-foot horizon and the abundance of leiospheres at this and at the 45-foot horizons. In the assemblages as a whole, dinoflagellates form 42.5 per cent., hystrichospheres 53.4 per cent., and genera *incertae sedis* 4.1 per cent.; the dinoflagellates are numerically dominant only in the uppermost (10-foot) horizon. Twenty-one species of dinoflagellates, twenty-seven species of hystrichospheres, and four species *incertae sedis* were recognized; several



TEXT-FIG. 1. Section through the Ampthill Clay of Messrs. G. & T. Earle's clay pit at Melton, near Hull. The horizons from which assemblages were examined are indicated by arrows.

HORIZONS	% Dinoflagellates	% Hystri ch o s p h e r e s				Microplankton Incertae Sedis
		Larger Forms	Microhystridia	Leiospheres	Total	
10 — Foot	53.0	25.4	16.2	1.4	43.0	4.0
25 — Foot	39.2	3.6	38.4	13.8	55.8	5.0
45 — Foot	40.8	19.6	10.0	25.6	55.2	4.0
62 — Foot	37.2	37.6	13.8	8.0	59.4	3.4

TABLE 1. The relative proportions of the groups of microplankton in the Melton assemblages.

other species of dinoflagellates are certainly present, each represented by a few poor specimens not suitable for full description. A list of species, with their numerical distribution by horizon, is given in Table 2.

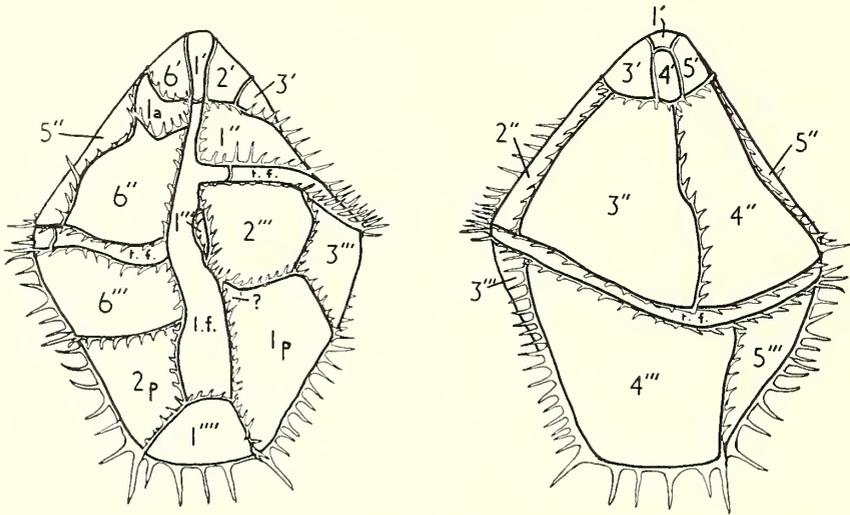
In this section, only new species, or species about which additional information was forthcoming, are dealt with. All holotypes of species described are to be lodged in the Laboratory of Sedimentology, University of Reading.

Class DINOPHYCEAE
Order PERIDINIALES
Family GONYAULACIDAE Lindemann
Genus GONYAULAX Diesing
Gonyaulax nealei sp. nov.

Plate 69, fig. 1; text-fig. 2

Holotype. M134/3/172, 62-foot horizon of Amphill Clay, Melton. *Dimensions of Type.* Overall: length 69μ , breadth 61μ . Without spines: length 64μ , breadth 50μ . Spines up to 5μ in length. Other specimens too damaged for satisfactory measurement.

Diagnosis. A species of fossil *Gonyaulax* with epitheca conical, rounded at the apex, and hypotheca in the form of a truncated cone. Tabulation 6', la, 6'', 6''', 2p, 1''':



TEXT-FIG. 2. *Gonyaulax nealei* sp. nov. Holotype (M134/3/172), $\times 900$. Left: in ventral view. Right: in dorsal view. *t.f.*, transverse furrow. *l.f.*, longitudinal furrow.

plate 1''' reduced and elongate. Sutures in the form of low ridges generally bearing simple spines of varying length and quite wide separation: the apical sutures, however, lack spines.

Description. Theca pale yellowish in colour, thin walled and without granulation. There is no apical horn: the six apical plates differ from those of the rest of the theca in that

the sutures between them lack spines, whereas the sutures separating them from the other epithelial plates are spinose. One anterior intercalary plate and six pre-equatorial plates are present: plates 1" and 6" are somewhat reduced.

The transverse furrow is of moderate breadth and extends round the theca in a laevo-rotatory spiral such that its two ends differ in antero-posterior position by twice the width of the furrow. The longitudinal furrow is narrow in its epithelial portion but broadens as it approaches the antapex. Of the six post-equatorial plates, plate 1''' is very reduced and not readily seen, and plates 2''' and 6''' are also somewhat reduced. Two large posterior intercalary plates are certainly present: a third (marked '?') may also be present in the angle formed by plate 1p against plate 2''' and the longitudinal furrow, but this could not be confirmed. The antapical plate is large and polygonal in shape.

The species is named after Dr. J. W. Neale of the Geology Department, University of Hull.

Remarks. Of the six specimens seen, only the holotype is well enough preserved to be capable of full study. In shape, tabulation, and ornamentation of crests, *Gonyaulax nealei* differs from all described fossil species. Those most closely comparable are *Gonyaulax cornigera* Valensi 1953, from the Bathonian of France, and *G. serrata* Cookson and Eisenack 1958, from Upper Jurassic to ?Neocomian of Western Australia. In neither of these species is the tabulation fully known: the former is distinguished by its longer and sometimes bifurcate sutural spines, the latter by the possession of grouped bifurcate processes on the apex.

Gonyaulax paliuros Sarjeant 1962

Plate 69, fig. 2

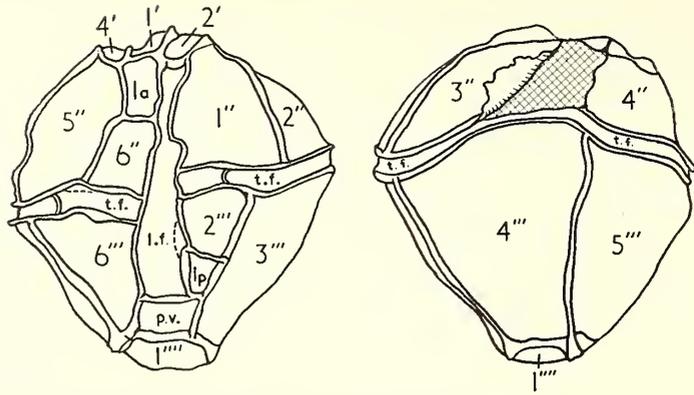
Remarks. This species, originally described from the Oxfordian (Corallian) (Sandsfoot Clay, *E. bimammatum* Zone) of Dorset, is abundant at all four horizons. The tabulation proved, as always, very difficult to determine, but observations made supported the earlier interpretation. This species has also now been found present in the assemblage from the Hambleton Oolite of Filey Brigg, Yorkshire, described earlier (Sarjeant 1960b).

Gonyaulax eumorpha Cookson and Eisenack 1960

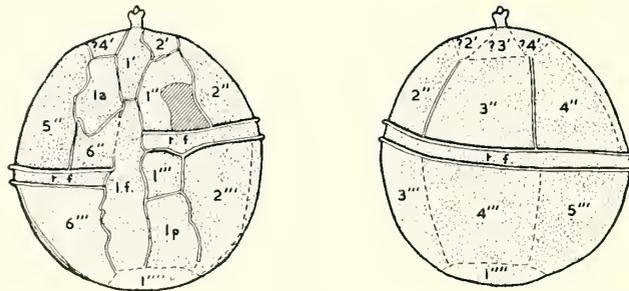
Plate 69, fig. 12; text-fig. 3

Remarks. This species, originally described from Oxfordian to Lower Kimmeridgian and probably Tithonian horizons of Western Australia, is recorded for the first time from Europe, representatives being present at three of the horizons studied.

The figured specimen (M132/8/61A) is the best preserved. Its tabulation corresponds in broad terms to that of the type; there are, however, several differences in detail. The boundary between plates 1a and 6" is well defined and plate 6" is clearly larger than plate 1a: in the type, the boundary is poorly defined and plate 1a considered larger. The transverse furrow shows a distinct subdivision by low sutures, a feature not observed in the type: and the posterior ventral plate (p.v.) is squarish and has a clearer relation to the antapical plate. Pre-equatorial plate 3" is torn open and may well represent an archaeopyle.



TEXT-FIG. 3. *Gonyaulax enmorpha* Cookson and Eisenack. The specimen figured (M132/8/61a) differs from the type description in detail of tabulation. Left: in ventral view. Right: in dorsal view. $\times 600$.



TEXT-FIG. 4. *Gonyaulax nuciformis* (Deflandre) comb. nov. Ventral tabulation (left) from specimen M134/1/37; dorsal tabulation (right) diagrammatic, reconstructed from several specimens studied. $\times 600$.

Gonyaulax nuciformis (Deflandre) comb. nov.

Plate 69, fig. 6; text-fig. 4

1938 *Palaeoperidinium nuciforme* Deflandre, p. 180, pl. viii, figs. 4-6.

Diagnosis. A species of fossil *Gonyaulax* having a spheroidal to ovoidal theca, thick walled and very coarsely granular, the granules in some cases so large as to be better regarded as very short spines. Tabulation ?4', 1a, 6'', 6''', 1p, 1''': extremely difficult to determine, since the sutural crests are very low and masked by the surface ornament. The apical process is short and broad, bifurcating briefly distally and giving rise to a short terminal process.

Remarks. This species was originally attributed to the genus *Palaeoperidinium* in absence of knowledge of the tabulation. In course of a recent visit to the Laboratoire de Micropaléontologie in Paris, I was courteously allowed by Prof. Deflandre to examine the holotype, which gives indication of a tabulation but no more. The species is present in the Middle Callovian of Dorset (Sarjeant 1962) and it occurs at all four Melton

Horizon within the Amphill Clay of Melton Species of microplankton	62 — foot M 134	45 — foot M 131	25 — foot M 133	10 — foot M 132
<u>Gonyaulax jurassica</u> Deflandre	31	17	16	49
<u>G. cladophara</u> Deflandre	3	13	17	49
<u>G. eisenacki</u> Deflandre	15	11	4	9
<u>G. ambigua</u> Deflandre	4	5	9	7
<u>G. paliuros</u> Sarjeant	19	9	29	12
<u>G. acanthosphaera</u> Sarjeant	9	—	11	14
<u>G. eumorpha</u> Cooksan & Eisenack	4	3	—	3
<u>G. nuciformis</u> (Deflandre) camb. nov.	25	9	2	18
<u>G. pachyderma</u> Deflandre	2	—	—	—

Species of microplankton	Horizon within the Amphill Clay of Melton			
	62 — foot M134	45 — foot M131	25 — foot M133	10 — foot M132
<i>Gonyaulax lurae</i> Deflandre	31	17	16	49
<i>G. cladophora</i> Deflandre	3	13	17	49
<i>G. elsenacki</i> Deflandre	15	11	4	9
<i>G. ambigua</i> Deflandre	4	5	9	7
<i>G. pallidus</i> Sarjeant	19	9	29	12
<i>G. acanthosphaera</i> Sarjeant	9	—	11	14
<i>G. eumorpha</i> Cookson & Eisenack	4	3	—	3
<i>G. nucleiformis</i> (Deflandre) comb. nov.	25	9	2	18
<i>G. pachyderma</i> Deflandre	2	—	—	—
<i>G. nopsis</i> sp. nov.	1	5	—	—
<i>Pluricarinatum oemingtonense</i> Sarjeant	—	—	1	—
<i>Cicadodinium ornatum</i> Deflandre	1	2	—	1
<i>Cf. Palaeogonystrichophora sphaerocoma</i> (Defl.)	1	—	—	—
<i>Paracadinia ceratophora</i> Deflandre	12	21	12	9
<i>Scrinodinium crystallinum</i> (Deflandre)	12	14	35	75
<i>S. lyridum</i> Deflandre	2	11	3	7
<i>S. galericum</i> Deflandre	3	13	9	—
<i>S. subvolutum</i> Sarjeant	3	7	—	—
<i>S. axfordianum</i> sp. nov.	—	7	5	2
<i>S. dictyotum</i> Cookson & Eisenack	6	12	4	10
<i>Nannoceratopsis pellucida</i> Deflandre	3	18	—	1
<i>Hyaliosphaera furcata</i> (Ehrenberg)	—	2	—	—
<i>Hyaliosphaeridium calpingapharum</i> (Defl.)	2	7	—	—
<i>Bailliosphaeridium pilosum</i> (Ehrenberg)	51	8	—	11
<i>B. etimuliferum</i> (Deflandre)	47	3	10	19
<i>B. veetium</i> (Deflandre)	23	12	1	34
<i>B. ehrenbergi</i> (Deflandre)	19	15	—	11
<i>B. trilobuliferum</i> sp. nov.	3	4	—	6
<i>B. polytrichum</i> (Valenel)	5	15	—	—
<i>B. parvifolium</i> (Deflandre)	—	—	—	4
<i>Bailliosphaeridium</i> sp.	1	—	—	—
<i>Cannosphaeropsis caulleryi</i> Deflandre	22	3	1	14
<i>Systematophora arbutera</i> Klement	1	1	—	—
<i>Dictyopyxide areolata</i> Cookson & Eisenack	2	3	—	—
<i>Chlamydomonada wallata</i> Cookson & Eisenack	—	—	—	4
<i>Cymatiosphaera parva</i> Sarjeant	—	—	3	2
<i>Pteropermapsihelias</i> Sarjeant	—	1	2	8
<i>P. cf. helias</i> Sarjeant	—	—	—	1
<i>Micrhystridium inconspicuum</i> (Deflandre)	17	30	114	62
<i>M. fragile</i> Deflandre	33	14	14	8
<i>M. recurvatum</i> Valenel	7	5	?	—
<i>M. stellatum</i> Deflandre	8	1	—	4
<i>M. rhopallium</i> sp. nov.	2	?	6	9
<i>M. rarispinum</i> Sarjeant	—	2	19	—
<i>M. sydus</i> Valenel	—	—	10	—
<i>M. cf. pluvetevi</i> Valenel	1	—	—	—
<i>M. deflandrei</i> Valenel	—	—	3	—
<i>Leiosphaeridia similis</i> Cookson & Eisenack	—	—	6	4
<i>L. ehytraeides</i> sp. nov.	40	128	32	3
<i>L.</i> sp.	—	—	25	—
<i>Palaeocostamocystis sinuata</i> Cook. & Eis.	—	—	2	—
<i>Stephanolirion starburburgense</i> Sarjeant	7	4	1	1
<i>S. redcliffense</i> Sarjeant	7	7	21	20
<i>Netrelirion elegatum</i> Sarjeant	6	10	—	3

TABLE 2. List of microplankton species present in the Melton assemblages, showing numerical distribution by horizon.



horizons: the majority of its representatives, like the type, show only traces of a tabulation, the thick walls, dark yellowish-brown colour and heavy granulation making study difficult. One specimen, however (M134/1/37), in which the dorsal surface is almost entirely lacking, allowed determination of details of the ventral tabulation, and indications on several other specimens enabled reconstruction of the dorsal tabulation. The species is clearly attributable to the genus *Gonyaulax* and resembles, in tabulation, the thickness and granular nature of its walls, and the possession of a short apical horn, the species *G. pachyderma* Deflandre of the French Lower Oxfordian (1938), differing from the latter in the shape of the apical horn, details of plate shape, and the presence of an anterior intercalary plate. A close systematic relationship between the two species is clearly indicated; *G. nuciformis* is known to occur earlier than *G. pachyderma* and might be visualized as giving rise to the latter species by loss of plate 1a, simplification of horn structure and emphasis of sutural crests. However, no intermediate forms are known to date. The range of dimensions exhibited (Melton specimens) is overall length 56–58 μ , breadth 50–64 μ : the specimens are more generally spheroidal than those whose dimensions are quoted by Deflandre (length 60–65 μ : breadth 47–53 μ).

Family HYSTRICHODINIDAE

Genus PALAEOHYSTRICHOPHORA Deflandre, 1934 (emend. Deflandre and Cookson, 1955)

Cf. *Palaehystrichophora spinosissima* (Deflandre 1938)

Remarks. A single specimen from the 62-foot horizon accords well with forms described under this name from North Yorkshire (Sarjeant 1960). The tabulation again proved incapable of determination.

?Order GYMNODINIALES

Family uncertain

Genus PAREODINIA Deflandre

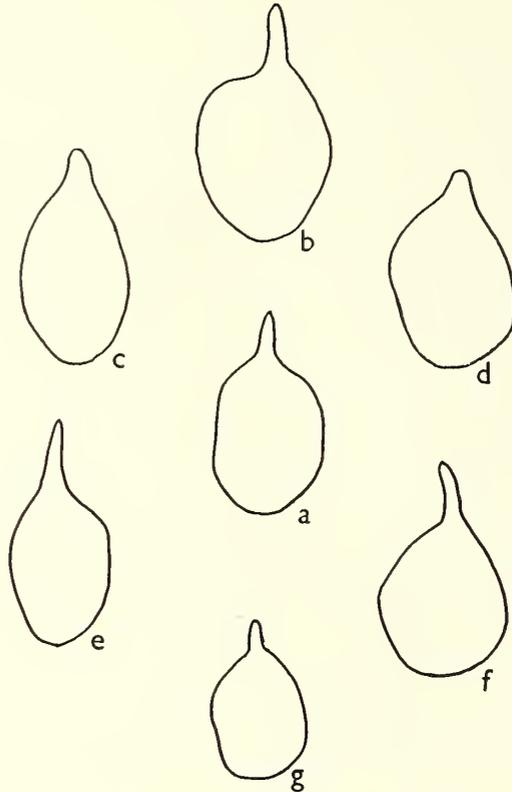
Pareodinia ceratophora Deflandre, 1947

Plate 69, fig. 8; text-fig. 5

Remarks. This species was originally described from the Callovian of the Baltic region and Bajocian of France (1947). It has subsequently been found represented, in its typical form, in British strata ranging in age from Middle Callovian to Upper Oxfordian (Lantz 1958, Sarjeant 1960, 1961, 1962) and a variety, *P. ceratophora* var. *pachyceras* Sarjeant, in the Lower Callovian and lowest Oxfordian (1959 and 1961).

This species is of extremely variable form, variation occurring in overall size, in granularity, in ratio of length to breadth, in shape of the apical horn, and in ratio of horn length to overall length. The variation in all characters save granularity is shown in text-fig. 5, where the outlines of individuals, drawn to a constant scale, are shown in pictogram form (variation in granularity proved independent of these dimensional variations). All intermediates between the figured extremes are known. Within the Melton assemblage, a very wide variation of form was observed, the variations typified by specimens in text-fig. 5 *b*, *c*, being especially frequent. The latter is indistinguishable in outline from the forms classed previously (1959) as var. *pachyceras*, differing only in

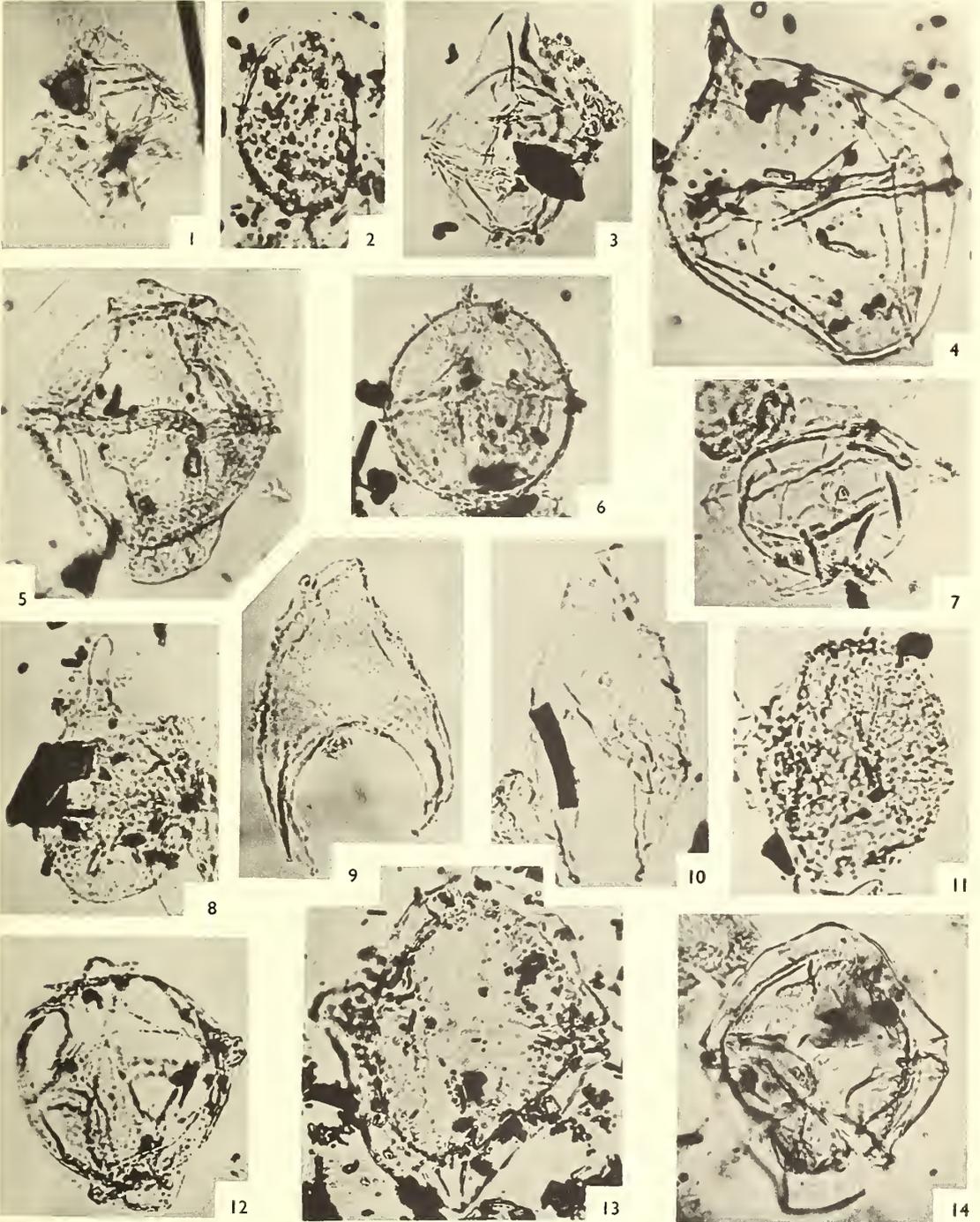
the less strongly coloured and more granular nature of the shell. *Pareodinia aphelia* Cookson and Eisenack 1958, from the Upper Jurassic and Lower Cretaceous of Western Australia, is known to vary in proportions in similar fashion to *P. ceratophora*, although the proportion of horn length to body length is generally smaller. It is probable



TEXT-FIG. 5. The range of variation exhibited by *Pareodinia ceratophora* Deflandre. Outlines of specimens from several horizons, drawn to a constant scale. *a*, CB81/6/4, from the Oxford Clay of Cayton Bay, Yorkshire. *b*, *c*, *f*, M134/1/92, M133/4/14, and M134/4/66, from the Amphill Clay of Melton. *d*, *e*, WC90/14/5 and WC90/1/1, from the Oxford Clay of Chickerell, Dorset. *g*, O130/9/2, from the Osmington Oolite of Osmington Mills, Dorset. All $\times 375$.

EXPLANATION OF PLATE 69

- Microplankton from the Amphill Clay of Melton, near Hull, Yorkshire. All figures $\times c. 500$.
- 1, *Gonyaulax nealei* sp. nov., M134/3/172, holotype, ventral view.
 - 2, *G. paliuros* Sarjeant, M133/2/24, ventral view.
 - 3, *G. eisenacki* Deflandre, M134/1/71, lateral view.
 - 4, *Pluriarvalium osmingtonense* Sarjeant, M133/5/13, dorsal view.
 - 5, *Scriniodinium subvallare* Sarjeant, M134/3/132, ventral view.
 - 6, *G. nuciformis* (Deflandre) comb. nov., M134/1/37, ventral view (interior view of half-shell).
 - 7, *S. luridum* (Deflandre), M134/2/131.
 - 8, *Pareodinia ceratophora* Deflandre, M134/1/92.
 - 9, 10, *Nannoceratopsis pellucida* Deflandre, M132/8/18A, M134/4/64.
 - 11, *S. dictyotum* Cookson and Eisenack, M132/8/88A.
 - 12, *G. eunorpha* Cookson and Eisenack, M132/8/61A.
 - 13, 14, *S. oxfordianum* sp. nov. 13, M131/1/58. 14, holotype, FB122/11/34 Hambleton Oolite, Carr Naze, Filey Brig, Yorks.



that both species are part of one continuous plexus and that the systematic distinction between them is wholly artificial.

Order Uncertain

Family DEFLANDREIDAE

Genus SCRINIODINIUM Klement

Subgenus ENDOSCRINIUM Klement 1960

Scriniodinium (?*Endoscrinium*) *oxfordianum* sp. nov.

Plate 69, figs. 13, 14

1960 *Scriniodinium* sp. A Sarjeant, p. 394, pl. 13, fig. 2.

1962 *Scriniodinium* (?*Endoscrinium*) sp. Sarjeant, p. 263, pl. 1, fig. 15.

Holotype. FB122/11/34, Hambleton Oolite (10 feet below top), Carr Naze, Filey Brigg. *Dimensions of type*. Cyst length 100 μ , breadth 82 μ . Theca length 82 μ , breadth 62 μ .

Diagnosis. A species of *Scriniodinium* having a cyst of broadly ellipsoidal shape, one face of whose hypothecal portion is somewhat flattened. Theca ellipsoidal, having a distinct tabulation, apparently 4', 6", 5"', 0p, 0''' ; the sutures of the ventral surface are unornamented, but sutures elsewhere bear raised crests formed by short spines, quite widely separated, whose tips are linked by a trabecula following the course of the suture.

Description. The cyst is ellipsoidal, pale yellowish or yellowish-brown in colour, smooth or very faintly granular. In some specimens there is a distinct equatorial bulge, the shape thus becoming biconical rather than ellipsoidal; in others, the space between theca and cyst is larger at one pole than at the other. The theca is somewhat darker in colour and broadly ellipsoidal in shape. Its surface may be areolate in patches; these patches are quite irregular in position and their distribution varies between individuals, the areolation being in all cases most pronounced near to a suture and dying out toward the centre of the plate.

The characteristic features of this species are its distinctive sutural crests, composed of widely spaced spines linked in T-fashion by a trabecula. The sutures of the ventral surface lack such crests, being marked only by low ridges, extremely hard to see even under the most favourable conditions: orientation and the establishment of a tabulation are thus difficult. From the examination of all available specimens, the tabulation was considered to resemble that established by Klement for his subgenus *Endoscrinium*, with four apical plates definitely present. The transverse furrow is of moderate breadth and only feebly laevo-rotatory, the longitudinal furrow narrow in its epithecal portion but broadening as it approaches the antapex. All specimens examined show some degree of damage, but the presence in constant position of an archaeopyle cannot be affirmed.

Remarks. Following study of the Melton specimens of *Scriniodinium oxfordianum*, representatives of this genus in the Yorkshire Corallian horizons were re-examined and the earlier interpretation of the crests of *Scriniodinium* sp. A (1960) corrected: these are as here described, and not 'perforated and in part areolate', as stated earlier. Indeed, specimen FB122/11/34 shows the form of the crests more clearly than any other seen;

for this reason, it has been chosen as type despite its damaged condition. The specimens from the Ringstead Waxy Clay (*E. bimammatum* Zone) of Dorset, earlier attributed to an undescribed species of *Scriniodinium* (1962), fall clearly within the range of variation of this species. The Melton specimens are generally somewhat larger than the type; specimen M131/1/58 (figured) has cyst $124 \mu \times 107.5 \mu$ and theca $98.5 \mu \times 75.5 \mu$.

Scriniodinium oxfordianum may represent an intermediate stage between species without a recognizable tabulation, such as the type species of the genus, *Scriniodinium* (*S.*) *crystallinum* (Deflandre) and clearly tabulate species, such as *S.* (*Endoscrinium*) *luridum*. In *S. oxfordianum*, the sutures of the ventral surface are poorly defined; in *S. crystallinum*, the transverse furrow cannot be traced across this surface and no longitudinal furrow is apparent. The flattening of one face of the hypothecal portion of the cyst of *S. oxfordianum* may be regarded as an approach to the projecting membranous 'cross-arching' of *S. luridum*: and the tabulation of the two species appears similar. In some poorly preserved specimens from Melton, there appears to be incomplete development of crests on sutures near the apex; these specimens could not be definitely attributed either to *S. crystallinum* or to *S. oxfordianum* and may well represent an intermediate stage of progressive crest development, leading from the former to the latter species. A process of filling in of the crests and modification of general shape might lead from *S. oxfordianum* to *S. luridum*. The forms from the Upper Calcareous Grit of Yorkshire, described as *Scriniodinium* sp. B (1960*b*) are similar in general shape to *S. luridum* but have crests of the type of *S. oxfordianum*: however, they occur in an assemblage in which the typical forms of these species are not present. Apparent intermediates of this character are not known from earlier horizons, and this second line of possible evolutionary development remains hypothetical.

Order HYSTRICHOSPHAERIDIA

Family HYSTRICHOSPHAERIDAE

Genus HYSTRICHOSPHAERA O. Wetzel 1933

Hystrichosphaera furcata (Ehrenberg 1838) O. Wetzel 1933

Remarks. The occurrences of this species in the Upper Jurassic, of which the Melton record is the third, are of interest in relation to the controversy with regard to the definition of this species and of *H. ramosa* (Ehrenberg 1838) O. Wetzel 1933. In the Upper Cretaceous, the two species form a continuously varying plexus (Lejeune-Carpentier 1937*a, b*); *H. ramosa* has not to date been recorded earlier. It appears that *H. furcata* is, as would be expected, the ancestral type and that the trend of increase in complexity of the spines, leading to *H. ramosa*, did not begin to operate until well into the Cretaceous.

Genus BALTISPHAERIDIUM Eisenack 1958

Baltisphaeridium ehrenbergi (Deflandre 1947) Sarjeant 1961

Plate 70, fig. 1; text-fig. 6*a*

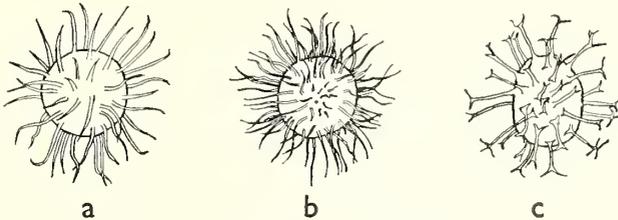
Remarks. This species, originally described from the Lower Oxfordian of Normandy, is present in three Melton assemblages. It has also now been noted from three horizons in the Yorkshire Oxford Clay (from the base, in the exposures in Scarborough Castle

Cliff: and from horizons respectively 25 feet and *c.* 100 feet above the base, in High Red Cliff, Cayton Bay; all within the *Q. mariae* Zone) and from the Hambleton Oolite of Filey Brigg, Yorkshire (*C. cordatum* Zone). These are the first British records of this species.

Baltisphaeridium polytrichum (Valensi 1947) Sarjeant 1960a

Plate 70, fig. 2; text-figs. 6b

Remarks. This species, originally described from the Bathonian of France, is present in the two lower Melton horizons and is also present in the Yorkshire Oxford Clay (lowest and 25-foot horizons: see above) and in the Osmington Oolite of Filey Brigg, Yorkshire (*P. plicatilis* Zone). These occurrences represent a considerable extension of the known range of this species within the Jurassic. A morphologically similar form from the Australian Upper Cretaceous has been placed in this species (Deflandre and Cookson 1955), but the stratigraphic separation remains immense. The forms from the Upper Kimmeridgian of Dorset, attributed to this species by Downie (1957), show clear morphological differences (Sarjeant 1960a).



TEXT-FIG. 6. Hystrichospheres from the Amphill Clay. *a*, *Baltisphaeridium ehrenbergi* (Deflandre) (M134/4/60). *b*, *B. polytrichum* (Valensi) (M134/3/67). *c*, *B. tribuliferum* sp. nov. Holotype, M134/2/29. All $\times 900$.



TEXT-FIG. 7. Variation in the form of spines of *Baltisphaeridium tribuliferum* sp. nov. Holotype, M134/2/29; $\times c.$ 1,800.

Baltisphaeridium tribuliferum sp. nov.

Plate 70, fig. 4; text-figs. 6c, 7

Holotype. M134/2/29, 62-foot horizon of Amphill Clay, Melton.

Dimensions of type. Overall: long diameter 59μ , short diameter 54μ . Shell: long diameter 33μ , short diameter 25.5μ . *Range of dimensions.* Overall: long diameters $53\text{--}62 \mu$, short diameters $48\text{--}58 \mu$.

Diagnosis. A species of *Baltisphaeridium* having an ovoid shell bearing widely spaced processes, attached proximally by root-like extensions on the shell surface and tapering somewhat distally, branching at a constant distance from the shell surface into bi-, tri-, or quadri-furcations of variable length and attitude.

Description. Shell smooth, without granulation or punctation, varying in hue from

yellowish to quite colourless. The spines are hollow but appear not to open directly into the shell's interior. They are of very variable form, never simple but having two to four branches of varying length: the branches appear flexible and may be directed outward from, or inward towards, the shell surface or may be roughly parallel to it (text-fig. 7). The branches are closed at their tips. The spines are widely spaced: the number present is between about forty-five and sixty; in length they exceed half the long diameter.

Remarks. *Baltisphaeridium tribuliferum* differs from all described species of this genus in its combination of form, and proportionate length, of processes with shell shape. The forms from the Lower Oxfordian of France, described by Deflandre as *Hystriochosphaeridium* cf. *intermedium* (1938), are probably attributable to this species, as also is the form from the Bathonian of France, described under this name by Valensi (1953).

This species is present in low numbers at three Melton horizons and has also been noted from all three horizons of the Yorkshire Oxford Clay (see above) and from the Lower Calcareous Grit and Hambleton Oolite of Filey Brigg, Yorkshire.

Baltisphaeridium parvispinum (Deflandre 1937) Cookson and Eisenack 1957

Text-fig. 9d

Remarks. This species, present at the 10-foot Melton horizon, is described for the first time from Britain and from the Jurassic: it has previously been recorded from the Lower Cretaceous (Aptian) of France (1937), Queensland, and Papua (Aptian: Cookson and Eisenack 1957) and the Upper Cretaceous of Belgium (Conrad 1941). In their dimensions, the Melton specimens fall between the range estimated by Cookson and Eisenack for the French specimens (shell $40\ \mu \times 20\ \mu$) and that quoted for the Australasian specimens (shell $73\text{--}76\ \mu \times 32\text{--}33\ \mu$); specimen M132/10/1 is typical—overall $63\ \mu \times 38\ \mu$, shell $57.5\ \mu \times 32.5\ \mu$.

Baltisphaeridium stimuliferum (Deflandre 1938) Sarjeant 1961

Plate 70, figs. 5, 17; text-figs. 8?c, e, g

Remarks. The range of forms depicted in text-fig. 8, all from the lowest (62-foot) horizon at Melton, well illustrates the difficulty of establishing a satisfactory morpholo-

EXPLANATION OF PLATE 70

Microplankton from the Amptill Clay of Melton, near Hull, Yorkshire. All figures (except fig. 12) $\times c. 500$; fig. 12, $\times c. 750$.

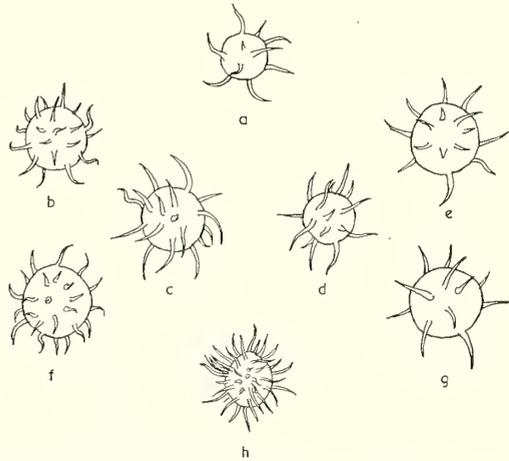
- 1, *Baltisphaeridium ehrenbergi* Deflandre, M134/4/60. 2, *B. polytrichum* (Valensi), M134/3/67. 3, *Cannosphaeropsis caulleryi* (Deflandre), M134/4/25. 4, *B. tribuliferum* sp. nov., Holotype, M134/2/29.
- 5, *B. stimuliferum* (Deflandre), M134/2/42. 6, *Micrhystridium fragile* Deflandre, M134/1/72. 7, *B. pilosum* (Ehrenberg) with *Stephanelytron redcliffense* Sarjeant, M132/8/105A and M132/8/105. 8, *B. sp.*, M134/3/73. 9, *Leiosphaeridia similis* Cookson and Eisenack, M133/7/48. 10, *B. pilosum* (Ehrenberg), M134/4/26. 11, *Stephanelytron scarburghense* Sarjeant, M134/2/104. 12, *S. redcliffense* Sarjeant, M134/4/16, in slightly oblique view, showing the mat of fibres within the corona. 13, *Leiosphaeridia chytrooides* sp. nov., holotype, M133/2/53. 14, *M. rhopalicum* sp. nov., holotype, M132/8/47. 15, *Pterospermopsis* cf. *helios* Sarjeant, M132/9/27. 16, *L. chytrooides* sp. nov., M134/2/80, showing organism emerging from cyst. 17, *B. stimuliferum* (Deflandre), M134/2/92. 18, *Netrelytron stegastum* Sarjeant, M132/5/2. 19, *Dictyopyxis areolata* Cookson and Eisenack, M134/4/16.



SARJEANT, Oxfordian microplankton

gical classification of those hystrichospheres with a spherical test and with simple spines present in moderate number. The size ranges of these forms overlap from above and below the artificial boundary ('size generally less than $20\ \mu$ ') separating *Micrhystridium* from *Baltisphaeridium*; and considerable variation in spine number and length is exhibited. Specimens *e* and *g* (text-fig. 8), in size and in spine number and character, are attributable to *Baltisphaeridium stimulierum*, which has a quoted range of shell diameters $20\text{--}26\ \mu$ and of spine lengths $10\text{--}23\ \mu$ (Deflandre 1938, Valensi 1953). Specimen *a* is clearly *Micrhystridium fragile*. Its author, Deflandre (1947), quotes for this species a range of overall diameters of $12\text{--}24\ \mu$, and shell diameters of $8\text{--}10\ \mu$. Valensi (1953) quotes ranges respectively of $15\text{--}40\ \mu$ and of $7\text{--}20\ \mu$: a similar range was exhibited by an assemblage studied earlier from the Yorkshire Hambleton Oolite (Sarjeant 1960*b*). Specimens *b* and *f* fall within the species *Micrhystridium recurvatum* Valensi (1953), which, with its described varieties, exhibits a range of overall diameters of $17\text{--}35\ \mu$ and shell diameters of $10\text{--}21\ \mu$. *Baltisphaeridium stimulierum* typically has about 15 spines; *Micrhystridium fragile*, 9 to 26; and *M. recurvatum*, 20 to 30. In known chronologic range, these species again overlap. *B. stimulierum* has been recorded from the Bajocian, Bathonian, and Lower Oxfordian of France (Valensi 1953, Deflandre 1938) and from the Lower Oxfordian of England (Sarjeant 1961); certain forms from the Upper Oxfordian of England have been classed as *B. cf. stimulierum* (Sarjeant 1962). *M. fragile* has been recorded from the Bajocian and Bathonian of France (Deflandre 1947, Valensi 1953) and from the Lower and Middle Callovian and the Lower and Upper Oxfordian of England (Sarjeant 1959, 1960*b*, 1961, 1962). *M. recurvatum* and its varieties have been recorded from the Bajocian and Bathonian of France (Valensi 1953) and from the Lower Callovian and Lower and Upper Oxfordian of England (Sarjeant 1960*b*, 1961, 1962).

At many horizons, the hystrichospheres of this general morphological type (shell spherical, spines not exceeding thirty in number, spine lengths from about one-quarter of the shell diameter to slightly greater than the diameter, shell diameter between $8\ \mu$ and $40\ \mu$) may be grouped without difficulty into one or more of the above species. Of the Melton assemblages, only that from the 62-foot horizon presented any difficulties: it is significant that hystrichospheres of the specified morphological type were commonest at this horizon. Specimen *d* is near the limit of spine number but may be classed as *M. fragile*; specimen *c* is morphologically most similar to *B. stimulierum* but has too many spines.



TEXT-FIG. 8. Hystrichospheres of closely comparable structure from the lowest (62-foot) Melton horizon. *a*, *Micrhystridium fragile* Deflandre (M134/1/72). *b*, *f*, *M. recurvatum* Valensi (M134/1/8 and M134/2/92). *c*, Cf. *Baltisphaeridium stimulierum* (Deflandre) (M134/2/81). *d*, *M. cf. fragile* Deflandre. *e*, *g*, *Baltisphaeridium stimulierum* (Deflandre) (M134/2/92 and M134/2/42). *h*, cf. *piveteaui* Deflandre (M134/3/17). $\times c. 750$.

Although the size boundary separating *Micrhystridium* and *Baltisphaeridium* is arbitrarily drawn, these genera appear nonetheless to express natural morphogenetic groupings and problems in allocation are rare. The mean and modal sizes of the three species here discussed fall clearly above or below the boundary; however, their very similar morphology suggests a relationship. *M. fragile* and *M. recurvatum* appear to be two parts of a single morphological plexus; and the degree of variation within the species *B. stimuliferum* is comparable.

Baltisphaeridium sp.

Plate 70, fig. 8; text-fig. 9c

Specimen. M134/3/73, 62-foot horizon of Amphthill Clay, Melton.

Dimensions. Overall: long diameter 62 μ , short diameter 60 μ . Shell: long diameter 32.5 μ , short diameter 25 μ .

Description. Shell oval, bearing simple, hollow spines; these open directly into the shell interior and have closed tips. The length of the spines exceeds half the long diameter of the shell; they number around thirty.

Remarks. The single specimen differs in its morphology from all described species. In view of lack of knowledge of the range of variation, it was decided not to designate this as a new species.

Genus SYSTEMATOPHORA Klement 1960

Systematophora orbifera Klement 1960

Remarks. The two specimens from Melton, placed within this genus and species, are both severely obscured by adherent organic debris, so that their attribution here, made on the basis of what could be seen of the process clusters, is somewhat doubtful.

Genus MICRHYSTRIDIUM Deflandre 1937

Remarks. The validity of this genus, as at present defined, is discussed above (see under *Baltisphaeridium stimuliferum*).

Micrhystridium rhopalicum sp. nov.

Plate 70, fig. 14; text-fig. 9f

Holotype. M132/8/47, 10-foot horizon of Amphthill Clay, Melton.

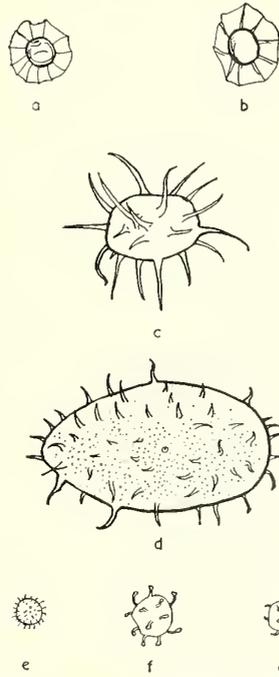
Dimensions of type. Overall diameter 21 μ ; diameter of shell 13.5 μ ; spines c. 4 μ in length.

Range of dimensions. Overall diameter 18–23 μ ; shell 10–15 μ .

Diagnosis. A species of *Micrhystridium* having a spherical shell, without surface ornamentation. Spines relatively few in number, short (less than half the shell diameter), with knob-shaped or briefly bifurcate tips.

Description. Shell yellowish in colour and of moderate thickness. The spines number 15–20: they taper from the base, but swell out at the tip in club-like form or into a T-shape with very brief arms.

Remarks. This species, present probably at all four Melton horizons, is also represented in an assemblage from the Osmington Oolite of Filey Brigg and may well have a much wider distribution than is at present known. However, at the high magnifications necessary for study of the processes, it has frequently proved difficult to confirm that the spines having a knobbed appearance are not merely recurved simple spines; at several horizons, more information must be awaited before its presence can be confirmed.



TEXT-FIG. 9. Hystrichospheres from the Amphill Clay. *a*, *Pterospermopsis helios* Sarjeant (M132/7/14). *b*, *P. cf. helios* Sarjeant (M132/9/27). *c*, *Baltisphaeridium* sp. (M134/3/73). *d*, *B. parvispinum* Deflandre (M132/10/1). *e*, *Micrhystridium deflandrei* Valensi (M133/3/23). *f*, *M. rhopalicum* sp. nov. (Holotype, M132/8/47). *g*, *M. rarispinum* Sarjeant (M133/2/25). $\times c. 750$.

In the form and number of its processes, *Micrhystridium rhopalicum* differs from all described fossil species of this genus. The only comparable species is *M. bigoti*, from the Bajocian and Bathonian of France (Deflandre 1947); however, in this latter species the processes are clearly capitate and are much shorter and more numerous.

Micrhystridium cf. piveteani Valensi 1953

Specimen. M134/3/17, 62-foot horizon of Amphill Clay, Melton.

Dimensions. Overall: long diameter 36 μ , short diameter 27 μ . Shell: long diameter 21.5 μ , short diameter 16 μ . Spines *c.* 9 μ long.

Description. Shell ovoidal, yellowish, bearing a large number (50–60) of simple processes whose length is equal to about half the long diameter. The surface of the shell lacks other ornament.

Remarks. The single specimen here described differs in shell shape and process number from all described species. It finds its closest comparison in *Micrhystridium piveteaui*, which has, however, somewhat fewer processes (about 40). In general morphology, there is considerable similarity to the *B. stimuliferum*—*M. fragile*—*M. recurvatum* type; but specimens of intermediate character were not found.

Family PTEROSPERMOPSIDAE
Genus PTEROSPERMOPSIS W. Wetzel 1952
Pterospermopsis cf. *helios* Sarjeant 1959

Plate 70, fig. 15; text-fig. 9b

Specimen. M132/9/27, 10-foot horizons of Amptill Clay, Melton.

Dimensions. Overall: long diameter 29 μ , short diameter 23 μ . Capsule: maximum diameter 9 μ .

Description. Capsule broadly oval, almost spherical, in outline: colour yellowish-brown. Wing oval in outline, thrown into nine radial folds; colour pale yellowish. Ratio of wing breadth to capsule radius: 2+ to 1.

Remarks. This species is closely comparable to forms present in the Hambleton Oolite of Filey Brigg, Yorkshire (Sarjeant 1960b). In wing outline and in ratio of wing breadth to capsule radius, it differs from the typical *P. helios*, specimens of which are present at three Melton horizons. (*P. helios* typically has a wing circular in outline and a ratio of 1.5 to 1.)

Family LEIOSPHAERIDIDAE Eisenack
Genus LEIOSPHAERIDIA Eisenack 1958
Subgenus LEIOSPHAERIDIA subgen. nov.

Type species. *Leiosphaeridia* (*L.*) *baltica* Eisenack 1958.

Diagnosis. A subgenus of *Leiosphaeridia* comprising species having a circular pylome or none at all.

Leiosphaeridia (*Leiosphaeridia*) cf. *similis* Cookson and Eisenack 1960

Plate 70, fig. 9; text-fig. 10

Remarks. Ten specimens in the two upper Melton horizons correspond in their morphology to this species, originally described from probably Tithonian and late Upper Jurassic horizons of Western Australia and Papua. They differ however in their much smaller size; the range of diameters is 38–45.5 μ , in comparison with a quoted range of 70–100 μ .

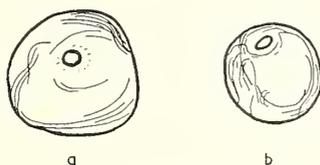
Subgenus CHYTROEISPHAERIDIA subgen. nov.

Type species. *Leiosphaeridia* (*Chytr.*) *chytrooides* sp. nov.

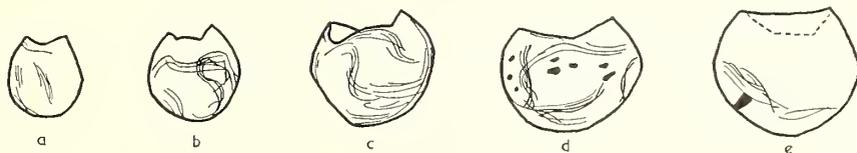
Diagnosis. A subgenus of *Leiosphaeridia* comprising species having a polygonal or

subpolygonal pylome, lateral or terminal in position. The pylome may not be present in all individuals of such species.

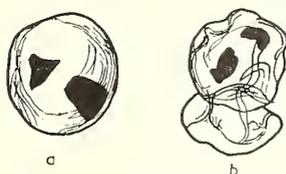
Remarks. Evitt (1961), discussing the significance of the pylome in fossil dinoflagellates and related organisms, proposed the term 'archaeopyle' for pylomes formed by the release of single plates or groups of plates. He lists *Leiosphaeridia* as a genus without definite dinoflagellate affinity, in which the pylome is most often absent or, where present, is of circular shape. The form of the pylome in *L. chytrooides* sp. nov. suggests an archaeopyle and thus also suggests dinoflagellate affinity; a taxonomic distinction from species having a circular pylome or no pylome is thus necessary. However, since a pylome is not constantly present, differentiation is not always possible. It is therefore considered best that all forms conforming in their morphology with Eisenack's generic diagnosis should remain in *Leiosphaeridia* and that distinction on pylome form should be made at subgeneric level only, the two subgenera being otherwise morphologically indistinguishable.



TEXT-FIG. 10. *Leiosphaeridia similis* Cookson and Eisenack. Specimens showing extremes of the size range exhibited in the Melton assemblages. *a*, M133/7/48 (45.5μ). *b*, M133/8/26 (34μ). $\times c. 750$.



TEXT-FIG. 11. The range of variation exhibited by *Leiosphaeridia chytrooides*, sp. nov. *a*, M133/8/51. *b*, M131/2/19. *c*, M134/3/18. *d*, Holotype, M133/2/52. *e*, M131/1/79. $\times 375$.



TEXT-FIG. 12. *Leiosphaeridia chytrooides* sp. nov. *a*, Specimen lacking a pylome (M133/1/6). *b*, Organism emerging from cyst (M134/2/80). $\times 375$.

Leiosphaeridia (Chytroeisphaeridia) chytrooides sp. nov.

Plate 70, figs. 13, 16; text-figs. 11, 12

Holotype. M133/2/53, 25-foot horizon of Amphill Clay, Melton.

Dimensions of type. Diameter (maximum) 50μ . *Range of dimensions.* Maximum diameters $30-60\mu$.

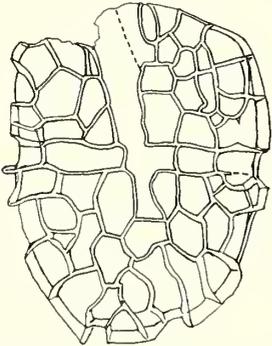
Diagnosis. A species of *Leiosphaeridia* having a smooth or faintly granular shell of

spherical to broadly ovoidal shape and variable thickness. A large pylome of polygonal outline, without a thickened rim, is characteristic.

Description. The shell is of pale to deep yellowish-brown colour. Its thickness is variable: the largest forms frequently have very thin walls, whereas the walls of smaller forms tend to be proportionately much thicker: however, thick-walled large forms are not uncommon. A pylome is frequently, though not uniformly, present; it is of approximately polygonal shape, the sides of the polygon curving inward. It varies in size with relation to shell diameter; the portion detached ranges from about one-third to just under two-thirds the longest radius. In ovoidal forms, the pylome is situated at one pole. In text-fig. 11, an arbitrary apical orientation has been given; the outline of the pylome suggests that of a plate, so that the term 'archaeopyle' may be preferable.

Some forms present in the Amphill assemblage, for example that figured in text-fig. 12a, have no pylome: their correspondence in all other morphological characters with *L. chytrooides* suggests their identity with the pylomate forms. One specimen encountered appears to represent the preservation of an individual actually in the stage of emerging from its cyst (Plate 70, fig. 16; text-fig. 12b); this interpretation is suggested by the lines of folding traversing both shells and the partial contraction of the upper one, presumed to be the cyst. The taxonomic character of the lower, emergent body is not clear.

Remarks. *Leiosphaeridia chytrooides* sp. nov. is abundant in the Melton assemblages. It differs, in the character of its pylome, from all other described species of leiospheres.



TEXT-FIG. 13. *Dictyopyxis areolata* Cookson and Eisenack, showing the median and longitudinal bands which are suggestive of a dinoflagellate cyst, M134/4/16. $\times c. 600$.

Family Uncertain

Genus DICTYOPYXIS Cookson and Eisenack 1960

Dictyopyxis areolata Cookson and Eisenack 1960

Plate 70, fig. 19; text-fig. 13

Remarks. This species, described originally from Oxfordian to Lower Kimmeridgian horizons of Western Australia, is recorded for the first time from Europe. It was regarded by its authors as *incertae sedis*: however, its possession of median and longitudinal bands, homologous with the furrows of a dinoflagellate albeit almost certainly functionless in this species, and the absence of one pole of the shell (text-fig. 13) in one specimen seen, suggesting a possible apical pylome, indicate that this may well be a dinoflagellate cyst. It is therefore here placed in the Order Hystrichosphaeridia, alongside other genera of presumed dinoflagellate cysts.

INCERTAE SEDIS

Genus NETRELYTRON Sarjeant 1961

Netrelytron stegastum Sarjeant 1961

Plate 70, fig. 18

Remarks. Two features noted in the original descriptions of this remarkable species are

confirmed from its Melton representatives; the oval perforation on one ? dorsal flank, which is clearly a pylome: and the investment of each individual in a mass of formless organic material. The former feature was observed with certainty in eleven specimens, the state of preservation and/or the orientation of the others seen not permitting certainty; and all specimens seen showed the latter feature, the cloak of debris presumably affording protection during encystment.

Genus *STEPHANELYTRON* Sarjeant 1961

Stephanelytron scarburghense Sarjeant 1961

Plate 70, fig. 11

Remarks. The presence of this genus at all four horizons at Melton shows that the original limited vertical range postulated for it is incorrect. It was originally described from the lowest Yorkshire Oxford Clay and was not represented in assemblages from higher horizons. The extension of its known range suggests that it may well have given rise to *S. redcliffense*, by disappearance of processes within fields and slight increase in ratio of shell length to breadth (the shell of *S. scarburghense* is typically almost spherical).

Stephanelytron redcliffense Sarjeant 1961

Plate 70, figs. 7, 12

Remarks. The specimen described as Organism A, from the Hambleton Oolite of Yorkshire (Sarjeant 1960*b*), is attributable to this species, which thus has a known range from the top of the *Q. mariae* Zone through the *C. cordatum* Zone (middle-upper Lower Oxfordian).

CONCLUSIONS

The principal aim in studying the Ampthill Clay assemblages was to determine whether a stratigraphic position could be allotted to these beds on the basis of their microplankton content. The known distribution by horizon of microplankton in British Callovian and Oxfordian horizons is given in Table 3; the known distribution of these species in other described assemblages is also shown, together with their distribution in the Melton assemblages. For the British horizons, stage names and ammonite zones are given, where known: for the non-British assemblages, only stage names are given, since ammonite zones were not quoted. The Australasian assemblages, obtained from borehole material, are often very vaguely dated. From examination of Table 3, it is evident that the Melton assemblages are exceptionally rich in number of species. Their age is clearly Oxfordian. The absence of several species recorded only from the Lower Oxfordian (*Gonyaulax areolata*, *Baltisphaeridium* cf. *fimbriatum*, *Cannosphaeropsis aemula*, *Polystephanophorus calathus*, *Wanaea fimbriata*, *Stephanelytron caytonense*) and the presence of others known only from the Upper Oxfordian (*Gonyaulax paliuros*, *Pluriarvalium osmingtonense*, *Scrinioidinium subvallare*, *Micrhystridium rarispinum*), together with the presence of species whose ranges overlap these horizons from above or below, indicate an uppermost Lower to Upper Oxfordian age. It would seem most probable, on the basis of these assemblages, that the age range of the Ampthill Clay succession examined is from uppermost *C. cordatum* to *P. plicatilis* Zone (approximately

equivalent to the Nothe Grit–Osmington Oolite range in the Dorset Corallian, or to the Hambleton Oolite–Osmington Oolite range in North Yorkshire). The Ampthill Clay is a facies equivalent of the Corallian: no ammonite zonation has to date been established for the Melton Clay Pit.

Seventeen species from Melton are also present in the assemblage described by Deflandre (1938) from the Lower Oxfordian (*C. cordatum* Zone) of Villers-sur-Mer, Calvados, France: and ten species in the Australasian assemblages described by Cookson and her associates. In contrast, only nine species occur in common with Klement's assemblages from the Malm of South-west Germany (1960); this degree of comparison is much smaller than was anticipated and may suggest some environmental barrier. None of the authors quoted here concerned themselves with the micrhystridia, a group of difficult systematics and doubtful stratigraphic value.

Acknowledgements. This research was conducted in the Department of Geology of the University College of North Staffordshire; thanks are offered to Professor F. Wolverson Cope and to Mr. T. G. Miller for profitable discussions, and to Mr. D. Leverett for technical services. The author would also like to thank Dr. J. W. Neale and Mr. Peter Kaye, of the University of Hull, and Mr. Harold Sarjeant for guidance and assistance in field work; and Professor L. R. Moore, of the University of Sheffield, for his courtesy in allowing use of the photographic facilities of the Laboratory of Micropalaeontology.

REFERENCES

- CONRAD, W. 1941. Quelques microfossiles des silex crétacés. Notes protistologiques 19. *Bull. Mus. roy. Hist. Nat. Belg.* **17**, 1–10.
- COOKSON, ISABEL C. and EISENACK, A. 1958. Microplankton from Australian and New Guinea Upper Mesozoic sediments. *Proc. Roy. Soc. Vic.* **70**, 19–79.
- — — 1960. Upper Mesozoic microplankton from Australia and New Guinea. *Palaeontology* **2**, 243–61.
- DEFLANDRE, G. 1934. Sur les microfossiles d'origine planctonique conservés à l'état de matière organique dans les silex de la craie. *C. R. Acad. Sci., Paris*, **119**, 966–8.
- — — 1937. Microfossiles des silex crétacés II. Flagellés incertae sedis, Hystrichosphaeridés, Sarcodiné, organismes diversés. *Ann. Paléont.* **26**, 51–103.
- — — 1938. Microplancton des mers jurassiques conservés dans les marnes de Villers-sur-Mer (Calvados). Étude liminaire et considérations générales. *Trav. Stat. zool. Wimereux*, **13**, (Vol. jub. M. Caullery), 147–200.
- — — 1941. Le microplancton kiméridgien d'Orbagnoux et l'origine des huiles naturelles. *Mém. Acad. Sci. Inst. Fr.* **65**, 1–32.
- — — 1942. Sur les hystrichosphères des calcaires siluriens de la Montagne Noire. *C. R. Acad. Sci. Paris*, **215**, 475–6.
- — — 1947. Sur quelques micro-organismes planctoniques des silex jurassiques. *Bull. Inst. Oceanogr. Monaco*, no. **921**, 1–10.
- DEFLANDRE, G. and COOKSON, ISABEL C. 1955. Fossil microplankton from Australian late Mesozoic and Tertiary sediments. *Austr. J. Mar. Freshw. Res.* **6**, 242–313.
- DOWNIE, C. 1957. Microplankton from the Kimeridge Clay. *Quart. J. geol. Soc. Lond.* **112**, 413–34.
- EISENACK, A. 1958. *Tasmanites* Newton 1875 and *Leiosphaeridia* n.g. als Gattungen der Hystrichosphaeridia. *Palaeontographica (A)*, **110**, 1–19.
- EVITT, W. R. 1961. Observations on the morphology of fossil dinoflagellates. *Micropaleontology*, **7**, 385–420.
- KLEMENT, K. W. 1957. Revision der Gattungszugehörigkeit einiger in die Gattung *Gymmodinium* Stein eingestufter Arten jurassischer Dinoflagellaten. *Neu. Jb. Min. u.s.w. Monatshefte*, 408–10.
- — — 1960. Dinoflagellaten und Hystrichosphaerideen aus dem Unteren und Mittleren Malm Südwestdeutschlands. *Palaeontographica (A)*, **114**, 1–111.

- LANTZ, J. 1958. Étude palynologique de quelques échantillons Mesozoïques du Dorset (Grande-Bretagne). *Rev. Inst. Fr. Pétrole*, **13**, 917-42.
- LEJEUNE-CARPENTIER, M. 1937*a*. L'étude microscopique des silex (2^{ième} note): Un fossile anciennement connu et pourtant méconnu: *Hystrichosphaera ramosa* Ehrbg. *Ann. Soc. géol. Belg.* **60**, B239-60.
- 1937*b*. L'étude microscopique des silex (3^{ième} note): Encore *Hystrichosphaera ramosa*; les coques 'dedoublées', le 'flagelle'. *Ibid.* **60**, B321-3.
- NEALE, J. W. 1960. Field meeting at Melton clay pit. *Yorks. Geol. Soc. Circular* no. **215**, 2.
- SARJEANT, W. A. S. 1959. Microplankton from the Cornbrash of Yorkshire. *Geol. Mag.* **96**, 329-46.
- 1960*a*. New hystrichospheres from the Upper Jurassic of Dorset. *Ibid.* **97**, 137-44.
- 1960*b*. Microplankton from the Corallian rocks of Yorkshire. *Proc. Yorks. Geol. Soc.* **32**, 389-408.
- 1961. Microplankton from the Kellaways Rock and Oxford Clay of Yorkshire. *Palaeontology*, **4**, 90-118.
- 1962. Upper Jurassic microplankton from Dorset, England. *Micropaleontology*, **8**, 255-68.
- VALENSI, L. 1947. Note préliminaire à une étude des microfossiles de la région de Poitiers. *C. R. Acad. Sci. Paris*, **225**, 816-18.
- 1953. Microfossiles des silex du Jurassique moyen. Remarques pétrographiques. *Mém. Soc. géol. Fr.* **68**, 1-100.
- WETZEL, O. 1933. Die in organischer Substanz erhaltenen Mikrofossilien des Baltischen Kreide-Feuersteins. *Palaeontographica*, **77**, 141-88, and **78**, 1-110.

WILLIAM A. S. SARJEANT
Department of Geology,
The University,
Reading.

SOME DIPLOGRAPTIDS FROM THE BRITISH LOWER SILURIAN

by G. H. PACKHAM

ABSTRACT. Diplograptids (seven species and nine subspecies) are described from various localities in the Lower Silurian of Great Britain, ranging in age from the zone of *Monograptus cyphus* to that of *M. turriculatus*. The study centres about *Glyptograptus tamariscus* (the genotype). From the time of its origin in the zone of *M. cyphus*, *G. tamariscus* displays considerable diversification along a number of different evolutionary lines. Other diplograptids which have some general similarity to *G. tamariscus* are also described, but they appear to be unrelated to it. The new forms described are *Glyptograptus tamariscus distans*, *G. tamariscus varians*, *G. tamariscus angulatus*, *G. tamariscus acutus*, *Clinacograptus tamariscoides*, *C. tangshanensis linearis*, *G. enodis enodis*, *G. enodis latus*, *G. elegans* and *C. alternis*.

THE Silurian diplograptids have been largely neglected since the publication of Elles and Wood's *Monograph of British Graptolites*. This neglect is possibly the result of the belief that they are of little stratigraphic value compared with the monograptids, but the work of Davies (1929) did show that there was considerably more variation in diplograptid species on any one horizon and throughout a sequence, than had been expected. The present study endorses Davies's findings.

The material used in this investigation has been drawn principally from the collection of the Sedgwick Museum in Cambridge, supplemented by specimens from the British Museum of Natural History, the University of Birmingham, the University of Aberdeen, and the Geological Survey of Scotland. The fossils described here range in age from the *Monograptus cyphus* Zone to the *M. turriculatus* Zone. The most valuable collections available to me were those from Dobb's Linn, near Moffat in the Southern Uplands of Scotland, and from Rheidol Gorge near Aberystwyth in Wales. The former was made several years ago by the Sedgwick Club; the graptolites here are flattened, or at best, preserved in very low relief; nevertheless, the collection has the advantage of being the most complete stratigraphically, covering all the zones of the Lower Llandovery. The Rheidol Gorge collection was made by Sudbury from the *M. gregarius* Zone at the time she was studying the triangulate monograptids of that zone (Sudbury 1958). All her material is preserved in pyrite in full relief. Other specimens are from the Lake District (Skelgill), the Cross Fell Inlier at Knock, Duffkinnel Burn in the Southern Uplands of Scotland, and isolated localities in Wales.

The identification of some of the graptolite zones in the Dobbs Linn Section has been based on the work of Sudbury (1958) at Rheidol Gorge. The zone of *M. cyphus* is thus the lower division of the zone of *M. gregarius* as Lapworth (1878) recognized it. The base of the zone of *M. gregarius*, thus restricted, is taken as the horizon at which *M. triangulatus* first appears. That part of the zone of *M. gregarius* which is referred to as the lower part in this paper is that containing *M. triangulatus* and lacking *Rastrites*. It corresponds approximately to horizons S (lowest) to H (highest) in the Rheidol Gorge section. *Rastrites* is present in addition to triangulate monograptids in what is referred to here as the upper part of the *M. gregarius* Zone. This latter can be correlated approx-

imately with horizons from G (lowest) to A (highest) of the Rheidol Gorge Section together with the *Diplograptus magnus* band and the *M. leptotheca* band at the same locality.

Method of study. Since no isolated specimens of the species under investigation are available for study, it has not been possible to determine any details of the development of the proximal portions of the rhabdosomes. Diagnoses of the forms here described thus depend on external morphology. So far as possible, however, special attention has been paid to the proximal end. In the description of thecal form, the term *geniculum* of Jaanusson (1960) has been used to describe the point of maximum flexure of the free ventral wall, the part above it being the supragenicular wall and the part below it the infragenicular wall. Two other conventions used in the description need some explanation. First, the width of the rhabdosome at, say, the fifth thecal pair, denotes the distance from the lip of the aperture of th_5^1 to that of th_5^2 measured perpendicular to the axis of the rhabdosome. Secondly, measurements involving the level of the aperture of a theca are taken from the axial extremity of the aperture, rather than the lip. The difference between the axial and lateral levels of the aperture will be noticeably different when the apertures are strongly everted.

In comparing compressed and uncompressed specimens, a geometric approach has been adopted. The cross-sectional profile of specimens preserved in relief is such that assuming simple flattening of the periderm, the width of the graptolite would be increased by about 30 per cent. Unfortunately it has not been possible to check this figure because no compressed and uncompressed specimens of the same form are available from the same locality, but specimens thought to be the same form, from different localities, confirm this assumption. The behaviour of the thecal profile during compression is variable. This is most marked in the infragenicular part of the theca. In specimens preserved in relief, the infragenicular wall varies from approximately planar to distinctly convex in horizontal section. Compression of the planar type could result in the infragenicular wall being folded inwards or outwards, while the convex type will almost certainly be folded outwards. If the infragenicular wall is folded outwards, there will be a tendency for the excavation to be decreased in depth, but this will be counterbalanced by the increase of width resulting from the flattening of the apertural region of the theca below (text-fig. 1*t*). If the infragenicular wall is folded inwards then the depth of the excavation will appear to be considerably greater after compression. This probably applies to *Climacograptus tangshanensis linearis*. For all these reasons little emphasis has been placed on the depth of the excavations.

The specimens preserved in relief are preserved as internal casts in pyrite. The form of this cast is clearly related to the external morphology in a general way, but there is no means of telling whether features like the interthecal septa had any external expression or not, nor whether the periderm was thick or thin. The pyrite has remnants of the periderm adhering to it, but is surrounded by a layer of chloritic mineral, as described by Sudbury (1958).

The text-figures have been prepared originally at a magnification of sixteen on graph paper, the specimen being studied at the same magnification by means of a binocular microscope with a graticule eye-piece.

SYSTEMATIC DESCRIPTIONS

Family DIPLOGRAPTIDAE Lapworth 1873

The species principally under consideration in this paper, *Glyptograptus tamariscus*, is the genotype and thus its morphological characters are of interest in determining the diagnostic features of the genus. The variation of the forms described below does raise some difficulties in nomenclature. The principal difficulty is in distinguishing between *Glyptograptus* and *Climacograptus*, a problem that has been made more difficult by some change in emphasis in the diagnostic features of the two genera by successive authors.

In erecting the genus *Climacograptus*, Hall (1865) drew attention to the thecal shape: 'cellules short and square; apertures apparently excavated in the margin of the stipe, and transversely oval or subquadrate; cell denticles or appendages, if present, usually on the upper side of the aperture'. Lapworth (1873) distinguished between *Climacograptus* and *Diplograptus* on the basis of the inclination of the thecae and the location of ornamental spines (if any), *Climacograptus* having 'thecae perpendicular: without ornament, or furnished proximally with a single, median, marginal spine. Polyary tapering; section circular or bilobate. Thecae free, section sub-oval.' *Diplograptus* has 'thecae inclined: without ornament, or furnished distally with two lateral apertural spines'. The sub-genus *Glyptograptus* was further distinguished by having the 'polyary usually styliform, section concavo-convex. Thecae usually free, section sub-oval.'

Elles and Wood (1906) shifted the emphasis to the degree of sigmoidal curvature of the thecal wall, and the disposition of the aperture. Their description of *Climacograptus* is: 'Thecae tubular, ventral walls with every degree of sigmoidal curvature; apertural margins typically horizontal situated within well-defined "excavations", occasionally introverted and rarely intortorted'. They describe the thecae of *Diplograptus* as 'sub-prismatic or sub-cylindrical tubes, ventral walls typically inclined and more or less straight; apertural margins even or undulated'. They also say (1907, p. 218) 'in the typical forms of the sub-genus *Glyptograptus* the theca is shorter and stouter [than in other sub-genera of *Diplograptus*], and the middle third of its ventral wall impressed to form a distinct "excavation" as in the genus *Climacograptus*; but the free edge is inclined instead of being vertical, the sigmoid ventral curve is flowing rather than sharp, and the "excavation" is wide instead of deep'. Elles and Wood also distinguish between different cross-sections of the rhabdosomes.

Subsequent definitions have been based on essentially the same characters as recognized by Elles and Wood. The problem of assigning difficult species to one genus rather than the other was recognized by Ruedemann (1904) and later implied by Elles (1922) when she wrote '?*Glyptograptus*' alongside several species of *Climacograptus* in the table accompanying that paper. More recently Jaanusson (1960) said that 'the morphological line from the orthograptid type to the climacograptid type is well documented. There exist all possible transitions between these extremes.' From this premiss he goes on to including the Climacograptinae in the Diplograptinae 'on account of the present difficulties in defining the former taxon.'

The difficulty of generic determination is apparent in species of British climacograptids, for example *C. scalaris miserabilis*, *C. wilsoni*, and *C. brevis*. In the first two cases

the supragenicular wall is vertical, but the geniculum is not so sharp as other species of the genus. The infragenicular wall is thus inclined at a relatively small angle (*c.* 45°) to the length of the rhabdosome. In *C. wilsoni* the proximal thecae at least are considerably inclined to the rhabdosome length and the geniculum is again not very sharp. Of the British species of *Glyptograptus* defined by Elles and Wood (1906, 1907), the only forms which present any real difficulty are *G. tamariscus* and possibly *G. teretiusculus siccatus*. Examination of the figures of *G. tamariscus* in Elles and Wood (1907) reveals the diversity of form of the thecae. The supragenicular walls vary from vertical (fig. 167*a*) to gently inclined (fig. 167*d*) and the geniculum from smooth and gentle (fig. 167*d*) to distinctly angular (some of the thecae of fig. 8*c*, plate xxx). The specimens examined in this study show a similar variation.

In this paper I have distinguished forms as *Climacograptus* which have an abrupt geniculum, with the infragenicular wall just beneath the geniculum inclined at an angle of at least 45 degrees to the rhabdosome length. The supragenicular wall in these forms is approximately parallel to the sides of the rhabdosome. This is not in any way an attempt to define the difference between the two genera; it is simply a rule of convenience for present purposes. At present it is probably best to regard the two genera as 'form genera' until far more isolated material becomes available.

The forms described here are divided into two groups: (*a*) narrow forms and (*b*) wider forms.

(*a*) *Narrow forms*

Genus GLYPTOGRAPTUS Lapworth 1873

Glyptograptus tamariscus (Nicholson)

Plate 71, figs. 1-4, 7-17; Plate 72, fig. 8; text-figs. 1*a-v*, 3*a-d*

- 1868 *Diplograptus tamariscus* Nicholson, p. 526, pl. 19, fig. 12 (*non* figs. 10, 11, 13).
 1872 *Diplograptus tamariscus* Nicholson; Nicholson, p. 117, text-fig. 4*c*.
 ?1876 *Diplograptus tamariscus* Nicholson; Lapworth, pl. 24, fig. 134.
 ?1877 *Diplograptus tamariscus* Nicholson; Lapworth, pl. 6, fig. 12.
 ?1897 *Diplograptus tamariscus* Nicholson; Perner, p. 4, pl. 9, fig. 16.
 ?1897 *Diplograptus tamariscus* Nicholson; Törnquist, p. 15, pl. 2, figs. 15-19.
 1907 *Diplograptus (Glyptograptus) tamariscus* Nicholson; Elles and Wood (*pars*), p. 247, pl. 30, fig. 8*d* (*non* text-figs. 164*a-d*, pl. 30, figs. 8*a-c*).
 1920 *Diplograptus tamariscus* Nicholson; Gortani, p. 17, pl. 1, figs. 22, 23.
 ?1920 *Diplograptus tamariscus incertus* Elles and Wood; Gortani (*pars*), p. 18, pl. 1, figs. 25, 26 (*non* figs. 24, 27).
 ?1920 *Diplograptus tamariscus laxus* Gortani, p. 19, pl. 1, fig. 28.
 1931*a* *Diplograptus (Glyptograptus) cf. tamariscus* Nicholson; Haberfelner, p. 104, pl. 3, fig. 16.
 1934 *Diplograptus (Glyptograptus) tamariscus* Nicholson; Hsü, p. 76, text-figs. 26*a, b*, pl. 6, figs. 1*a-f*.
 1949 *Diplograptus (Glyptograptus) tamariscus* Nicholson; Harris and Thomas, p. 54, figs. 13-14*a*.
 1954 *Diplograptus (Glyptograptus) tamariscus* Nicholson; Sherrard, p. 98, pl. 11, fig. 19.
 Note. The above can only be referred to *G. tamariscus* s.l.
non 1927 *Glyptograptus* aff. *tamariscus* (Nicholson); Whittard, p. 469, text-figs. A-C, pl. 13, 14.
non 1931*b* *Diplograptus* cf. *tamariscus* Nicholson; Haberfelner, p. 47, pl. 1, fig. 8.

Lectotype. Nicholson (1868) did not select a type specimen when he described the species, but subsequently Přibyl (1948) selected fig. 10 of plate 19 of Nicholson (1868) as the lectotype. The specimen probably corresponding to this figure has been located in the collection of the British Museum of

Natural History (BM (NH) 24925) and is figured here as text-fig. 1*q* and Plate 71, fig. 13. This specimen is flattened and incomplete; it is a young colony the proximal tip of which is missing. Přebyl's lectotype comes from Duffkinnel Burn, near Wamphray, in southern Scotland, as does this specimen. The horizon cannot be determined with any accuracy because all of the zones from *Akidograptus acuminatus* to *Monograptus turriculatus* are apparently present in that stream (judging from the fauna listed by Peach and Horne in 1899).

Horizon. Specimens of all the various varieties described below range from the *M. cyphus* Zone to the *M. turriculatus* Zone.

Revised diagnosis. Narrow rhabdosome, reaching possibly 2 mm. in width in the widest forms, thecae alternating with small overlap, excavations occupying approximately half the width of the rhabdosome, apertures horizontal or everted, supragenicular wall near perpendicular and longer than the length of the excavation, geniculum more or less rounded, median septum absent from the reverse side of the rhabdosome.

Description. There is considerable variation in the length of the rhabdosomes of specimens of this species, the shortest being several millimetres and the longest being over 4 centimetres. The width of the broadest forms may reach 2 mm. The rhabdosome is either parallel-sided or gently tapering.

The thecae vary considerably in spacing, from about seven to approximately fourteen per centimetre. The thecal shape is likewise very variable, but in all forms of the species, the thecae are moderately to strongly sigmoidally curved with the supragenicular wall more or less perpendicular. The interthecal spacing (measured between one aperture and the next in the same series) is almost constant throughout any rhabdosome except at the proximal end where the first and second thecae in each series are sometimes a little closer than succeeding thecae.

The depth of the excavations increases along the rhabdosome so that as the rhabdosome widens they occupy about the same proportion (about one-half) of the width throughout. They occupy less than half the margin of the rhabdosome, measuring them from the lip of the aperture to the geniculum of the theca above.

In specimens preserved in relief the septum is absent from the reverse side; in flattened

TEXT-FIG. 1. *a-f.* *Glyptograptus tamariscus varians* subsp. nov. *a*, Obverse of specimen in relief SM. A24925. *b*, Reverse of same specimen. *c*, Reverse of flattened specimen, SM. A51430. *d*, Holotype, reverse of specimen in relief, SM. A51439. *e*, Reverse of flattened specimen, SM. A51437. *f*, Reverse of flattened specimen, SM. A51435.

g-j. *G. tamariscus tamariscus* (Nicholson), form A. *g*, Reverse of flattened specimen, SM. A51412. *h*, Reverse of specimen in relief, SM. A24934. *i*, Obverse of same specimen. *j*, Reverse of flattened specimen, SM. A51417.

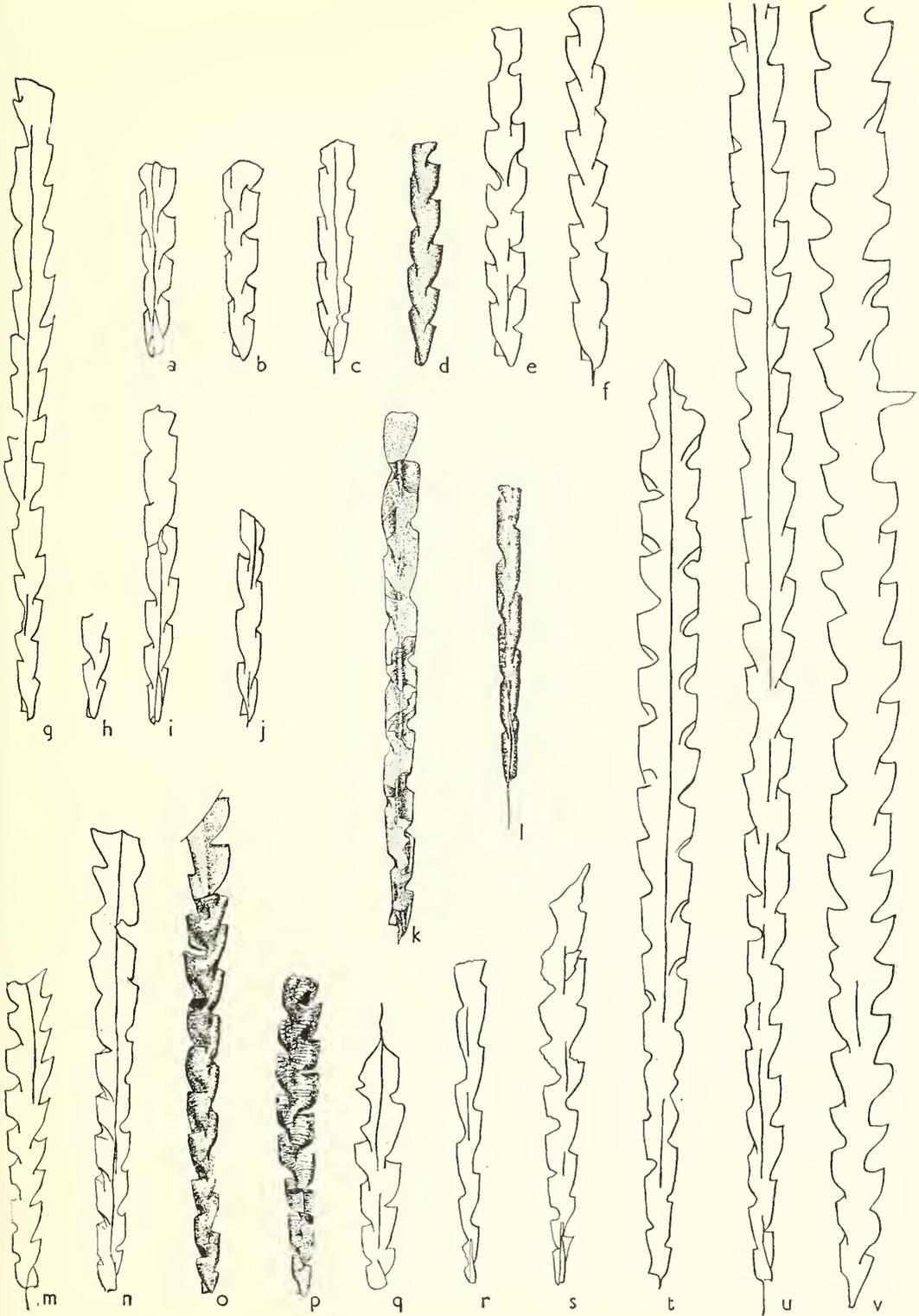
k-l. *G. tamariscus distans* subsp. nov. *k*, Reverse of flattened specimen, SM. A51428. *l*, Holotype, obverse of specimen in relief, SM. A24942.

m-p. *G. tamariscus tamariscus* (Nicholson), form B. *m*, Impression of reverse of flattened specimen, SM. A51419. *n*, Obverse of flattened specimen, SM. A51418. *o*, Reverse of specimen in half relief, SM. A20383. *p*, Reverse of specimen in half relief, SM. A51421.

q-u. *G. tamariscus tamariscus* (Nicholson), form C. *q*, Possible holotype, obverse of flattened specimen, BM (NH) 24953. *r*, Obverse of flattened specimen, SM. A51425. *s*, Obverse of flattened specimen, SM. A51424. *t*, Reverse of flattened specimen, Scot. Survey 5619. *u*, Proximal part of flattened specimen, SM. A51003.

v. *G. tamariscus linearis* Perner. Reverse, flattened specimen, BU. 1272.

All figures $\times 7.5$. Horizons and localities given in text.



TEXT-FIG. 1

specimens, there is some evidence of the septum, but this is probably a result of compression. In all the flattened specimens the periderm is thin—much thinner than in, say, *G. incertus* in the same band. Half-rings are distinctly visible in some specimens, notably those from Skelgill in half relief. Although it is not possible in the specimens available to count the half-rings precisely, it can be said that they are more closely spaced and more numerous in the proximal than the distal thecae. The sicula is normally a little over a millimetre long and exposed throughout its length.

Remarks. In this paper a number of subspecies are described; they are *G. tamariscus tamariscus* (Nicholson), *G. tamariscus linearis* Perner, *G. tamariscus distans* nov., *G. tamariscus angulatus* nov., *G. tamariscus acutus* nov., and *G. tamariscus varians* nov. Wide forms assigned to this species have been reported from central Europe (Münch, 1952) and Sardinia (Gortani, 1922). The Chinese species *Glyptograptus luushanensis* Hsü (1934) might include these forms.

The graptolite described as *Glyptograptus* aff. *tamariscus* by Whittard (1927) has not been included in *G. tamariscus* in this paper because of the presence of a complete septum and the strongly climacograptid aspect of the thecae.

The form described by Haberfelner (1931*b*) as *G. cf. tamariscus* has glyptograptid thecae at the proximal end, and orthograptid thecae at the distal end, and for that reason has been excluded from *G. tamariscus* in this paper. It may, however, be related to *G. elegans* sp. nov. described later.

Glyptograptus tamariscus tamariscus (Nicholson)

Plate 71, figs. 1-4, 11, 13; text-figs. 1*g-j*, *m-u*

1868 *Diplograptus tamariscus* Nicholson, p. 526, pl. 19, figs. 10, 11, 13 (*non* fig. 12).

1897 *Diplograptus tamariscus* Nicholson; Perner, p. 4 pl. 9, fig. 16.

1907 *Diplograptus* (*Glyptograptus*) *tamariscus* Nicholson; Elles and Wood, pl. 247, text-figs. 167*a-c*, pl. 30, fig. 8*a* (*non* text-fig. 167*d*, pl. 30, fig. 8*b-d*).

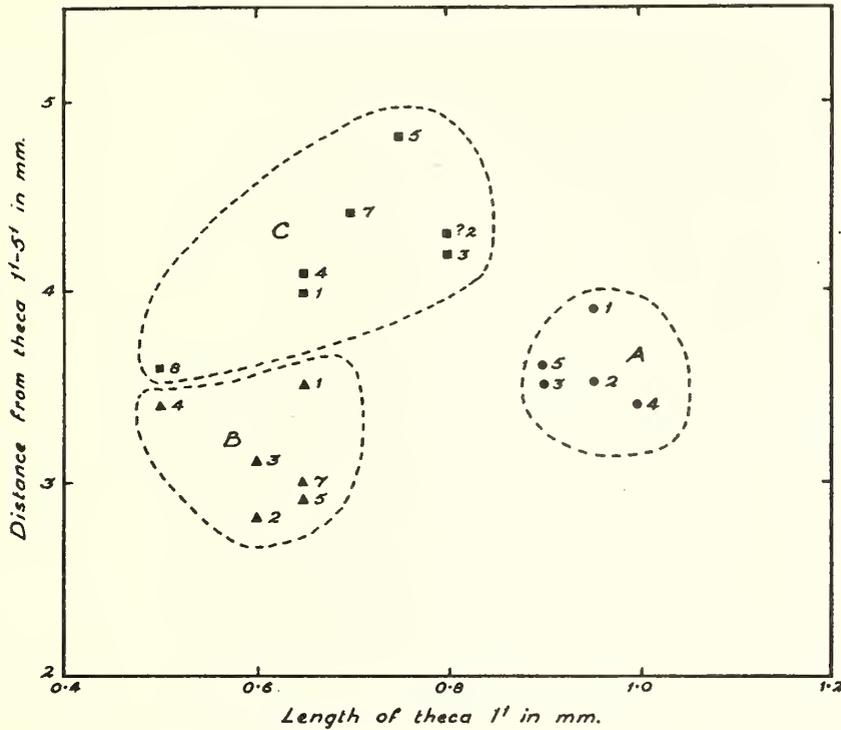
Lectotype. Nicholson (1868), plate 19 fig. 10, was selected by Přibyl (1948) as lectotype. The corresponding specimen is probably BM (NH) 24953 in the British Museum of Natural History. It is figured here as text-fig. 1*g* and Plate 71, fig. 13.

Horizons and localities. The specimens studied range from the base of the zone of *Monograptus cyphus* to the lower part of the zone of *M. turriculatus*. Dobb's Linn: base of the zone of *M. cyphus* (SM. A51411), near top of the zone of *M. cyphus* (SM. A51412), lower part of the zone of *M. gregarius* (SM. A51413, SM. A51414), upper part of the zone of *M. gregarius* (SM. A51417), band of *Cephalograptus cometa* (SM. A51418, SM. A51003, SM. A51422, SM. A51423, SM. A51424, SM. A51425, SM. A51426), lower part of the zone of *M. sedgwicki* (SM. A51419). Duffkinnel: zone of *M. convolutus* (Scotland Survey 5619) and BM (NH) 24953 (horizon unknown). Skelgill: zone of *M. fimbriatus* (SM. A20382), zone of *M. argenteus* (SM. A51421), zone of *M. convolutus* (SM. A20383, SM. A22487). Knock: low in the zone of *M. turriculatus* immediately downstream from the smash belt between the Ashgill shales and the Browgill beds on Swindale Beck, the bed contains a fauna similar to that recorded by Shotton (1935) at his locality c, but is stratigraphically below it (SM. A51420). Rheidol Gorge: zone of *M. gregarius*, horizon H (SM. A24934).

Revised diagnosis. Tapering form of *G. tamariscus* reaching 1.3 mm. in flattened specimens, theca 1¹ has its aperture between 0.5 and 1.0 mm. from the proximal end of the rhabdosome. Thecal excavations deep and relatively long.

Description. This subspecies is variable and within it three ill-defined forms can be recognized. These forms have some stratigraphic significance, so their separation is of some value. The principal dimensions of selected specimens are quoted in the table and some of these are plotted in text-fig. 2.

Throughout the group, the wider specimens have their thecae more closely spaced suggesting that the volume of the theca might be roughly constant.



TEXT-FIG. 2. The three forms of *Glyptograptus tamariscus tamariscus* Nicholson. The numbers correspond to those in the table in the text.

In form A the supragenicular wall is slightly inclined to the vertical, the excavations are deep and the apertures are horizontal to slightly everted. Form B appears to have been more circular in cross-section since all the specimens are preserved in a position slightly removed from the biprofile view. This peculiar mode of flattening may have been enhanced by a greater strength of the median septum resulting in twisting on compression so that the apertures on one series of thecae are more or less facing the observer. The thecae are more closely spaced than in the other two forms. Form C resembles form A in general features but the thecae are more distant and the first theca is shorter.

Sufficient of the probable type specimen is preserved to be able to identify it with form C. Other specimens of this form from the same locality are rather broader than the specimens of the same form from Dobb's Linn and text-fig. 1*u* is more typical of the broader specimens.

Dimensions (in millimetres)

Specimen Number	Flat or relief	Length of rhabdosome	Width			Length		Sicula	th5 ¹ to th1 ¹	Th/cm.	
			th1	th5	maxi-mum	th1 ¹	th1 ²			th1-2	th4-5
Form A											
1. SM. A51411	F	4.7	0.5	0.85	0.85	0.95	1.25	..	3.9	13	10
2. SM. A51412	F	13	0.5	0.8	0.9	0.95	1.2	..	3.5	13	c.10
3. SM. A51413	F	13	0.5	0.8	1.1	0.9	1.5	?0.95	3.5	13	c.10
4. SM. A51414	F	11	0.5	0.9	1.1	1.0	?1.5	..	3.4	13	c.10
5. SM. A24934	R	6.5	0.5	0.6	0.65	0.95	1.35	1.25	3.6	c.12	c. 9
6. SM. A51417	F	4.5	0.4	..	?0.5	0.9	1.3	12	..
Form B											
1. SM. A51418	F	9.5	0.5	0.7	1.1	0.65	0.75	1.0	3.5	13	c.11 $\frac{1}{2}$
2. SM. A51419	F	6.5	0.5	0.9	1.0	0.65	1.0	..	2.8	14	c.12
3. SM. A20382	$\frac{1}{2}$ R	6.0	0.4	0.7	0.75	0.65	0.95	..	3.1	14	12
4. SM. A20383	$\frac{1}{2}$ R	10.0	0.45	0.6	0.9	0.5	0.7	..	3.4	13	10
5. SM. A22478	$\frac{1}{2}$ R	7.5	0.4	0.75	0.9	0.65	0.95	0.95	2.9	15	12 $\frac{1}{2}$
6. SM. A51420	F	11.0	0.45	..	0.9	0.85	1.15	14	12
7. SM. A51421	$\frac{1}{2}$ R	6.5	0.4	0.8	0.9	0.65	0.85	..	3.0	13	12
Form C											
1. SM. A51003	F	43	0.4	0.8	1.2	0.65	1.1	?0.9	4.1	10	9
2. SM. A51422	F	12	0.45	0.75	0.9	?0.8	?1.1	?0.9	?3.8	..	9
3. SM. A51423	F	10	0.4	0.7	0.8	0.8	1.2	..	4.2	13	10
4. SM. A51424	F	8	0.45	0.75	1.0	0.65	1.0	?0.9	3.6	13	c.10
5. SM. A51425	F	8	0.35	0.6	0.7	0.75	1.25	1.0	4.8	10	7
6. SM. A51426	F	12	0.4	0.55	0.8	4.4	..	8
7. Scot. Sur. H1615	F	18	0.5	0.9	1.3	0.7	1.0	..	4.4	11	9
8. BM (NH) 24953	F	5.5	0.6	?1.1	?1.1	0.5+	0.85+	..	3.6	12	c. 9

Remarks. The other two long subspecies of *G. tamariscus* are *G. tamariscus linearis* and *G. tamariscus distans*. Both are essentially parallel-sided, but *G. tamariscus linearis* is rather broader than *G. tamariscus tamariscus*, tapering suddenly in the proximal end. *G. tamariscus distans* has smaller excavations and longer supragenicular walls than the typical form.

Glyptograptus tamariscus linearis Perner

Plate 72, fig. 8; text-fig. 1v

?1868 *Diplograptus tamariscus* Nicholson, p. 526, pl. 19, fig. 13 (*non* figs. 10–12).?1876 *Diplograptus tamariscus* Nicholson; Lapworth, pl. 2, fig. 34.?1877 *Diplograptus tamariscus* Nicholson; Lapworth, pl. 6, fig. 12.?1897 *Diplograptus tamariscus* Nicholson; Törnquist, p. 15, pl. 11, figs. 15–19.1897 *Diplograptus tamariscus linearis* Perner, p. 4, text-fig. 2 (? pl. 9, fig. 23).1907 *Diplograptus (Glyptograptus) tamariscus* Nicholson; Elles and Wood (*pars*), p. 247, pl. 30, fig. 8c (*non* text-figs. 167a-d, pl. 30, figs. a, b, d).

Lectotype. Specimen figured by Perner (1897) as *G. tamariscus linearis* (text-fig. 2) was designated lectotype by Přibyl (1948); it is from the zone of *Monograptus convolutus*.

Number of specimens. One (the specimen figured by Elles and Wood, pl. 30, fig. 8c). Birmingham Univ. 1272.

Horizon and locality. Dobb's Linn. Probably the zone of *M. cyplus* (*Orthograptus mutabilis*, cf. *Dinorhograptus decussatus*) and monograptid fragments on the same slab).

Revised diagnosis. Long, broad, parallel-sided, width almost constant beyond the first few millimetres, excavations deep.

Description. The only specimen available is preserved flattened, it has a length of 34.5 mm. and reaches a maximum width of 1.5 mm. The rhabdosome is slightly tapering, but is essentially parallel-sided. The width at the first pair of thecae is 0.7 mm. and at the fifth pair of thecae 1.25 mm. The thecae are spaced at the rate of eleven thecae per centimetre decreasing distally to nine per centimetre. The excavations are deep and occupy slightly more than half of the width of the rhabdosome and about half the margin of the rhabdosome. The geniculum is rounded and the supragenicular wall is inclined to the rhabdosome length. The apertures appear to be approximately horizontal. The overlap is apparently very small. Some trace of the septum can be seen although the view preserved is the reverse; this is apparently the result of intense flattening. The proximal end is damaged, so that the lengths of the first thecae cannot be determined with any accuracy, but the aperture of $th1^1$ is at least 1 mm. above the proximal end of the rhabdosome.

Dimensions (in millimetres)

Specimen Number	Flat or relief	Length of rhabdosome	Width			Length		Sicula	$th5^1$ to $th1^1$	Th/cm.	
			$th1$	$th5$	maxi-mum	$th1^1$	$th1^2$		 $th1-2$ $th4-5$
B.U. 1272	F	34.5	0.7	1.5	1.5	1.0+	1.4+	..	3.8	11	c.9

Remarks. This is the largest form of *G. tamariscus* in this collection. It differs from the other forms in the distinct inclination of the thecae, in which respect it resembles *G. serratus*, but *G. serratus* is a much larger and coarser species. The specimen of *G. tamariscus linearis* described here is from a horizon considerably lower than the one at which the form occurs in Bohemia, the zone of *Deuirastrites convolutus* (Příbyl 1948). Other distinguishing features have been mentioned above (see *G. tamariscus tamariscus*).

Glyptograptus tamariscus distans subsp. nov.

Plate 71, figs. 9–10; text-figs. 1k–l

Holotype. The specimen figured as text-fig. 1l and Plate 71 fig. 9, from F horizon (Sudbury 1958) of the *Monograptus gregarius* zone, Rheidol Gorge, near Aberystwyth, SM. A24942.

Number of specimens. Two.

Horizons and localities. Approximately the base of the zone of *Monograptus cyphus* at Dobb's Linn (SM. A51428) and the *Monograptus gregarius* Zone (F horizon) at Rheidol Gorge.

Diagnosis. Narrow form of *G. tamariscus* (0.8 mm. flattened), parallel-sided, inter-apertural distance a little over a millimetre, thecal excavations narrow, supragenicular wall long and perpendicular.

Description. Both specimens have a preserved length of approximately 10 mm. (the holotype is preserved partly as a cast). The width at $th1^1$ is 0.5 mm. in the flattened specimen and 0.4 mm. in the specimen in relief. Both specimens are almost parallel-sided distally to the first pair of apertures and tapered proximally to them. The base

of $th1^1$ extends about 0.1 mm. below the aperture of the sicula and proximal to it is a stout virgella. The flattened specimen from Dobb's Linn shows the reverse view so that the length of the sicula cannot be determined, but it is visible for 0.45 mm. before being obscured by $th1^2$. In the Rheidol Gorge specimen the sicula is apparently exposed for its entire length (1.4 mm.) extending upwards to a little above the aperture of $th1^2$. There are eight or nine thecae per centimetre at the proximal end, decreasing to about seven per centimetre by the fifth pair of thecae.

The supragenicular walls are straight and parallel to the sides of the rhabdosome, averaging 0.8 mm. long. The excavations are shallow, occupying less than half of the width of the stipe even in the flattened specimen. The excavation has an average length of 0.3 mm. being somewhat less for the first couple of thecae. The sigmoidal curvature of the thecae is gentle and the thecal overlap is of the order of a quarter of the thecal length. The apertures are everted. The septum is developed only on the obverse side.

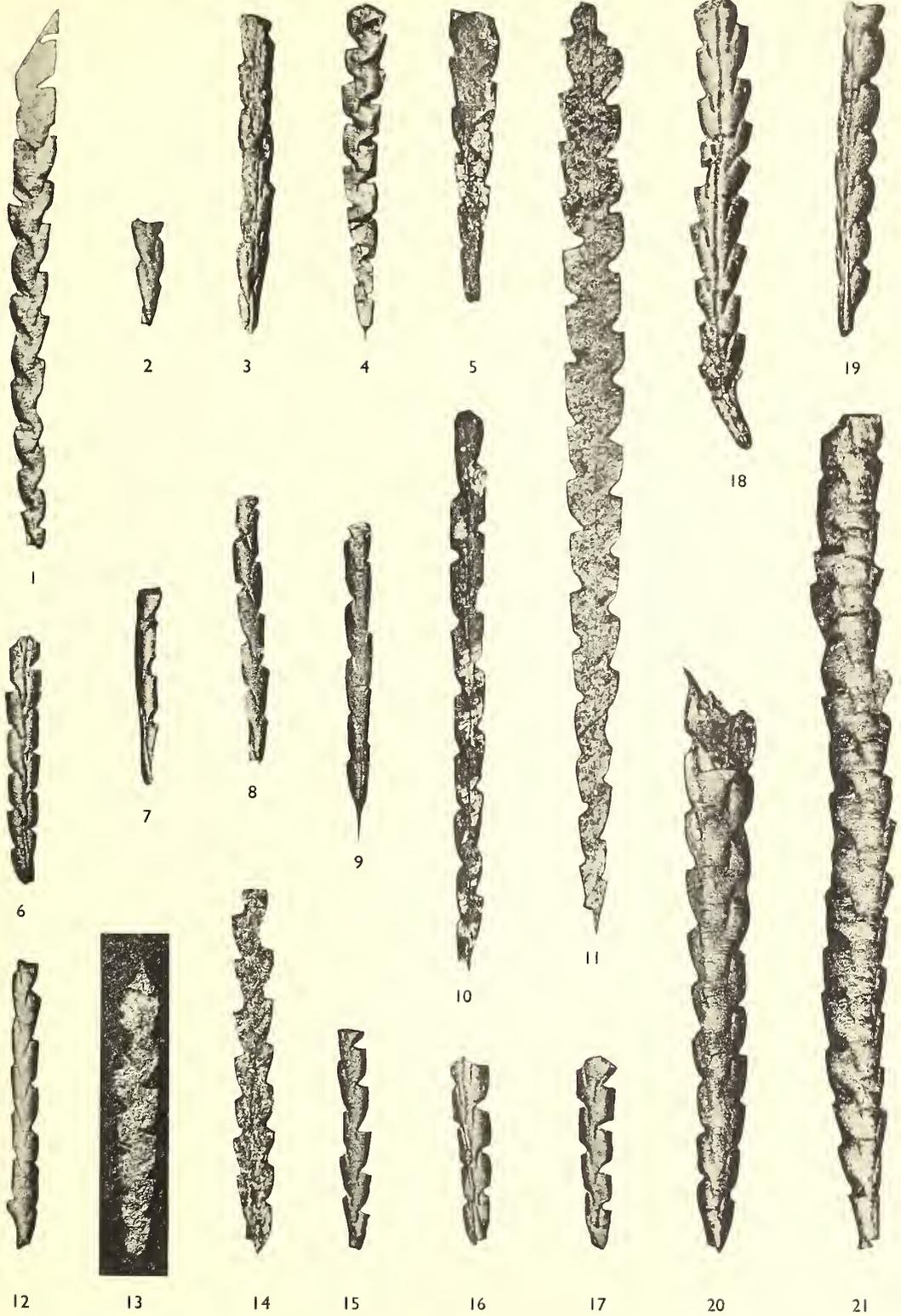
Dimensions (in millimetres)

Specimen Number	Flat or relief	Length of rhabdosome	Width			Length		Sicula	$th5^1$ to $th1^1$	Th/cm.	
			$th1$	$th5$	maxi-mum	$th1^1$	$th1^2$			$th1-2$	$th4-5$
SM. A51428	F	11	0.5	0.65	0.8	1.0	1.4	.	4.9	8	7
SM. A24942	R	10	0.4	0.5	0.5	1.05	1.5	1.4	4.9	9	7½

EXPLANATION OF PLATE 71

All figures except fig. 13, $\times 7.5$. Horizons and localities given in text.

- Fig. 1. *Glyptograptus tamariscus tamariscus* (Nicholson), form B; SM. A20383, reverse of specimen in half relief.
- Figs. 2-3. *Glyptograptus tamariscus tamariscus* (Nicholson) form A. 2, SM. A24934, reverse of specimen in relief. 3, obverse of same specimen.
- Fig. 4. *Glyptograptus tamariscus tamariscus* (Nicholson), form B; SM. A51421, reverse of specimen in half relief.
- Fig. 5. *Glyptograptus* sp. cf. *G. tamariscus fastigans* (Haberfelner); SM. A51443, impression of reverse of flattened specimen.
- Fig. 6. *Climacograptus tamariscoides* sp. nov. SM. A24924, obverse of specimen in relief.
- Figs. 7-8. *Glyptograptus tamariscus angulatus* subsp. nov. 7, SM. A51440, obverse of specimen in relief. 8, SM. A24926, holotype, reverse of specimen in relief.
- Figs. 9-10. *Glyptograptus tamariscus distans* subsp. nov. 9, SM. A24924, holotype, obverse of specimen in relief. 10, SM. A51428, reverse of flattened specimen.
- Fig. 11. *Glyptograptus tamariscus* (Nicholson), form C. SM. A51003, proximal part of long flattened specimen.
- Fig. 12. *Glyptograptus tamariscus acutus*; SM. A24952, reverse of specimen in relief.
- Fig. 13. *Glyptograptus tamariscus tamariscus* (Nicholson), form C. BM (NH) 24953, possible holotype, obverse of flattened specimen, $\times 8.75$.
- Figs. 14-17. *Glyptograptus tamariscus varians* subsp. nov. 14, SM. A51435, reverse of flattened specimen. 15, SM. A51439, holotype reverse of specimen in relief. 16, SM. A24925, obverse of specimen in relief. 17, reverse of same specimen.
- Figs. 18-19. *Glyptograptus enodis enodis* subsp. nov. 18, SM. A24973, holotype, obverse in relief. 19, SM. A51450, obverse in relief.
- Fig. 20. *Glyptograptus enodis latus* subsp. nov. SM. A24967, holotype, reverse in relief.
- Fig. 21. *Glyptograptus enodis enodis* subsp. nov. SM. A51453, reverse of specimen in relief.



PACKHAM, Lower Silurian diplograptids

Remarks. In size and general form *G. tamariscus distans* is closest to *G. tamariscus angulatus*, but differs from it in having a much shallower and shorter excavation. *G. tamariscus angulatus* also has a more abrupt geniculation.

Glyptograptus tamariscus varians subsp. nov.

Plate 71, figs. 14–17; text-figs. 1a–f

Holotype. The specimen figured as text-fig. 1d and Plate 71, fig. 5, from C horizon (Sudbury 1958) of the *Monograptus gregarius* Zone, Rheidol Gorge, near Aberystwyth, SM. A51439.

Number of specimens. Twelve.

Horizons and localities. Dobb's Linn; low in the zone of *M. cyplus* (SM. A51429, SM. A51430), middle of the same Zone (SM. A51431, SM. A51432), top of the zone (SM. A51434, SM. A51435), lower part of the *M. gregarius* zone (SM. A51436, SM. A51437). Rheidol Gorge; zone of *M. gregarius*, horizon D (SM. A51738), horizon C (SM. A24925, SM. A24927, SM. A51439).

Diagnosis. Short narrow form of *Glyptograptus tamariscus* reaching maximum width by at least the third pair of thecae and thereafter parallel-sided or decreasing in width, geniculum becoming more gentle distally.

Description. The longest specimen is 8 mm. in length. The width of the rhabdosome is approximately uniform throughout the length or narrows distally. The widest specimen reaches a maximum width of 1.1 mm. Accompanying the tendency for the rhabdosome to narrow distally there is a change in the thecal shape; distally the geniculum is rounder and the excavation a little deeper, giving the thecae a more gentle sigmoidal curvature. The proximal end of the rhabdosome is robust and $th1^1$ varies in length between 0.75 and 1.15 mm. The sicula has between 1.0 and 1.4 mm. of its length visible on the obverse side, this could be as high as 1.6 mm. in one specimen. Thecae are at the rate of eleven to fourteen per centimetre at first, decreasing somewhat in most specimens towards the distal end.

Dimensions (in millimetres)

Specimen Number	Flat or relief	Length of rhabdosome	Width			Length		Sicula	$th5^1$ to $th1^1$	Th/cm.	
			$th1$	$th5$	maximum	$th1^1$	$th1^2$			$th1-2$	$th4-5$
SM. A51430	F	4	0.65	0.7	0.7	0.95	1.2	..	3.6	12½	10½
SM. A51429	F	6.5	0.65	c.1.0	1.0*	0.90	1.15	..	3.0	14	10½
SM. A51431	F	8	1.0	0.95	1.1 (th2)	1.1	1.6	?1.6	3.0	13	12
SM. A51432	F	7	0.7	0.75	0.8	1.15	1.5	1.4	3.2	13	11
SM. A51434	F	5	0.65	0.8	0.8	0.95	1.15	..	3.0	13	13
SM. A51435	F	7	0.7	0.75	0.8 (th3)	0.95	1.5	..	3.3	12	10½
SM. A51436	F	6	0.7	0.75	0.9	1.1	1.6	?1.0	3.3	14	11
SM. A51437	F	6.5	0.7	0.85	0.85	0.75	1.35	..	3.5	11½	10½
SM. A51438	R	4.3	0.6	0.6†	0.7	?0.9	1.2	..	3.4†	12	11†
SM. A51439	R	4.5	0.55	0.6	0.65	0.9	1.2	..	3.5	12½	11½
SM. A24925	R	4.1	0.55	0.8	0.80	0.85	1.25	1.0	3.2†	12½	c.10
SM. A24927	R	2.5	0.45	..	0.55	?1.0	1.4	?1.4	..	12	..

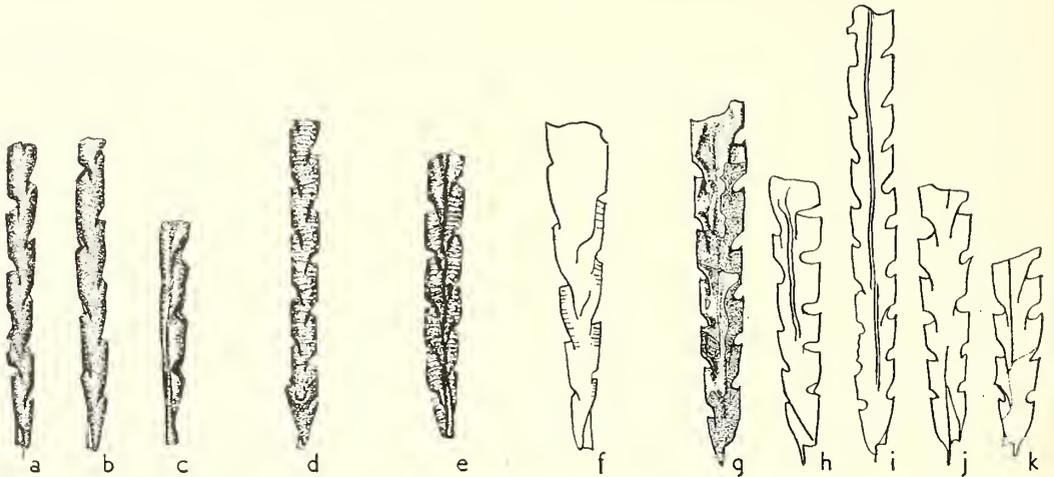
* Specimen preserved in twisted position. † Extrapolated.

Remarks. The parallel-sided nature of the rhabdosome with its relatively robust proximal end distinguishes this form from all others. It is shorter and more robust than *Glyptograptus tamariscus tamariscus*, its thecae are more closely spaced than *G. tamariscus distans* and it is a broader form than *G. tamariscus angulatus*.

Glyptograptus tamariscus angulatus subsp. nov.

Plate 71, figs. 7-8; text-figs. 3a-c

Holotype. The specimen figured as text-fig. 3b and Plate 71, fig. 8, from horizon C (Sudbury 1958) of the zone of *Moulograptus gregarius* from Rheidol Gorge near Aberystwyth, SM. A24926.



TEXT-FIG. 3. *a-c.* *Glyptograptus tamariscus angulatus* subsp. nov. *a*, Reverse of specimen in relief, SM. A24976. *b*, Holotype, reverse of specimen in relief, SM. A24926. *c*, Obverse of specimen in relief, SM. A51440.
d, *G. tamariscus acutus*. Reverse of specimen in relief, SM. A24952.
e, *Climacograptus tamariscoides* sp. nov. Holotype, obverse of specimen in relief, SM. A24924.
f, *Glyptograptus* sp. cf. *G. tamariscus fastigans* Haberfelner. Impression of reverse of flattened specimen, SM. A51443.
g-k. *Climacograptus tangshaneensis linearis* subsp. nov. *g*, Holotype, obverse of flattened specimen, SM. A51448. *h*, Obverse of flattened specimen, SM. A51446. *i*, Impression of reverse of flattened specimen, SM. A51444. *j*, Obverse of flattened specimen, SM. A51449. *k*, Reverse of flattened specimen, SM. A51447.

All figures $\times 7.5$. Horizons and localities given in text.

Number of specimens. Five.

Horizons and localities. Dobb's Linn; near the top of the zone of *M. cyphus* (SM. A51441). Rheidol Gorge; at the top of the *M. cyphus* Zone (SM. A24976) from horizon T, and the *M. gregarius* Zone, horizon G (SM. A51441) and horizon C (SM. A24926, SM. A51442).

Diagnosis. Narrow, short form, parallel-sided, geniculum relatively abrupt, supra-genicular wall long and perpendicular, thecal excavation deep.

Description. The length of the longest specimen of this form is 7 mm. and the width of specimens preserved in relief at the first pair of thecae is 0.4 mm. and 0.5 mm. in the

flattened specimen (Dobb's Linn), distally the form widens slightly, but proximally it tapers evenly to a pointed proximal extremity. The base of $th1^1$ extends slightly below the aperture of the sicula and there is a short virgella.

The supragenicular walls are straight and parallel to the sides of the rhabdosome averaging 0.7 mm. in length. The geniculum is abrupt rather than flowing, but not angular. The infragenicular wall is moderately to slightly concave longitudinally and planar transversely. The excavations occupy approximately half the width of the rhabdosome in specimens preserved in relief. The apertures are everted, the overlap of the thecae is less than a third. There are between 9 and $11\frac{1}{2}$ thecae per centimetre initially, decreasing distally.

Dimensions (in millimetres)

Specimen Number	Flat or relief	Length of rhabdosome	Width			Length		Sicula	th5 ¹ to th1 ¹	Th/cm.	
			th1	th5	maximum	th1 ¹	th1 ²			th1-2	th4-5
SM. A24976	R	5.5	0.4	0.5	0.5	0.95	1.4	..	3.9	$11\frac{1}{2}$	$10\frac{1}{2}$
SM. A24926	R	5.6	0.45	0.5	0.5	1.1	1.5	..	4.3	10	$8\frac{1}{2}$
SM. A51440	R	4.0	0.4	..	0.55	1.35	?1.7	1.45	..	$9\frac{1}{2}$..
SM. A51441	F	3.7	0.5	..	0.65	1.0	1.6	c.1.5	..	9	..
SM. A51442	R	3.3	0.4	..	0.5	1.0	c.1.35	1.5	..	9	..

Remarks. The geniculum of this subspecies is the most angular of any of the subspecies of *G. tamariscus* and hence comes closest to *Climacograptus*, but there is still some rounding of the geniculum. *Glyptograptus tamariscus angulatus* is close to *G. tamariscus distans*, but differs from it in two respects, the sharper geniculation, and the deeper and longer excavation.

Glyptograptus tamariscus acutus subsp. nov.

Plate 71, fig. 12; text-fig. 3d

Number of specimens. One.

Locality and horizon. Rheidol Gorge; *Monograptus gregarius* Zone, horizon H of Sudbury (1958), SM. A24952.

Diagnosis. Narrow (0.5 mm.), parallel-sided, interapertural distance averages 0.9 mm. for the first five thecae. Thecal overlap small, geniculation abrupt proximally becoming gentle distally. Supragenicular wall parallel to sides of rhabdosome. Theca 1¹ has its aperture 0.8 mm. from proximal end of rhabdosome.

Description. The specimen is 6 mm. long and has a uniform width of 0.5 mm. but it is distorted in the region of $th1^2$. Below the first pair of thecae the form tapers sharply. The base of theca 1¹ is level with the aperture of the sicula. The length of the sicula is not known since only the reverse side is visible, but here it is exposed for 0.2 mm. before being obscured by $th1^2$. The thecae are closely spaced at first (fifteen per centimetre) decreasing to ten per centimetre by the fifth pair of thecae. The supragenicular walls are straight and parallel to the side of the rhabdosome averaging 0.65 mm. long. The geniculation is abrupt at first, but appears to become slightly more flowing distally.

The infragenicular wall is approximately planar. The excavations are moderately deep, occupying half of the width of the rhabdosome, and the apertures are strongly everted.

Dimensions (in millimetres)

Specimen Number	Flat or relief	Length of rhabdosome	Width			Length		Sicula	th5 ¹ to th1 ¹	Th/cm.	
			th1	th5	maximum	th1 ¹	th1 ²			th1-2	th4-5
SM. A24952	R	6	?	0.5	0.5	0.8	1.1	..	3.5	15	10

Remarks. This form is clearly closely related to *G. tamariscus angulatus* and *G. tamariscus varians*. The geniculum is more angular than *G. tamariscus angulatus* proximally, and the thecae are more closely spaced. Like *G. tamariscus varians* the thecae change in shape distally becoming more gently curved, but *G. tamariscus varians* is a much more robust form.

Glyptograptus sp. cf. *G. tamariscus fastigans* Haberfelner

Plate 71, fig. 5; text-fig. 3f

1931a *Glyptograptus tamariscus* mut *fastigans* Haberfelner, p. 105, pl. 3, figs. 17a-e.

Number of specimens. One.

Locality and horizon. Knock, Swindale Beck, immediately downstream from the smash belt between Ashgill shales and Browgill Beds, stratigraphically below locality *c* of Shotton (1935), zone of *Mono-graptus turriculatus*, SM. A51443.

Description. The rhabdosome is wedge-shaped, 5.6 mm. long, tapering evenly throughout and reaching a width of a fraction over 1 mm. at the distal end. The periderm is robust, preserved as a thick, shiny, carbonaceous film. The specimen is partly an obverse view and partly a reverse view. It appears that no septum is present. The proximal end of the rhabdosome is finely pointed leaving the sicula prominent. The sicula is visible in the reverse view for 0.7 mm. before being obscured by th1². The aperture of th1¹ is 1.0 mm. from the proximal end of the rhabdosome and that of th1² is 1.2 mm. from the proximal end. The thecae are narrow in the apertural region, with everted apertures. The excavations are long and shallow, of approximately the same depth throughout the rhabdosome (0.15 mm.), thus occupying a much smaller proportion of the width of the rhabdosome distally than proximally. The length of the thecae is difficult to determine; the overlap appears to be at least a third and could be well over a half. The interthecal distance is 0.9 mm. (eleven thecae per centimetre) for th1 to th2 increasing to 1.1 mm. (nine thecae per centimetre) distally.

Dimensions (in millimetres)

Specimen Number	Flat or relief	Length of rhabdosome	Width			Length		Sicula	th5 ¹ to th1 ¹	Th/cm.	
			th1	th5	maximum	th1 ¹	th1 ²			th1-2	th4-5
SM. A51443	F	5.6	0.5	1.05	1.10	1.0	1.25	..	4.1	11	10½

Remarks. This specimen is very similar to *G. tamariscus fastigans*, but differs from it in having its apertures everted rather than introverted, and the thecal overlap in this present specimen could be larger. The horizon of the specimen from Knock is the same as Haberfelner's specimens from the Carnic Alps.

The narrowness of the apertural region of this form and the consequent shallowness of the excavations, makes it doubtful whether it should be referred to *G. tamariscus* at all. It has much in common with *G. elegans* especially in the way that the axial part of the rhabdosome increases distally. The apertures are more restricted than those of *G. elegans*.

Genus CLIMACOGRAPTUS Hall 1865

Climacograptus tamariscoides sp. nov.

Plate 71, fig. 6; text-fig. 3e

Holotype. The specimen figured as text-fig. 3e and Pl. 71, fig. 6, from horizon C of Sudbury (1958) in the zone of *Monograptus gregarius*, Rheidol Gorge near Aberystwyth, SM. A24924.

Number of specimens. Two.

Localities and horizons. The locality and horizon of the holotype is given above, the other specimen is from Skelgill probably from the *Monograptus argenteus* subzone of the *M. gregarius* Zone BM (NH) H. 1626.

Diagnosis. Short parallel-sided *Climacograptus*, width about 0.7 mm. in relief, geniculation abrupt, slightly less so distally, thecae closely spaced, with average interapertural distance 0.8 mm. (twelve thecae per centimetre).

Description. The holotype is 5 mm. long and attains a width of 0.7 mm. This width is reached by the second pair of thecae, proximally to this the rhabdosome tapers regularly. The obverse view is preserved showing the sicula and a slightly undulating septum. The sicula has an exposed length of 1.2 mm., the top reaching the level of the top of the excavation of $th1^2$, and a width at the apertural end of 0.15 mm. The base of theca 1^1 extends proximally only as far as the aperture of the sicula. The apertures of thecae 1^1 and 1^2 are 0.75 and 1.15 mm. from the proximal end of the rhabdosome and the average interapertural distance is 0.8 mm. The supragenicular wall is about 0.65 mm. long and slightly convex but generally parallel to the sides of the rhabdosome. The geniculation is abrupt proximally, but becomes gentler distally. The excavations are small giving the thecae the appearance of being restricted in the apertural region. The overlap is of the order of one-fifth.

Dimensions (in millimetres)

Specimen Number	Flat or relief	Length of rhabdosome	Width			Length		Sicula	th5 ¹ to th1 ¹	Th/cm.	
			th1	th5	maxi-mun	th1 ¹	th1 ²			th1-2	th4-5
SM. A24924	R	5	0.45	0.7	0.7	0.75	1.15	1.2	3.4	12	12

Remarks. This species is clearly related to *Glyptograptus tamariscus*, but differs from it in the abruptness and angularity of the geniculum, it is this feature which suggests reference to the genus *Climacograptus*. Further, the thecae in *C. tamariscoides* are more closely spaced than any form of *G. tamariscus* except *G. tamariscus tamariscus* form B.

Like some of the forms of the latter species the thecal profile changes in shape towards the distal end. It is distinct from other species of *Climacograptus* occurring at the same horizon; *C. hughesi* has very distinctive thecae and a strongly undulating septum, *C. minutus* has a tapering rhabdosome and more closely set thecae, and all the other forms of *Climacograptus* at this horizon are much larger.

Climacograptus tangshanensis linearis subsp. nov.

Plate 72, figs. 2-3; text-figs. 3g-k

Holotype. The specimen figured as text-fig. 3g from Dobb's Linn in the upper part of the zone of *M. gregarius* probably about the equivalent of horizons A to J of Sudbury (1958) at Rheidol Gorge, SM. A51448.

Number of specimens. Six.

Locality and horizons. All the specimens are from Dobb's Linn from the zone of *M. gregarius*. One specimen (SM. A51444) is from the lower part of the zone, the remainder are from the same horizon as the holotype.

Diagnosis. *Climacograptus* with short rhabdosome, parallel-sided or gently tapering proximally, proximal end robust, apertures introverted showing a suggestion of an apertural spine.

Description. All the specimens are preserved in very low relief. The longest specimen is 8 mm. in length and is almost parallel-sided; the others are shorter and rather more tapering in form. Nevertheless, the tapering ones are still robust at the proximal end. The proximal end of the rhabdosome is prolonged by a short stout virgella and the proximal extremity of $th1^1$ is below the aperture of the sicula. The septum appears to be developed only on the obverse side of the rhabdosome. The inter-thecal interval is about 0.75 mm. for the first two pairs of thecae (about thirteen thecae per centimetre) increasing to about 0.85 distally (about $11\frac{1}{2}$ thecae per centimetre). The geniculum is abrupt, formed by the junction of the straight supragenicular wall and the concave infragenicular wall. The supragenicular wall is approximately perpendicular or slightly inclined to the rhabdosome sides. The apertures are very distinctly introverted and the apertural lip is concave so that in some views the aperture seems to extend into a short spine. The excavations are of moderate depth averaging about 0.2 mm. and about the same length, varying only very slightly in size from one end of a rhabdosome to the other. The alternation of the thecae varies; in the holotype they are strongly alternating, but in some other specimens they are sub-opposite. In all specimens the periderm is preserved as a thick, shiny, carbonaceous film, suggesting that it was relatively thick.

Dimensions (in millimetres)

Specimen Number	Flat or relief	Length of rhabdosome	Width			Length		Sicula	$th5^1$ to $th1^1$	Th/cm.	
			$th1$	$th5$	maxi-mum	$th1^1$	$th1^2$			$th1-2$	$th4-5$
SM. A51444	F	8.5	0.65	0.8	0.8	0.9	1.1	..	3.0	$14\frac{1}{2}$	$11\frac{1}{2}$
SM. A51445	F	5	0.65	0.95	0.95	0.9	1.2	..	3.0	15	12
SM. A51446	F	5	0.65	0.95	0.95	0.9	1.1	..	3.1	15	$11\frac{1}{2}$
SM. A51447	F	3.5	0.70	..	0.9	0.9	1.0	$13\frac{1}{2}$..
SM. A51448	F	6	0.65	0.90	0.95	0.9	1.2	..	3.4	$12\frac{1}{2}$	11
SM. A51449	F	4.5	0.65	0.95	0.95	0.8	1.0	1.0	3.0	$14\frac{1}{2}$	$11\frac{1}{2}$

Remarks. This subspecies seems most closely related to the parent species *Climacograptus tangshanensis* Hsü, described by Hsü (1934) from the Koachiapien shale near Nanking, from the zone of *Monograptus leei* Hsü, which he regards as the equivalent of the zone of *M. gregarius* in the British sequence. *C. tangshanensis* is of the same order of length as the rhabdosome of the present subspecies, which differs principally from the typical form in being narrower (1.0 mm. as against 1.5 mm.) and having its supragenicular walls rather more vertical. It is not clear whether Hsü's specimens have a complete median septum or not. The characters of *C. tangshanensis linearis* are quite different from other described British Silurian climacograptids with the possible exception of *C. scalaris miserabilis*, which has thecae slightly farther apart and horizontal apertural margins.

(b) *Wider forms*

Genus GLYPTOGRAPTUS Lapworth 1873

Glyptograptus euodis sp. nov.

Plate 71, figs. 18–22; Plate 72, fig. 1; text-fig. 4e, g–j

Holotype. The specimen figured as text-fig. 4g, Plate 71, fig. 18, from horizon P of Sudbury (1958) of the zone of *Monograptus gregarius* (i.e. near the base of the zone), Rheidol Gorge, near Aberystwyth, SM. A24973.

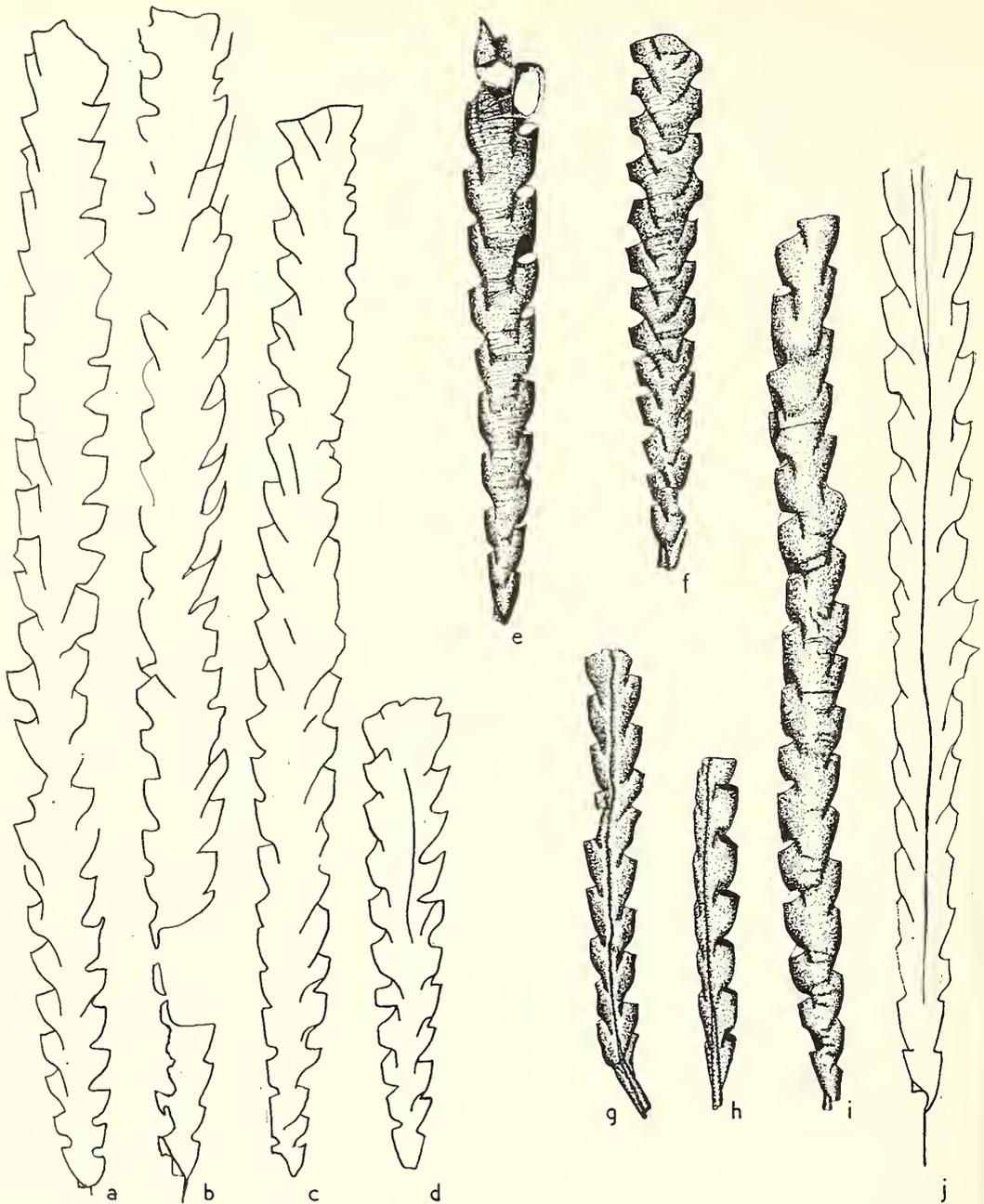
Number of specimens. Eight (both subspecies).

Horizons and localities. Rheidol Gorge, horizons O and P of Sudbury (1958) of the zone of *Monograptus gregarius* (near the base of the zone). Dobb's Linn, horizon unknown.

Diagnosis. Glyptograptid with gently sigmoidally curved thecae overlapping one-third, inclined to the rhabdosome at a low angle, apertures everted strongly, excavations long and of moderate depth, approximately uniformly deep throughout, proximal end of rhabdosome tapered.

Description. Rhabdosomes attain a length of 37 mm. The rhabdosomes widen rapidly for the first few thecae, then remain constant or gradually increase in width up to a maximum of 1.5 mm. in uncompressed specimens. The thecae range in frequency from eight to eleven per centimetre, in the mature portions of specimens. The thecae overlap about a third and have everted apertures. The geniculum is very gentle, occurring rather distally on the specimen so that the thecal excavation is long and open, giving the theca an appearance of being inclined to the rhabdosome length rather than strongly sigmoidally curved. The sicula is long and slender in one form at least, the apex reaches over halfway between $th1^1$ and $th2^1$ and is exposed for what is apparently its entire length. The median septum is incomplete, being absent from the reverse side, but complete on the obverse side. If the rhabdosome widens distally then the excavations remain approximately the same depth. Thus, because of the widening of the common canal, the excavations occupy a smaller proportion of the width of the rhabdosome distally.

Remarks. This species can be distinguished from *G. tamariscus* by the more gentle curvature of the thecae, the longer and less definite excavations occupying a smaller proportion of the rhabdosome width, and by a greater overlap of the thecae. *G. incertus* also has thecae with a more pronounced sigmoidal curvature. Apart from their



TEXT-FIG. 4. *a-d*. *Glyptograptus incertus* Elles and Wood. *a*, Lectotype, reverse of flattened specimen BU. 1274. *b*, Reverse of flattened specimen, SM. A51055. *c*, Reverse of flattened specimen, BU. 1273. *d*, Reverse of flattened specimen, SM. A51454.
e, g, Glyptograptus enodis subsp. nov. Holotype, reverse in relief, SM. A24967.
f, Climacograptus alternis sp. nov. Holotype, reverse in relief, SM. A24957.
g-j. Glyptograptus enodis enodis subsp. nov. *g*, Holotype, obverse in relief, SM. A24973. *h*, Obverse in relief, SM. A51450. *i*, Reverse in relief, SM. A51453. *j*, Reverse of flattened specimen, BU. 1271.
 All figures $\times 7.5$. Horizons and localities given in text.

somewhat wider rhabdosomes and differently shaped thecae, *G. persculptus* and *G. sinuatus* differ from *G. enodis* in having a greater thecal overlap (about a half).

Glyptograptus enodis enodis subsp. nov.

Plate 71, figs. 18–19, 21; Plate 72, fig. 1; text-figs. 4g–j

1907 *Diplograptus* (*Glyptograptus*) *tamariscus* Nicholson; Elles and Wood, p. 247, text-fig. 167d, pl. 30, fig. 8b (*non* text-figs. 167a–c, pl. 30, figs. 8a, c, d).

Holotype. The specimen figured as text-fig. 4g, and Plate 71, fig. 18, from horizon P (Sudbury 1958) of the zone of *Monograptus gregarius*, Rheidol Gorge, near Aberystwyth, SM. A24973.

Number of specimens. Seven.

Horizons and localities. Rheidol Gorge, the zone of *M. gregarius*. SM. A24973, 51427 from horizon P and SM. 51450–3 from horizon O. Dobb's Linn, horizon unknown, BU.1271 (the specimen figured by Elles and Wood 1907, as *G. tamariscus* in text-fig. 167d and plate 30, fig. 8b).

Diagnosis. *G. enodis* in which width increases quickly until about the fifth pair of thecae, then parallel-sided or slowly widening.

Description. The longest specimen (Elles and Wood's specimen from Dobb's Linn) attains a length of 37 mm. All the specimens preserved in relief reach their maximum width or very close to it by the fifth pair of thecae. The flattened specimen from Dobb's Linn continues to widen slowly beyond this level. The proximal extremity of the first theca extends slightly beyond the aperture of the sicula, the flattened specimen has a stout virgella. The sicula is long and slender, exposed for its entire length or close to it, and extends distally to about half-way between $th1^1$ and $th2^1$. The thecae have gentle sigmoidal curvature, everted apertures and an overlap of approximately one-third. The supragenicular walls are inclined to the margins of the rhabdosome. The common canal is roughly uniform in width beyond the fifth pair of thecae and occupies about half the width of the rhabdosome in that region and less proximally. The median septum is absent on the reverse side, but complete on the obverse side.

Dimensions (in millimetres)

Specimen Number	Flat or relief	Length of rhabdosome	Width			Length		Sicula	$th5^1$ to $th1^1$	Th/cm.	
			$th1$	$th5$	maxi-mum	$th1^1$	$th1^2$			$th1-2$	$th4-5$
SM. A24973	R	9	0.5	0.95	1.0	1.1	c.1.8	1.7	3.5	c.11	10
SM. A51450	R	6.5	0.6	0.9	0.9	1.3	1.5	1.9	3.6	10	10
BU. 1271	F	37	0.65	1.2	1.7	c.1.1	c.1.2	..	3.7	c.10	9½*
SM. A51451	R	3.5	0.65	..	0.95	c.1.0	c.1.4	11	..
SM. A51452	R	12	0.65	1.1	1.1	1.1	1.7	..	4.1	10	10
SM. A51427	R	6.5	0.65	1.1	1.1	1.1	1.4	1.4	4.2	10	8½
SM. A51453	R	17	c.0.7	1.2	1.3	?1.0	?1.5	..	4.0	11	10*

* Decreasing distally to 9.

Remarks. This form can be distinguished from *G. enodis latus* by its deeper excavations and the different forms of the rhabdosome.

Glyptograptus enodis latus subsp. nov.

Plate 71, fig. 20; text-fig. 4e

Holotype. The specimen figured as text-fig. 4e, and Plate 71, fig. 20, from horizon O (Sudbury 1958) of the zone of *Monograptus gregarius*, Rheidol Gorge, near Aberystwyth, SM. A24969.

Number of specimens. One (the holotype).

Diagnosis. Long form of *G. enodis*, increases in width throughout its length, common canal widens distally.

Description. The specimen, which is preserved in relief, is 10.8 mm. long, increasing in width throughout its length, reaching a maximum width at the distal end of 1.4 mm. The rhabdosome is sub-rectangular in cross-section. The common canal widens steadily throughout the rhabdosome and occupies a greater proportion of the width distally than proximally. It occupies about half the width at the distal end. The thecae overlap about a third and have a very gentle sigmoidal curvature and everted apertures. The excavations are relatively shallow, they would occupy about a third of the width of the rhabdosome in a full bi-profile view. The length of the sicula is unknown, but its aperture is a little distal to the proximal end of the rhabdosome. The septum is incomplete, it is present at the distal end of the rhabdosome on the obverse side but is absent on the reverse side of the rhabdosome. The specimen shows distinct growth-lines.

Dimensions (in millimetres)

Specimen Number	Flat or relief	Length of rhabdosome	Width			Length		Sicula	th5 ¹ to th1 ¹	Th/cm.	
			th1	th5	maxi-mum	th1 ¹	th1 ²			th1-2	th4-5
SM. A24969	R	10.8	0.65	1.1	1.4	1.0	1.4	..	3.7	11	9

Remarks. Apart from the general resemblance to the typical form, this subspecies has a thecal shape a little reminiscent of *G. sinuatus* and *G. persculptus*, but its thecae are considerably shorter and inclined to the rhabdosome at a smaller angle.

Glyptograptus incertus Elles and Wood

Plate 72, figs. 6-7; text-figs. 4a-d

1907 *Diplograptus (Glyptograptus) tamariscus* var. *incertus* Elles and Wood p. 249, text-fig. 168a, b, pl. 30, figs. 9a-d.

1922 *Diplograptus tamariscus incertus* Elles and Wood; Gortani, p. 104, pl. 17, fig. 24.

Lectotype. The specimen illustrated by Elles and Wood (1907) as plate 30, fig. 9c, and figured here as text-fig. 4a, and Plate 72, fig. 6, from the Birkhill shale, Garple Linn, near Moffat (*Monograptus sedgwicki* Zone), Birmingham Univ. Coll. 1274.

Number of specimens. About 100.

Horizons and localities. Dobb's Linn: specimens seen from the zones of *M. convolutus* and *M. sedgwicki* (SM. A51055, which was figured by Elles and Wood, 1907, on pl. 30, fig. 9a, and SM. A51454 are from the latter zone). Garple Linn; *M. halli* beds (the lectotype, BU. 1274) and horizon unknown (BU. 1273, figured by Elles and Wood, 1907, on pl. 30 fig. 9b).

Diagnosis. Robust glyptograptid, essentially parallel-sided with broad proximal end,

thecae with distinct sigmoidal curvature, more pronounced proximally than distally, overlap approximately one-third, eleven thecae per centimetre in the distal part.

Description. Rhabdosomes are normally long, reaching a length of 22 mm. They have blunt, rather than pointed proximal extremities, with a width of 0.6 to 0.8 mm. at the first pair of thecae, widening gradually to about 1.4 mm. at 5 mm. from the proximal end, eventually reaching a maximum of about 1.6 mm. The length of the sicula is unknown, as it is not clearly preserved in any of the specimens examined. It is possible, judging from the shape of the proximal end of the rhabdosome, that only a small proportion of its length was exposed. Normally, there is no evidence of a septum of the specimens, but one or two show some traces, e.g. text-fig. 4d. The thecal profile varies throughout the rhabdosome; in the proximal end the sigmoidal curvature is very strong in some specimens, but decreases in intensity towards the distal end of the rhabdosome. This results in a lengthening of the excavation towards the distal end. Overlap is not easy to determine because of the rather poor state of preservation of the specimens, but it appears to be generally of the order of a third, though in some it could be as high as a half. The interthecal interval is about 0.7 mm. between the first two thecae (about fourteen thecae per centimetre) but increases over the interval in which the width increases rapidly, to 0.9 mm. between the apertures (eleven thecae per centimetre). The excavations are deeper distally, but considerably longer, and occupy a smaller proportion of the width of the rhabdosome (a half or more at the proximal end, and a little over a third at the distal end). The apertures are horizontal or slightly everted and the supra-genicular walls are inclined to the rhabdosome margin. The periderm is moderately thick.

Dimensions (in millimetres)

Specimen Number	Flat or relief	Length of Rhabdosome	Width			Length		Sicula	th5 ¹ to th1 ¹	Th/cm.	
			th1	th5	maximum	th1 ¹	th1 ²			th1-2	th4-5
SM. A51055	F	22.5	c.0.8	c.1.2	1.6	0.6	30.6	..	?	?	?
BU. 1273	F	20.5	0.6	1.2	1.7	?	?	..	2.8	15	11
BU. 1274	F	23	0.8	1.3	1.7	0.6	0.8	..	2.9	15	11
SM. A51454	F	9.8	0.6	1.3	1.7	0.6	0.9	..	2.8	14	12

Remarks. This species is very distinctive. Comparison with *Glyptograptus tamariscus* reveals sufficient points of difference to warrant its being regarded as a separate species, and Elles (1922) apparently regarded it as a separate species rather than a variety of *G. tamariscus*, since it is cited as such in the table accompanying that paper. The shape and size of the rhabdosome, the change in thecal interval and thecal shape are all distinctive characters, distinguishing it from not only *G. tamariscus*, but other species of *Glyptograptus*. It is also distinct from *Mesograptus* because the proximal thecae of *G. incertus* are never truly amplexoid, nor are the distal thecae truly orthograptid.

Glyptograptus elegans sp. nov.

Plate 72, figs. 4, 10-12; text-figs. 5a-i

1920 *Diplograptus tamariscus incertus* Elles and Wood; Gortani, p. 18, pl. 1, fig. 24 (non figs. 25-27).

1922 *Diplograptus tamariscus* Nicholson; Gortani, p. 105, pl. 17, fig. 25.

Holotype. The specimen figured here as text-fig. 5c, and Plate 72, fig. 12, from the zone of *Monograptus sedgwicki*, Dobb's Linn, near Moffat, SM. A51455.

Number of specimens. Ten.

Horizons and localities. Dobb's Linn: lower part of the zone of *M. gregarius* (SM. A51416), zone of *M. convolutus* (SM. A51458), zone of *M. sedgwicki* (SM. A51455, SM. A51456, SM. A51459, SM. A20411). Knock; Swindale Beck, immediately downstream from the smash belt between the Ashgill shales and the Browgill beds, stratigraphically below locality C. of Shotton (1935), zone of *M. turriculatus* (SM. A51457). Torver Beck; zone of *M. sedgwicki* (SM. A20386a, b). Rheidol Gorge; zone of *M. gregarius* D horizon (SM. A24933 doubtfully referred to this species).

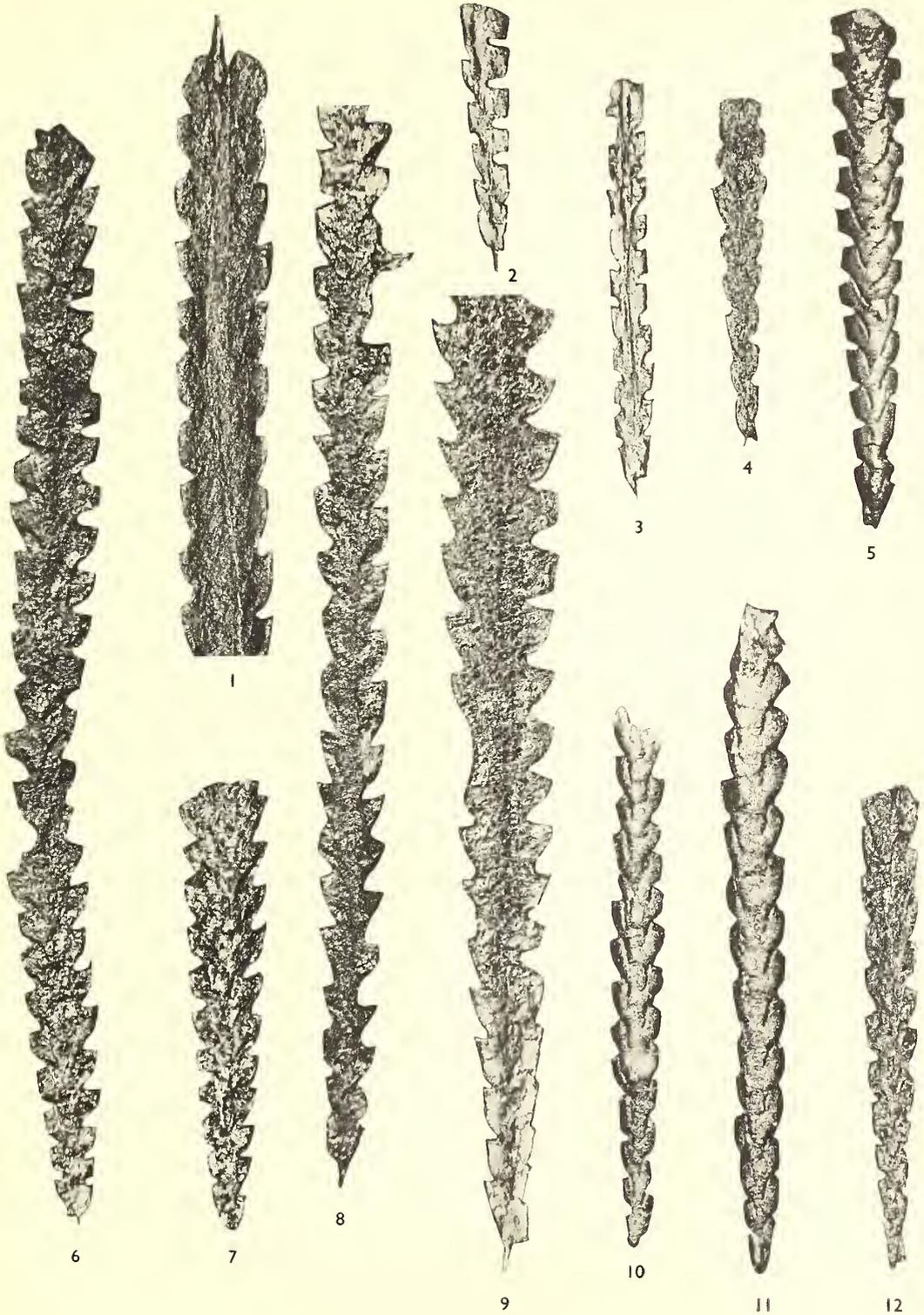
Diagnosis. *Glyptograptus* with rhabdosome tapering to a fine point proximally, may reach its maximum width in as little as 5 mm., thecae considerably more sigmoidally curved proximally than distally.

Description. The rhabdosomes are normally short, 8 mm. or so in length, reaching a maximum length of 15 mm. They widen gradually over the first 5 millimetres of their length to about 1 mm., from a width of about 0.5 mm. at the first pair of thecae. Proximal to the first pair of thecae, the rhabdosome is finely tapered; this feature is more apparent in flattened specimens, in which the sicula is evident in both obverse and reverse views. Distally, the rhabdosome either continues to widen throughout its length or else becomes parallel-sided. The maximum width observed is 1.4 in an uncompressed specimen. The sicula is quite prominent and has an exposed length of 1 millimetre. About half the specimens show some trace of a septum, but one specimen (Text-fig. 6a), although well preserved, shows no trace of a septum on the obverse side. The thecal profile is strongly sigmoidal at the proximal end, with narrow and often deep excavations. In this region the supragenicular walls are parallel to the sides of the rhabdosome. Distally the sigmoidal curvature is only moderate, the excavations are longer, more open and a little deeper, and the supragenicular walls are inclined gently to the margins of the rhabdosome. The overlap appears to be of the order of a third. The thecal interval decreases slightly from the proximal to the distal end; between the fourth and the fifth thecae it is between ten and twelve per centimetre. The apertures are everted. The periderm appears to have been of moderate thickness.

EXPLANATION OF PLATE 72

All figures $\times 7.5$. Horizons and localities given in text.

- Fig. 1. *Glyptograptus enodis enodis* subsp. nov.; BU. 1271, distal thecae of flattened specimen.
 Figs. 2-3. *Climacograptus tangshanensis linearis* subsp. nov. 2, SM. A51446, obverse of flattened specimen. 3, SM. A51444, impression of reverse of flattened specimen.
 Fig. 4. *Glyptograptus elegans* sp. nov. SM. A51457, obverse of flattened specimen.
 Fig. 5. *Climacograptus alternis* sp. nov. SM. A24957, holotype, reverse in relief.
 Fig. 6-7. *Glyptograptus incertus* Elles and Wood. 6, BU. 1274, lectotype, reverse of flattened specimen. 7, SM. A51454, reverse of flattened specimen.
 Fig. 8. *Glyptograptus tamariscus linearis* Perner; BM 1272, Reverse of flattened specimen.
 Fig. 9. *Glyptograptus serratus* Elles and Wood; SM. A20388b, reverse of flattened specimen, counterpart of specimen figured by Elles and Wood (1907) as text-fig. 169, Belcraig Burn, zone of *Monograptus sedgwicki*.
 Figs. 10-12. *Glyptograptus elegans* sp. nov. 10, SM. A20386a, ? reverse of specimen in relief. 11, SM. A20386b, obverse in relief, specimen lacking septum. 12, SM. A51455, holotype, obverse of flattened specimen.



PACKHAM, Lower Silurian diplograptids

Dimensions (in millimetres)

Specimen Number	Flat or relief	Length of Rhabdosome	Width			Length		Sicula	th5 ¹ to th1 ¹	Th/cm.	
			th1	th5	maxi-mum	th1 ¹	th1 ²			th1-2	th4-5
SM. A51416	F	6	0.5	1.0	1.0	1.0	1.4	..	3.4	12	11
SM. A51455	F	10	0.5	1.0	1.1	0.9	1.4	?1.0	3.1	11	11
SM. A51456	F	4	0.5	c.1.0	1.0	0.7	1.0	..	3.1	14	12
SM. A51457	F	7.3	0.5	0.85	c.1.1	0.7	1.0	..	3.2	?13	11
SM. A51458	F	..	0.6	1.1	1.5	0.7	0.95	..	3.2
SM. A51459	F	6.8	0.5	1.0	1.2	1.0	1.2	..	3.0	..	12
SM. A20411	F	8.5	0.6	0.9	1.0	0.9	1.2	0.9	c.3.3	12	11
SM. A20386a	R	10.8	?0.5	?0.95	1.0	?0.7	?1.1	..	3.2	14	12
SM. A20386b	R	13.5	0.4	0.9	1.4	0.7	1.0	..	3.3	c.14	c.10
SM. A24933	R	15.2	0.6	0.9	1.3	1.1	1.5	..	3.6	12	10

Remarks. This species has some affinity with *G. incertus* and *G. enodis enodis*. It differs from the former in having a narrower proximal end, and from the latter in having thecae which vary along the rhabdosome length. A detailed comparison of the descriptions of the three forms will reveal a number of less striking differences.

Genus CLIMACOGRAPTUS Hall 1865

Climacograptus alternis sp. nov.

Plate 72, fig. 5; text-fig. 4f

Holotype. The specimen figured as text-fig. 4f, and Plate 72, fig. 5, from horizon J (Sudbury 1958) of the zone of *Monograptus gregarius*, Rheidol Gorge, near Aberystwyth, SM. A24957.

Number of specimens. One (the holotype).

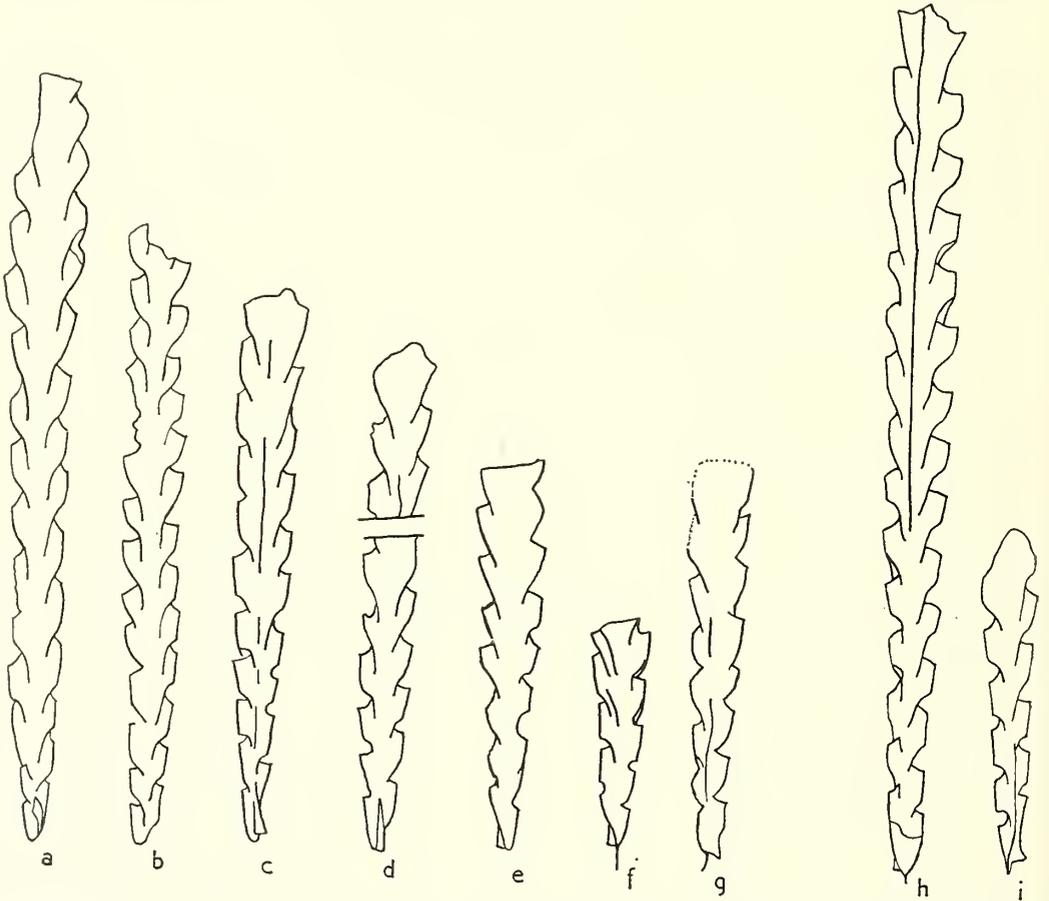
Diagnosis. *Climacograptus* with a narrow proximal end attaining a width of about 1.4 mm. at 1 cm. from the proximal end (specimen in relief), about fourteen thecae per centimetre throughout the rhabdosome, excavations becoming longer in proportion to their depth distally.

Description. The specimen is 10.4 mm. long, widening gradually over the first 5 millimetres and thereafter is nearly parallel-sided. The obverse side of the specimen is displayed and at the proximal end, the base of th1¹ is relatively restricted, as also is the proximal end of th1²; thus the sicula is prominent even on the obverse side. The sicula is visible for nearly half a millimetre before being totally obscured by th1². There is no septum on the obverse side of the rhabdosome. The appearance of the thecae changes throughout the rhabdosome. At the proximal end the excavations are shorter than distally. The supragenicular walls of the proximal thecae are inclined to the rhabdosome margins distally. They are in general parallel to the rhabdosome margin, but are somewhat variable. The length of the supragenicular wall decreases slightly distally so that the excavations become longer in proportion to their depth towards the distal end. The apertures are everted throughout. The overlap of the thecae is a little over a third. The intertheical septa are inclined at about 25° to the rhabdosome axis. The appearance of the outer surface of the rhabdosome is unknown. The type specimen is an internal

cast in pyrite. Prominent but rather irregular growthlines are apparent, particularly at the axial part of the rhabdosome.

Dimensions (in millimetres)

Specimen Number	Flat or relief	Length of Rhabdosome	Width			Length		Sicula	th5 ¹ to th1 ¹	Th/cm.	
			th1	th5	maximum	th1 ¹	th1 ²			th1-2	th4-5
SM. A24957	R	10.4	0.75	1.2	1.4	0.75	1.2	..	3.0	14	13½



TEXT-FIG. 5. *a-i*, *Glyptograptus elegans* sp. nov. *a*, Obverse in relief lacking sicula and septum SM. A20836*b*. *b*, ? Reverse in relief, SM. A20386*a*. *c*, Holotype, obverse of flattened specimen, SM. A51455. *d*, Obverse of flattened specimen SM. A20411*b*. *e*, Reverse of flattened specimen, SM. A51459. *f*, Reverse of flattened specimen, SM. A51456. *g*, Obverse of flattened specimen, SM. A51457. *h*, Reverse of specimen in relief doubtfully referred to this species, SM. A24933. *i*, Obverse of flattened specimen, SM. A51416.

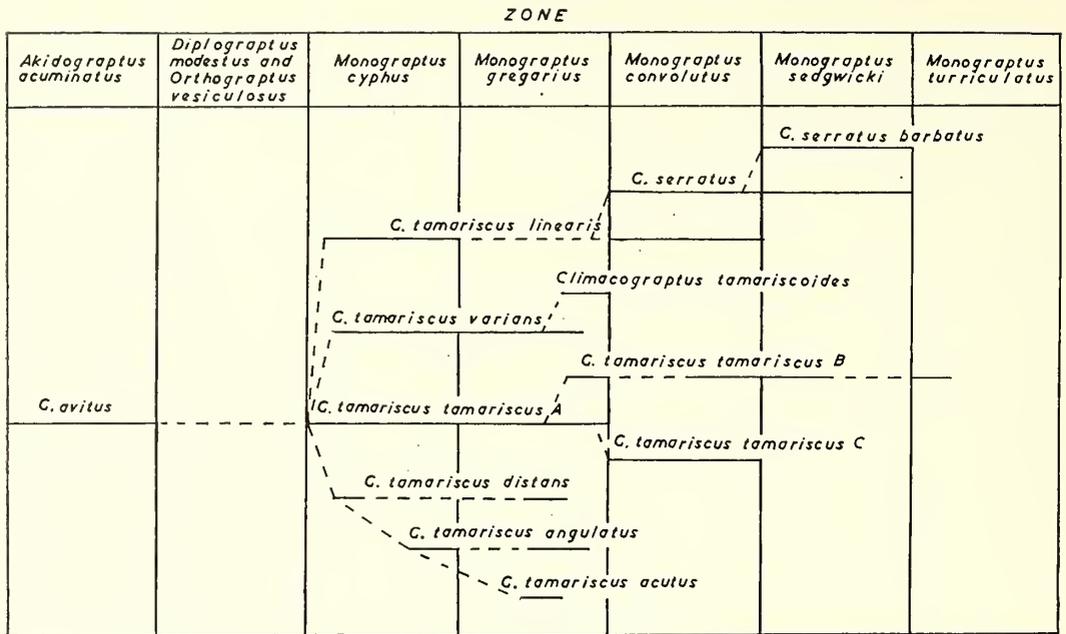
All figures $\times 7.5$. Horizons and localities given in text.

Remarks. *C. alternis* resembles *C. rectangularis* in the general shape of the rhabdosome, but the latter attains a greater width. The thecae of *C. alternis* distinguish it readily from *C. rectangularis*, which has narrower excavations which are uniform throughout the rhabdosome. The inclination of the supragenicular walls and the absence of a septum are further distinguishing features.

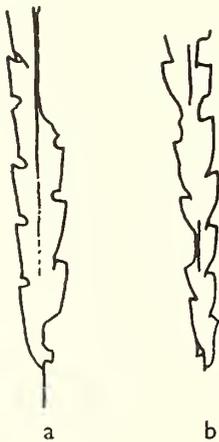
EVOLUTION OF THE FORMS DESCRIBED

Before making suggestions regarding the phylogeny of the forms described, it would be as well to explain the use of the term subspecies in this paper. There is of course, very little chance of determining the true taxonomic status of these forms. Some case can be made out for this being subspecies in the zoological sense. A succession of forms in any one locality could be acceptable as subspecies, but where a number of these forms occur on the same horizon at the same locality, some explanation is required. Assuming that these graptolites are pelagic and attached to floating objects, it might be difficult to argue that the various contemporaneous subspecies were isolated from each other by living at different depths in the sea, but it is possible to suggest other isolating mechanisms. Perhaps different bodies of water of the same sea were characterized by each of the contemporaneous subspecies, and the presence of the various subspecies in one locality could be a function of the forms which passed over the site of deposition. The distribution might have been partly climatic so that there would be a seasonal change in the forms present. Further, since graptolites are relatively light organisms, they could have floated considerable distances after death before they finally came to rest on the sea-floor. Isolation just as effective could exist if the various forms had different breeding seasons. Some isolation mechanism must be assumed if any branching phyletic tables, such as the one given by Sudbury (1958) or the one given here, are to be meaningful.

Amongst the species and subspecies described in this paper, there are apparently several phylogenetic lines (text-fig. 6). The most complicated is the one to which *Glyptograptus tamariscus* and all its subspecies belong. No immediate ancestor to *G. tamariscus* is known in the zone of *Orthograptus vesiculosus* and *Diplograptus modestus*, but in the preceding zone of *Akidograptus acuminatus*, *Glyptograptus (?) avitus* Davies (1929), from Dobb's Linn, has a number of features in common with *G. tamariscus*. The proximal part of the holotype of *G. (?) avitus* and that of a specimen of *G. tamariscus tamariscus* A are figured here for comparison (text-fig. 7). The first theca of *G. (?) avitus* is longer, the thecae are farther apart, and the geniculum appears to be more abrupt. The forms apparently derived from *G. tamariscus tamariscus* A are very varied in their characters. There seems to be one trend common to the various phyletic lines and that is the shortening of $th1^1$. This feature occurs in three of the four suggested lines of descent and marks the endpoint of each line. Examination of the sequence of forms of *G. persculptus* figured by Davies (1929) also reveals this trend which is apparently accompanied by progressive delay in the appearance of the median septum on the reverse side. *G. tamariscus tamariscus* forms B and C have $th1^1$ shorter than form A, but form B has its thecae more closely spaced and form C further apart. The second line from *G. tamariscus tamariscus* A contains *G. tamariscus varians* and *Climacograptus tamariscoides*. *Glyptograptus tamariscus varians* has more prominent genicula than does



TEXT-FIG. 6. Suggested lines of evolution of forms related to *Glyptograptus tamariscus*.



TEXT-FIG. 7. *a*, Proximal end of holotype of *Glyptograptus* (?) *avitus* Davies (flattened specimen), SM. A10019. $\times 7.5$. *b*, Proximal end of flattened specimen of *G. tamariscus tamariscus* (Nicholson) form A, SM. A51412. $\times 7.5$.

G. tamariscus tamariscus A, particularly at the proximal end, and the rhabdosome is parallel-sided or actually narrows distally. This line leads with increase in the degree of geniculation to *C. tamariscoides* which shows some decrease in the length of th^1 . The third line contains *G. tamariscus distans* which has its thecae more distantly spaced than *G. tamariscus tamariscus A* and shallower excavations. In this line too, the forms are parallel-sided. *G. tamariscus angulatus*, the next form, has more angular genicula, deeper excavations, and thecae more closely spaced. The last form on this series, *G. tamariscus acutus*, has still more angular genicula, closer thecae and th^1 shorter. The fourth line suggested involves an increase of size. The sequence of forms suggested is *G. tamariscus tamariscus A*, *G. tamariscus linearis*, *G. serratus*, and *G. serratus barbatus*. A specimen of *G. serratus* is figured on Plate 72, fig. 9, for comparison. The change of the length of the first theca is uncertain because of the poor state of preservation of the specimens available, but there is a suggestion that the increase of general size of the rhabdosome is accompanied by the increase of the length of th^1 .

The phylogeny of the other forms described in this paper is very problematical; none of them are apparently closely related to *G. tamariscus*. Of

the six remaining forms, five are first known in the zone of *Monograptus gregarius*, while *Glyptograptus incertus* appears in the zone of *Monograptus convolutus*. The variation of the thecae of *G. elegans* and *G. incertus* along their rhabdosomes suggests, at first sight, that they have been derived from a species of *Diplograptus*, but this kind of thecal variation on a modest scale is found in forms apparently derived from *G. tamariscus*. Nevertheless, perhaps the closest, morphologically, to these two forms is *Diplograptus modestus*, though it is considerably larger.

The presence of a septum in some specimens of *G. elegans* seems to have little relation to stratigraphic horizon. This is contrary to the conclusion of Davies (1929) that there was a progressive loss of the median septum in *G. persculptus* and *Climacograptus scalaris*. That this is not always the case is demonstrated by specimens of *G. sinuatus* in the Sedgwick Museum collected by Sudbury from the zone of *M. gregarius* at Rheidol Gorge. The position of commencement of the septum is as follows:

<i>Sudbury's horizon</i>	<i>Thecal pair opposite which septum starts</i>
G (highest)	9
H	4
J	7, 6, 6
O (lowest)	8

Waern (1948) described progressive delay in the development of the median septum on the reverse side in the following morphological series: *Climacograptus scalaris* var. *normalis*, *C. scalaris* var. *transgrediens* formae α , β , γ , and δ , *C. medius*. Although Waern does not give all the details, it appears from his stratigraphic table (p. 453) that the first occurrence of the forms γ and δ is slightly earlier than that of form β and that all three can occur with *C. medius*. Form β , however, survives a shorter time than forms γ and δ . In collections of specimens from successively higher horizons, there would be a progressive delay in the development of the septum, but there would be variation in its point of commencement at any horizon. The same could be true for the variation observed in *G. sinuatus* and *G. elegans*, but the number of specimens available is so small that no significant trend can be detected.

Glyptograptus enodis is possibly related to *G. sinuatus*, the elongation of the first thecae is similar. *Climacograptus alternis* could also have a similar ancestry since some specimens of *G. sinuatus* look peculiarly climacograptid.

The last form *C. tangshanensis linearis* might be related to the *C. scalaris* group.

Acknowledgements. This work was carried out at the Sedgwick Museum, Cambridge. I wish to thank Professor O. M. B. Bulman for his interest, friendly advice, and assistance, and Mr. A. G. Brighton for the loan of specimens from the Sedgwick Museum Collections. I would also like to thank the curators of the following museums for making specimens available to me; British Museum (Natural History), Palaeontological Department; Geological Survey, Edinburgh Office; Department of Geology, Birmingham University; Department of Geology, Aberdeen University. I am grateful to Dr. H. W. Ball for supplying photographs of specimens in his keeping at the British Museum of Natural History and to Mr. A. Barlow for assistance in photographing specimens from the Sedgwick Museum collections.

Repositories. BU—Department of Geology, Birmingham University; BM (NH)—British Museum (Natural History); Scot. Surv.—Geological Survey, Edinburgh Office; SM—Sedgwick Museum, Cambridge.

REFERENCES

- DAVIES, K. A. 1929. Notes on the graptolite faunas of the Upper Ordovician and Lower Silurian. *Geol. Mag.* **66**, 1–27.
- ELLES, G. L. 1922. The graptolite faunas of the British Isles. *Proc. Geol. Ass.* **33**, 168–200.
- and WOOD, E. M. R. 1901–18. A monograph of British graptolites. *Palaeont. Soc. Lond.* 1906, part 5, 181–216; 1907, part 6, 217–72.
- GORTANI, M. 1920. Contributo allo studio del paleozoico carnico. Parte VI. Faune a Graptoliti. *Palaeontogr. Ital.* **26**, 1–56.
- 1922. Faune paleozoiche della Sardegna. Parte II. Graptoliti della Sardegna orientale. *Ibid.* **28**, 85–112.
- HABERFELNER, E. 1931a. Graptolithen aus dem Obersilur der Karnischen Alpen. *Sitzb. Ak. Wiss. Wien*, Ab. 1, 140, 89–168.
- 1931b. Eine Revision der Graptolithen der Sierra Morena (Spanien). *Abh. Seuckenber. Nat. Ges.* **43**, (2), 1–66.
- HALL, J. 1865. Graptolites of the Quebec Group. *Canada Geol. Surv. Canad. Organic Remains*, dec. 2, 1–151.
- HARRIS, W. J. and THOMAS, D. E. 1949. Victorian graptolites (n.s.) Pt. II. Silurian graptolites from Jackson's Creek, Victoria. *Victoria Dept. of Mines, Mining and Geol. Jour.* **3** (5), 52–55.
- HSÜ, S. C. 1934. The graptolites of the Lower Yangtze Valley. *Monogr. Nat. Research Inst. Geol. A*, **4**.
- JAANUSSON, V. 1960. Graptoloids from the Ontikan and Viruan (Ordovician) Limestones of Estonia and Sweden. *Bull. Geol. Inst. Univ. Uppsala*, **38**, 289–366.
- LAPWORTH, C. 1873. On an improved classification of the Rhabdophora. *Geol. Mag.* **10**, 500–4, 555–60.
- (in Armstrong, Young, and Robertson) 1876. *Catalogue of the Western Scottish Fossils*. Glasgow.
- 1877. On the graptolites of County Down. *Proc. Belfast Nat. Fld. Cl.* Appendix, 125–44.
- 1878. The Moffat series. *Quart. J. geol. Soc.* **34**, 240–346.
- MÜNCH, A. 1952. Die Graptolithen aus dem anstehenden Gotlandium Deutschlands und der Tschechoslowakei. *Geologica*, Berlin, **7**, 1–157, 62 pls.
- NICHOLSON, H. A. 1868. On the graptolites of the Coniston Flags; with notes on the British species of the genus *Graptolites*. *Ibid.* **24**, 521–45.
- 1872. *Monograph of British graptolites*. Blackwood and Sons. Edinburgh and London.
- PEACH, B. N. and HORNE, J. 1899. The Silurian Rocks of Britain. Vol. 1. *Scotland Mem. Geol. Surv.*
- PERNER, J. 1897. *Études sur les Graptolites de Bohême*. Part III, section (a) Monographie des Graptolites de l'Étage E.
- PŘIBYL, A. 1948. Bibliographic index of Bohemian Silurian graptolites. *Knihovna Geol. Ústav. Česk.* **22**, 1–95.
- RUEDEMANN, R. 1904. Graptolites of New York State, Pt. 1. *New York State Mus. Mem.* **7**, 457–803.
- SHERRARD, K. M. 1954. The assemblages of graptolites in New South Wales. *J. Proc. Roy. Soc. N.S.W.* **87**, 73–101.
- SHOTTON, F. W. 1935. The stratigraphy and tectonics of the Cross Fell Inlier. *Quart. J. geol. Soc.* **91**, 639–704.
- SUDBURY, M. 1958. Triangulate Monograptids from the *Monograptus gregarius* zone of the Rheidol Gorge. *Phil. Trans. Roy. Soc. London*, **B**, **241**, 485–555.
- TÖRNQUIST, S. L. 1893. Observations on the structure of some Diprionidae. *Lunds. Univ. Årsskrift.*, **B**, **29**, 3, 1–14.
- WAERN, B. 1948. In WAERN *et al.* Deep boring through Ordovician and Silurian strata at Kinnekulle, Västergötland. 5. The Silurian strata of the Kullatorp core. *Bull. geol. Inst. Uppsala*, **32**, 433–74, 1 pl.
- WHITTARD, W. F. 1927. On the structure of *Glyptograptus* aff. *tamariscus*. *Ann. Mag. Nat. Hist.* **9**, **19**, 469–77.

G. H. PACKHAM
 Department of Geology and Geophysics,
 University of Sydney,
 Australia

NEW AMMONITES FROM THE BARREMIAN OF NORTH BULGARIA

by J. R. MANOLOV

ABSTRACT. In the Barremian of North Bulgaria are found some new ammonite genera and species; *Phyllopachyceras bontshevi* sp. nov. occurs in the Upper Barremian, *Costidiscus recticostatus* Zone. *Pseudothurmannia karakaschi* sp. nov. and *Holcodiscus caseyi* sp. nov. are found in the Lower Barremian. *Eoleptoceras* (*Tzankoviceras*) *tzankovi* gen. et sp. nov., *Eoleptoceras* (*Wrightites*) *wrighti* gen. et sp. nov., *E. (W.) parvulum kraptshevis* gen. and subsp. nov., and *Hemibaculites zaharievae* sp. nov. occur in the Lower Barremian of North-western Bulgaria, in the *Crioceratites emericianus* Zone. *Eoleptoceras* gen. nov., with its subgenera *Tzankoviceras* subgen. nov. and *Wrightites* subgen. nov., represents one of the latest members of the morphological series of Leptoceratinae. The latter is a new subfamily of Ancyloceratidae, created for the unification of the early representatives of the family, and showing close relations with *Leptoceras*. *Acanthoptyhoceras spinatocostatum* gen. et sp. nov., described from the Lower Barremian of North Bulgaria, is one of the earliest representatives of the Ancyloceratinae. It appears to be an intermediate link between *Acantholytoceras* Spath and *Lithancylus* Casey, and shows the origin of the Ancyloceratinae from a group of coarsely sculptured Ptyhoceratidae.

THE genera and species described in this paper are of Barremian age and are based on new discoveries. This work is the result of the study of a rich collection of Barremian ammonites, collected by the author in North Bulgaria and recently prepared for publication.

My best thanks are due to Mr. C. W. Wright and Dr. R. Casey (Geological Survey of Great Britain) who kindly helped me to solve questions connected with some of the genera and species described below.

The type-specimens of the newly named species are kept in the State's Geological Museum, which is situated in the University of Sofia, in the author's collection. When mentioning the name of the Museum the abbreviation S.G.M. will be used.

Order AMMONOIDEA Zittel, 1884
Suborder PHYLLOCERATINA Arkell, 1950
Superfamily PHYLLOCERATACEAE Zittel, 1884
Family PHYLLOCERATIDAE Zittel, 1884
Subfamily PHYLLOCERATINAE Zittel, 1884
Genus PHYLLOPACHYCERAS Spath, 1925

Phyllopachyceras bontshevi sp. nov.

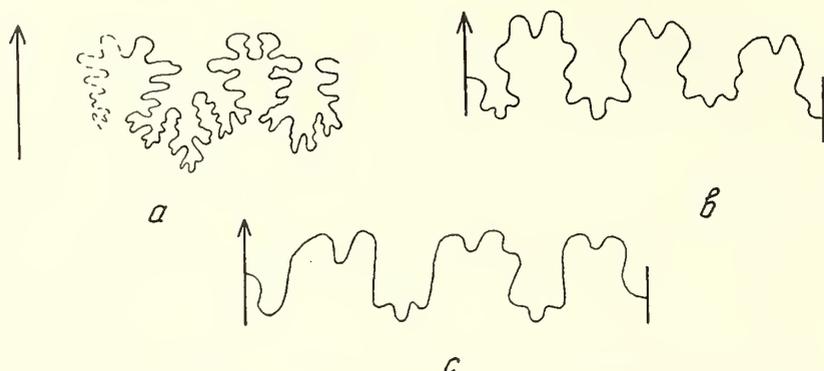
Plate 73, figs. 1-3; text-fig. 1a

Holotype. S.G.M., No. Cr₁ 1, Upper Barremian, North Bulgaria (my Collection); paratype 1—S.G.M., No. Cr₁ 2, paratype 2—S.G.M., No. Cr₁ 3.

Material. I have named this species after my teacher Academician Prof. Dr. Ek. Bontshev. I possess five well-preserved specimens, two of which show the suture clearly.

Description. Very involute, rather inflated, with feeble ornamentation consisting of broad slightly projecting rounded ribs, which extend over the outer two-thirds of the

whorl-height. The ribs are straight, divided by broad interspaces and bending sharply backward in the umbilical area where they disappear, so that a wide, smooth, rapidly expanding funnel-shaped area forms, which occupies the inner third of the whorl-height. Fine striae like prolongations of the ribs are observed here. The venter, as far as discernible on our specimens, is rounded and the ribs pass over it without interruption. Deep, narrow umbilicus. Suture-line moderately complex. Ventral saddle and lobe unknown. The first and second lateral saddles tetraphyllic, the first and second lateral lobes complex-triphyllic. The other saddles and lobes unknown.



TEXT-FIG. 1. External suture-lines of some new species; *a*, *Phyllopachyceras bontshevi* sp. nov. at 45 mm. diameter (holotype, S.G.M., No. Cr₁ 1, my Collection). *b*, *Eoleptoceras (Wrightites) wrighti* gen. et sp. nov. (holotype, S.G.M., No. Cr₁ 33, my Collection). *c*, *E. (W.) parvulum kraptschenensis* gen. et subsp. nov. (holotype, S.G.M., No. Cr₁ 30, my Collection).

Dimensions (given in millimetres; the figures in brackets give the dimensions as percentage of the diameter):

	Holotype (Pl. 73, fig. 1)	Paratype 1 (Pl. 73, fig. 2)	Paratype 2 (Pl. 73, fig. 3)
Diameter	64	34	41
Whorl-height	36 (0.56)	20 (0.58)	24 (0.58)
Whorl-thickness	?15 (0.23)	?	?10 (0.24)
Umbilicus	3 (0.05)	2.4 (0.07)	?

EXPLANATION OF PLATE 73

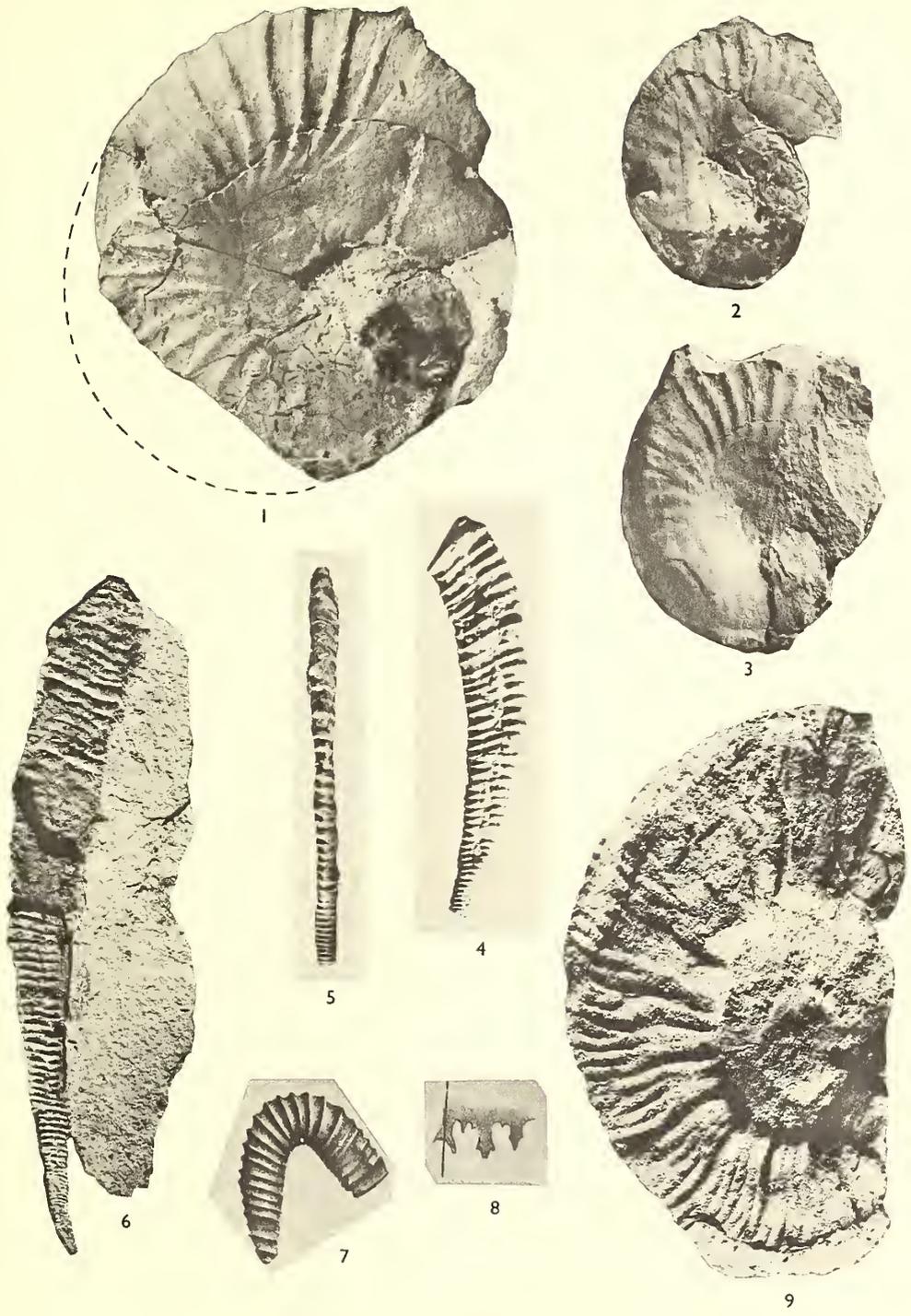
All figures are of natural size. Photo V. Makariev (Geol. Inst., Bulg. Acad. of Sci.).

Figs. 1-3. *Phyllopachyceras bontshevi* sp. nov.; Upper Barremian, zone of *Costidiscus recticostatus*, Bistriliza, North-western Bulgaria. 1, Side view of holotype. 2, Side view of paratype 1. 3, Side view of paratype 2.

Figs. 4-6. *Hemibaculites zaharievae* sp. nov. Lower Barremian, zone of *Crioceratites emericanus*, Kraptshe, North-western Bulgaria. 4, Side view of holotype. 5, Ventral view of holotype. 6, Side view of a specimen from the same locality.

Figs. 7-8. *Eoleptoceras (Tzankoviceras) assimilis* (Uhlig); Lower Barremian, Mistrowitz, Silesia (Copy of Uhlig, 1883, pl. xxxii, fig. 9a-b). 7, Side view of holotype. 8, Suture of holotype (enlarged).

Fig. 9. *Pseudothurmannia karakaschi* sp. nov., side view of holotype. Lower Barremian, Jablanitza, North Bulgaria.



MANOLOV, Barremian ammonites

Comparisons. Differs from *Phyllopachyceras infundibulum* (d'Orbigny) by lacking secondary ribs, the less prominent main ribs that bend backward, the wide funnel-shaped smooth area around the umbilicus and the suture.

Occurrence. *Phyllopachyceras bontshevi* sp. nov. was collected from the Upper Barremian marls of the gully near the school of the village of Bistrilitza, Mihailovgrad district (North-western Bulgaria) and was found with *Macroscaphites yvani* (Puzos), *Costidiscus recticostatus* (d'Orbigny), *Silesites seranonis* (d'Orbigny), *Phyllopachyceras infundibulum* (d'Orbigny), and others.

Distribution. Upper Barremian (*Costidiscus recticostatus* Zone).

Suborder LYTOCERATINA Hyatt, 1889
Superfamily ANCYLOCERATAEAE Meek, 1876
Family ANCYLOCERATIDAE Meek, 1876

Discussion. The definition and the subdivision of *Ancyloceratidae* into subfamilies has been revised lately. Casey (1960, p. 17) eliminates the subfamily Crioceratitinae from the Ancyloceratidae in which it was placed by Wright (1957, p. L208), and treats it as a separate family. He divides the Ancyloceratidae (Ancyloceratinae of Wright 1957) into two subfamilies, Ancyloceratinae s.s. and Helicancylinae (Helicancyliidae of Hyatt 1894—see Casey's footnote, 1960, p. 18) and takes out of the family the genera *Uhligia* Koenen, *Aspinoceras* Anderson, and *Dirrynoceras* Hyatt which he attaches to the Heteroceratidae. In this way he considerably narrows the family Ancyloceratidae. I agree, in this respect, with Casey (1960, pp. 17–19) but, in my opinion, the inclusion of *Leptoceras* Uhlig in the Helicancylinae (Casey, 1961, p. 76) is rather doubtful. The separation of the above-mentioned genus, together with *Eoleptoceras* gen. nov., in a new subfamily called the Leptoceratinae, seems more appropriate. Here also, in my opinion, must be included *Karsteniceras* Royo y Gomez and *Veleziceras* Wright, which show characters much closer to *Leptoceras* than to *Crioceratites*, and their inclusion in the Crioceratitidae seems very uncertain.

Subfamily ANCYLOCERATINAE Meek, 1876
Genus ACANTHOPTYCHOCERAS gen. nov.

Type-species. *Acanthoptychoceras spinatocostatum* gen. et sp. nov., Lower Barremian, North Bulgaria.

Generic characters. With straight, slowly increasing shafts, which are parallel but not touching; very sharply ribbed, main ribs spinous and simple secondary ribs. The main ribs high, excessively projecting like bars, with long spines. The section is elliptical, with greater width than height. The suture is unknown.

Remarks. *Acanthoptychoceras* is one of the earliest representatives of the Ancyloceratinae. In its type of coiling it resembles a *Ptychoceras* which is very highly ornamented. The existence of an initially spirally coiled part (as in *Ancyloceras*) is equally probable or not; my specimen cannot distinguish between the two possibilities. However, the difference between it and *Ancyloceras* is evident. In the latter the younger shaft of the hook is approximately as wide as the older shaft and is slightly arched inwards, while in *Acanthoptychoceras* it widens gradually, and is straight and parallel to the second shaft.

In its type of ribbing and the shape of its shell, it is an intermediate link between *Lithancyllus* Casey and *Acantholytoceras* Spath (concerning *Acantholytoceras* see Casey's footnote 1, 1960, p. 16). While in the latter a considerable number (8–12) of well-expressed simple ribs come between the spinous main ribs, in *Acanthoptychoceras* the main ribs are strengthened, greatly projecting, and among them are only three to four weak simple ribs. In *Lithancyllus* the intermediate ribs disappear and the distant main ribs only remain, having as have the above-mentioned genera, three rows of spinae on each side. The cross-section of *Acanthoptychoceras* is transversely elliptical, while in *Lithancyllus* it is almost circular and in *Ancyloceras* it is longitudinally elliptical.

The discovery of *Acanthoptychoceras* comes to support Casey's opinion (1960, p. 16) about the origin of the Ancyloceratinae from an extreme group of coarsely sculptured Ptychoceratidae like the group of *Acantholytoceras alpinum* (d'Orbigny). I agree with Casey's opinion (1961, p. 91), that the Ptychoceratidae must be taken out of the Turritellaceae and be included in the Ancylocerataceae.

Distribution. Lower Barremian, Lovetsh district, North Bulgaria.

Acanthoptychoceras spinatocostatum gen. et sp. nov.

Plate 74, fig. 1; Plate 75, fig. 1; Plate 76, fig. 1; text-fig. 2

Holotype. S.G.M., No. Cr₁ 8, Lower Barremian, North Bulgaria (my Collection). I possess an incomplete but perfectly well-preserved specimen of this species.

Description. A very strongly ornamented Ptychoceratid consisting of two straight, slowly increasing shafts, running parallel to each other, not touching. The ornamentation consists of very prominent, thick, bar-like main ribs passing over the venter without interruption. Each main rib has six long spines, three on each side. The spines are distributed almost regularly, near the dorsal area, in the middle of the side and near the venter. The spines are long, with an almost round section, somewhat flattened on one side at the base where they are hollow; higher up, however, they become solid. They are 14–16 mm. long with a diameter of 5–6 mm. at the base and project at a slight angle from the ribs. Three or four secondary ribs are to be observed between the main ribs. They are low, broad, rounded, free of spines. All ribs (main and secondary) pass over the venter without interruption. The section is elliptical, with greater width than height. The suture is unknown.

Dimensions of the holotype (in millimeters):

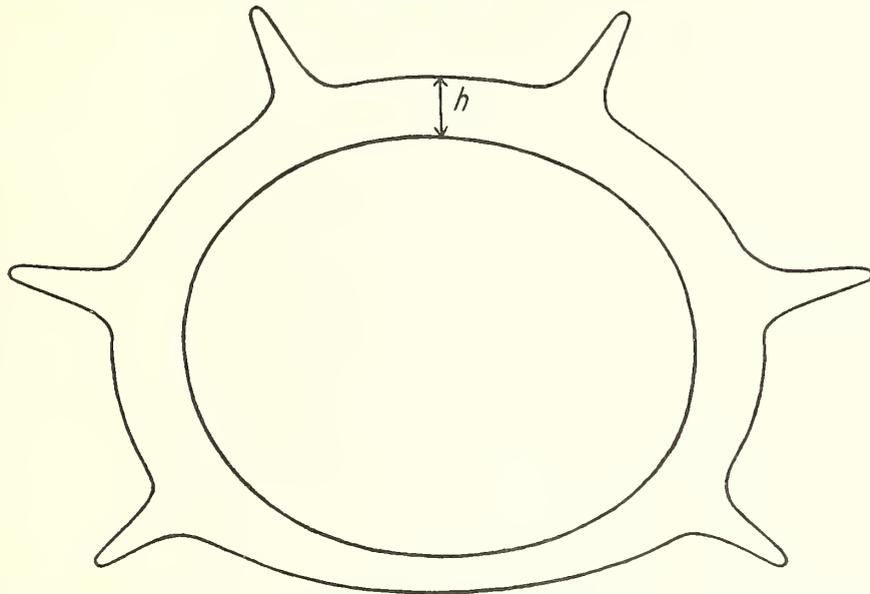
Length of the young shaft		160
Length of the adult shaft		139
Height of section of the young shaft (without tubercles)		34
Width of section of the young shaft	„	45
Height of section of the adult shaft	„	55
Width of section of the adult shaft	„	68
Height of main rib		9
Width of main rib		9

Remarks. *Acanthoptychoceras spinatocostatum* gen. et sp. nov. was collected from the marls which appear in alternation with limy sandstones in the lower part of the Lower Barremian (its thickness is about 350 metres) near the village of Jablanitz, about 10

metres above the beds with *Pseudothurmannia karakaschi* sp. nov., *Calliphylloceras ponticuli* (Rousseau), and *Barremites difficilis* (d'Orbigny).

Distribution. Lower Barremian.

Locality. The valley near the hamlet of Darvena Koshara, 2 km. to the west of the village of Jablanitza, Lovetsh district (North Bulgaria).



TEXT-FIG. 2. Cross-section of *Acanthoptychoceras spinatocostatum* gen. et sp. nov. (venter up); h , height of the main rib.

Subfamily LEPTOCERATINAE nov.

Type genus. *Leptoceras* Uhlig, 1883, Barremian, Silesia.

Discussion. The creation of a new subfamily within the family Ancyloceratidae is necessary to bring together the early representatives of the family, which show close relations among themselves. As mentioned above, included here are *Leptoceras* Uhlig, *Karsteniceras* Royo y Gomez, *Veleziceras* Wright, and *Eoleptoceras* gen. nov.

These are ammonites of small size (very rarely more than 5 cm.). At the beginning, the shell of all of them is smooth but later on, little by little, it is covered with ribs. The ribs are simple, straight, equal, and non-tuberculate. The ammonites of the Leptoceratinae are defined with a simplified suture-line, with simple or slightly indented bifid saddles and uneven (trifid to finger-like) lobes with slight indentation.

The subfamily *Leptoceratinae* is limited in its distribution to the Barremian only. The beginning of the subfamily should be sought, probably, in the Upper Hauterivian in some representative of the Crioceratitidae, small in size and with simple ribs. The members of the subfamily originate from this prototype. Morphologically the earliest type is *Leptoceras*, followed on one side by *Eoleptoceras* (*Wrightites*), and *Eoleptoceras* (*Tzankoviceras*), and on the other hand by *Karsteniceras*. For the present,

the position of *Veleziceras* remains unexplained. Parallel with the simplifying of the sculpture went on the simplifying of the suture-line. This is most clearly shown in *Karsteniceras* where the lobes are quite simple and finger-like. The divergence of the genera has taken place probably very quickly, as in the Lower Barremian they already all exist together.

Representatives of the subfamily in the Hauterivian have not yet been found, but their establishment in the Upper Hauterivian must be expected, as in the Lower Barremian the subfamily is greatly developed. The presence of *Leptoceras* in the Berriasian (Nikolov 1960, p. 192) is rather doubtful, because this genus has not been established in the Valanginian and the Hauterivian. The presence of the same genus in the Lower Aptian is also uncertain, because the forms described by Drushchitz (1960, p. 295) from the Lower Aptian of the Northern Caucasus are poorly preserved and their application to *Leptoceras* is doubtful. All the remaining genera of the Leptoceratinae are known from the Barremian only, and mainly from the Lower Barremian. Towards the end of the Barremian the representatives of the subfamily disappear.

Genus EOLEPTOCERAS gen. nov.

Type species. Crioceras (Leptoceras) parvulum Uhlig, 1883, Lower Barremian, Silesia (Plate 75, fig. 3).

Generic characters. Small with Ancyloceratid coiling and slowly increasing shafts. The shell makes initially one to one and a half whorls around the protoconch and then forms an Ancyloceratid hook. The young shaft is initially smooth and later ornamented by dense simple non-tuberculate ribs, which become more spaced on the second shaft and pass over the venter without interruption. The section is elliptical to rounded quadrate. The suture is simple, with slightly indented bifid saddles and trifid lobes.

Remarks. *Leptoceras* was created by Uhlig [1883, pp. 259-60 (135-6)] as a subgeneric name in order to denote a group of ammonites, small in size, with a Crioceratitid or Ancyloceratid coiling, which he included in *Crioceras* in a wide sense. Basse (1952, p. 609) and Luppov and Mikhailov (1958, p. 105) consider *Leptoceras* as an independent genus (with type species *Crioceras brunneri* Ooster) in the same sense as Uhlig takes it. Wright (1957, p. L211) points out as a type species of the genus, *Leptoceras pumilum* Uhlig which has typical Crioceratitid coiling. In the diagnosis of the genus, however, Wright includes both types of coiling of the shell. Observations on rich material from the Lower Barremian of North-western Bulgaria prove that one species never appears with the two different types of the shell, i.e. it always keeps the type of coiling of its shell. This fact is especially pointed out by Uhlig (1883, p. 259). In my opinion, however,

EXPLANATION OF PLATE 74

All figures are of natural size. Photo V. Makariev.

Fig. 1. *Acanthoptychoceras spinatocostatum* gen. et sp. nov., side view of holotype; Lower Barremian, Jablanitza, North Bulgaria.

Fig. 2. *Pseudothurmamia karakaschi* sp. nov., side view of cast of the holotype; Lower Barremian, Jablanitza, North Bulgaria.

Figs. 3-4. *Eoleptoceras (Tzankoviceras) assimilis* (Uhlig); Lower Barremian, zone of *Crioceratites emericianus*, Kraptshe, North-western Bulgaria. 3, Side view of plesiotype, S.G.M., No. Cr₁ 9. 4, Side view of other specimen, S.G.M., No. Cr₁ 10.



2

3

4

the separation of the species with an Ancyloceratid coiling in a different genus appears to be necessary, and *Eoleptoceras* gen. nov. fills this requirement.

Eoleptoceras includes two groups of ammonites clearly distinguished by the morphology of their shell. In one of the groups the young shaft is characterized by a bending in its lower part and by forming an acute angle when it joins the old shaft. This group is enclosed under the subgeneric name of *Tzankoviceras*. In the second group, enclosed under the subgeneric name of *Wrightites*, the two shafts are slightly arched and run subparallel to each other, without forming an acute angle when joining at the hook.

Distribution. Lower Barremian, Mihailovgrad district, North-west Bulgaria (*Crioceratites emericianus* Zone).

Subgenus TZANKOVICERAS subgen. nov.

Type species. *Crioceras (Leptoceras) assimile* Uhlig, 1883, Lower Barremian, Silesia (Plate 73, figs. 7–8, Pl. 74, figs. 3–4).

Subgeneric characters. *Eoleptoceras* in which the young shaft proceeds initially straight or is slightly arched for some distance, after that forming a bend of a very characteristic obtuse angle in its lower part and then grows straight to the final acute angled hook. The section is rounded quadrate. The suture is simple with slightly indented trifid lobes and bifid saddles.

Remarks. *Tzankoviceras* is the latest known member of the morphological series of the Leptoceratinae. On one side, *Tzankoviceras* preserves the ancestor's characters of simple ribs, bifidity of the saddles and trifidity of the lobes. On the other hand, in its straight shafts it recalls some representatives of the Ptychoceratidae from which it differs in the characteristic bending of its shell and in the formation of an acute angle when the young shaft joins the old shaft.

Distribution. Lower Barremian, Mihailovgrad district, North-western Bulgaria (*Crioceratites emericianus* zone).

Eoleptoceras (Tzankoviceras) tzankovi gen. et sp. nov.

Plate 75, figs. 2, 7–8

Holotype. S.G.M., No. Cr₁ 12, Lower Barremian, North Bulgaria (my Collection), paratype 1—S.G.M., No. Cr₁ 13.

Material. I have named this species after my teacher Prof. Dr. V. Tzankov. I possess seven specimens, three very well preserved, but all laterally flattened.

Description. Small, with a well-defined bend at the beginning of the young shaft. The two shafts form an acute angle at the final hook. The shell makes one and a half whorls around the protoconch and proceeds slightly arched to a bend after which it straightens up to the hook. The second shaft is likewise straight and forms an acute angle with the first. The young shaft is initially smooth, but later has sharp dense somewhat oblique ribs. The ribs on the second shaft are sharper and more spaced. The suture is unknown.

Comparison. Resembles *Eoleptoceras (Tzankoviceras) assimilis* (Uhlig) but differs from it by the more acute angle at which the two shafts meet in the hook, 5° to 6° compared

with 14° to 15° in *E. (Tz.) assimilis*, and the angle of bend of the young shaft, about 145° compared with about 115° in *E. (Tz.) assimilis*.

Distribution. Lower Barremian (*Crioceratites emericianus* Zone).

Locality. The thin bedded marls in the base of the Barremian at the southern end of the village of Kraptshene and the same marls in the valley North-west of Vlashki vrah, 2 km. to the west of the village of Bistrilitza, Mihailovgrad district (North-west Bulgaria).

Subgenus WRIGHTITES subgen. nov.

Type species. *Crioceras (Leptoceras) parvulum* Uhlig, 1883 [p. 273 (149), pl. xxix, fig. 3a-c, non fig. 10], Lower Barremian, Silesia (Plate 75, figs. 3a-c, 11-12).

Subgeneric characters. *Eoleptoceras* in which the young shaft forms a slight arch, in which it differs from *Anahamulina*, where it is straight, and from *Tzankoviceras*, where it bends at an obtuse angle. The second shaft is slightly arched too, subparallel to the first and does not meet it at an angle in the final hook. The ribs are more prominent and more spaced on the older shaft. The section is elliptical, almost circular. The suture is simple, with slightly indented trifold lobes and bifid saddles.

Remarks. *Wrightites* is very closely related to *Tzankoviceras* in the form of its ribbing and its suture-line. Morphologically it represents an earlier degree of passing towards an uncoiled shell. It differs from *Leptoceras* in the greater indentation of the lobes as well as in the Ancyloceratid type of coiling of the shell.

Distribution. Lower Barremian, Mihailovgrad district, North-west Bulgaria (*Crioceratites emericianus* Zone).

EXPLANATION OF PLATE 75

All figures, except fig. 10, natural size. Photo V. Makariev.

- Fig. 1. *Acanthoptychoceras spinatocostatum* gen. et sp. nov., ventral view of holotype; Lower Barremian, Jablanitza, North Bulgaria.
- Fig. 2. *Eoleptoceras (Tzankoviceras) tzankovi* gen. et sp. nov., side view of holotype; Lower Barremian, zone of *Crioceratites emericianus*, Kraptshene, North-western Bulgaria.
- Fig. 3. *Eoleptoceras (Wrightites) parvulum* (Uhlig); Lower Barremian, Wernsdorf, Silesia (Copy of Uhlig, 1883, pl. xxix, fig. 3). 3a, Side view of holotype. 3b, Ventral view of holotype. 3c, Suture of holotype (enlarged).
- Figs. 4-6. *Eoleptoceras (Wrightites) parvulum kraptshenensis* gen. et subsp. nov.; Lower Barremian, zone of *Crioceratites emericianus*, Kraptshene, North-western Bulgaria. 4, 6, Side views of holotype. 5, Ventral view of holotype.
- Figs. 7-8. *Eoleptoceras (Tzankoviceras) tzankovi* gen. et sp. nov. 7, Side view of an adult specimen; Lower Barremian (*Crioceratites emericianus* Zone), Kraptshene. 8, Side view of paratype 1; Lower Barremian (*Crioceratites emericianus* Zone), west of Bistrilitza, North-western Bulgaria.
- Figs. 9-10. *Eoleptoceras (Wrightites) wrighti* gen. et sp. nov.; Lower Barremian, zone of *Crioceratites emericianus*, Kraptshene, North-western Bulgaria. 9, Side view (reconstructed) of holotype. 10, Side view of holotype ($\times 2$).
- Figs. 11-12. *Eoleptoceras (Wrightites) parvulum* (Uhlig); Lower Barremian, zone of *Crioceratites emericianus*, Kraptshene, North-western Bulgaria. 11, Side view of pleseiotype, S.G.M., No. Gr₁ 19. 12, Side view of other specimen, S.G.M., No. Cr₁ 20.



MANOLOV, Barremian ammonites

Eoleptoceras (Wrightites) parvulum kraptshevensis gen. et subsp. nov.

Plate 75, figs. 4–6; text-fig. 1c

Holotype. S.G.M., No. Cr₁ 30, Lower Barremian, North Bulgaria (my Collection). I possess three specimens, one of which is perfectly preserved.

Description. Small in size with arched, slowly increasing shafts. Shell initially smooth, then ornamented by sharp simple oblique ribs passing over the dorsum and venter without interruption and having wide rounded interspaces. The ribs on the hook and older shaft are still more spaced. The section is elliptical, almost circular, somewhat higher than wide. The last suture is situated before the hook at a distance approximately equal to a quarter of the entire length of the shell. The suture is simple with trifid lobes and bifid saddles. The first lateral lobe is clearly trifid, the second is hardly perceptibly denticulate. The first and third lateral saddles are simply bifid, the second having a slight accessory inflection in its backward half.

Dimensions of the holotype (in millimeters):

Entire length	28
Height of section at the last suture	3·6
Width of section at the last suture	3·3

Comparison. Differs from *E. (W.) parvulum* (Uhlig) in its less denticulate suture, the almost circular section and the greater distance from the last suture to the hook.

Distribution. Lower Barremian (*Crioceratites emericianus* Zone).

Locality. The thin bedded marls in the base of the Barremian at the southern end of the village of Kraptshe, Mihailovgrad district (North-western Bulgaria).

Eoleptoceras (Wrightites) wrighti gen. et sp. nov.

Plate 75; figs. 9–10; text-fig. 1b

Holotype. S.G.M., No. Cr₁ 33, Lower Barremian, North Bulgaria (my Collection).

Material. I have named this species after Mr. C. W. Wright. I possess an incomplete but very well-preserved specimen.

Description. Small, of slow growth, ornamented by thin, slightly projecting oblique ribs, with wide interspaces between them, which pass without interruption over the dorsum and venter. At every three to five ribs the interspace becomes almost twice as wide, so that between every pair of wide interspaces there is a group of three to five ribs. The section is elliptical, almost circular. The suture is simple. The saddles are bifid, laterally complicated with shallow accessory lobes. The lobes are trifid.

Comparison. It differs from *E. (W.) parvulum* (Uhlig) in its suture, its almost circular section, and the less prominent ribs which form groups.

Distribution. Lower Barremian (*Crioceratites emericianus* Zone).

Locality. The thin-bedded marls in the base of the Barremian at the southern end of the village of Kraptshe, Mihailovgrad district (North-western Bulgaria).

Family HETEROCERATIDAE Hyatt, 1900

Genus HEMIBACULITES Hyatt, 1900

Hemibaculites saharievae sp. nov.

Plate 73, figs. 4-6

Holotype. S.G.M., No. Cr₁ 34, Lower Barremian, North Bulgaria (my Collection).*Material*. I have named this species after my teacher Dr. Kr. Sahariva. I possess twelve adult and four juvenile specimens of this species, all laterally flattened.*Description*. A toxicone of medium size, of rapidly expanding section, ornamented by simple, straight, rather prominent, rounded, oblique ribs, which pass without interruption over the dorsum and venter. Tubercles are not present. The section is elliptical, with greater height than width. The suture is unknown.*Dimensions of the holotype (in millimetres)*:

Entire length	57
Height of section at the base	3.2
Width of section at the base	2.8

Comparison. Differs from *Hemibaculites obliquatus* (d'Orbigny) in its smaller size, rounder section, and type of ribbing; its ribs are denser and more prominent than in *H. obliquatus* and pass without interruption over the dorsum, where in *H. obliquatus* they are interrupted.*Distribution*. Lower Barremian (*Crioceratites emericianus* Zone).*Locality*. The thin-bedded marls in the base of the Barremian at the southern end of the village of Kraptshene, Mihailovgrad district (North-western Bulgaria).

Family HEMIOPLITIDAE Spath, 1924

Genus PSEUDOTHURMANNIA Spath, 1923

Pseudothurmannia karakaschi sp. nov.

Plate 73, fig. 9; Plate 74, fig. 2.

1907 *Crioceras angulicostatum* d'Orbigny; Karakasch, p. 134, pl. xv, fig. 1 (*non* pl. xiv, figs. 4, 7 = *Pseudoth. picteti* Sarkar)*Holotype*. S.G.M., No. Cr₁ 50, Lower Barremian, North Bulgaria (my Collection).*Material*. I have named this species after the great Russian palaeontologist N. I. Karakasch, since he was the first to figure a specimen of this species. I possess a comparatively well-preserved specimen with an absolute likeness to the specimen figured by Karakasch (1907, pl. xv, fig. 1) and very different from the other species of this genus.

EXPLANATION OF PLATE 76

Photo V. Makariev.

Fig. 1. *Acanthoptychoceras spinatocostatum* gen. et sp. nov., side view of holotype (of natural size); Lower Barremian, Jablanitza, North Bulgaria.Figs. 2-5. *Holcodiscus caseyi* sp. nov.; Lower Barremian, south of Dobrevtzi, North Bulgaria. 2, Side view of holotype ($\times 1.5$). 3, Ventral view of holotype ($\times 1.5$). 4, Side view of holotype ($\times 3$). 5, Ventral view of holotype ($\times 3$).



2

3

4

5

1

Description. Medium in size, with evolute coiling, slowly increasing whorls, slightly overlapping to just touching, laterally flattened, with an almost rectangular section as in the other species of *Pseudothurmannia*. The ornamentation consists of main ribs, with elongated bullae in the umbilical area, bending slightly forwards towards the venter, some bifurcating; between the main ribs come three to four intercalatory ribs, some of which reach the umbilical area, while the rest spread only over the outer two-thirds of the whorl-height. The umbilical wall is steep, almost vertical. The ribbing, main and intercalatory, as far as discernible, passes without interruption over the venter. The suture is unknown.

<i>Dimensions (in millimeters)</i>	<i>Holotype</i> (Pl. 73, fig. 9)	<i>Karakasch's specimen</i> (1907, pl. xv, fig. 1)
Diameter	81	80
Whorl-height	28 (0.34)	27 (0.34)
Whorl-thickness	?	22 (0.27)
Umbilicus	32 (0.40)	32 (0.40)

Comparison. The species described differs from *Pseudothurmannia angulicostata* (d'Orbigny) in having more and longer intercalatory ribs, usually three to four, while in *P. angulicostata* they are one to two, occupying one-third of the whorl-side. It differs from *P. picteti* Sarkar by the greater number of the intercalatory ribs and the lack of ventral tubercles.

Remarks. The described species was collected from the marls of the alternation of limy sandstones and marls in the lowermost part of the Lower Barremian near the village of Jablanitza (see Manolov, 1960) together with *Calliphylloceras ponticuli* (Rousseau), *Barrenites difficilis* (d'Orbigny), and others.

Distribution. Lower Barremian.

Locality. The Lower Barremian marls in the valley near the hamlet of Darvena Koshara, 2 km. to the west of the village of Jablanitza, Lovetsh district (North Bulgaria).

Suborder AMMONITINA Hyatt, 1889
 Superfamily DESMOCERATAEAE Zittel, 1895
 Family HOLCODISCIDAE Spath, 1924
 Genus HOLCODISCUS Uhlig, 1882

Holcodiscus caseyi sp. nov.

Plate 76, figs. 2-5

Holotype. S.G.M., No. Cr₁ 51, Lower Barremian, North Bulgaria (my Collection).

Material. I have named this species after Dr. R. Casey. I possess a perfectly well-preserved juvenile specimen of this species.

Description. Somewhat involute with slowly increasing, richly ornamented whorls of a rounded whorl-section, with greater height than width. Each whorl has seven constrictions at each side on which there is a thick rib, so that it resembles *Spitidiscus*. Each rib situated in front of the constrictions has a big elongated club-shaped bulla, that almost reaches the middle of the whorl. Four intercalatory ribs come between the

thicker ribs situated at the constrictions. They are straight, rounded, and bifurcate in the umbilical area at one-third of the whorl-height into two equally strong ribs. All ribs pass over the rounded venter without interruption. The suture is unknown.

Dimensions of the holotype (in millimeters)

Diameter	12.5
Whorl-height	4.3 (0.34)
Whorl-thickness	3.2 (0.26)
Umbilicus	3.8 (0.30)

Comparison. It resembles *Holcodiscus gastaldinus* (d'Orbigny) in the bifurcation of the ribs but differs in the slower growth of the whorls and the wider umbilicus, the constrictions with thicker ribs flanking them, the presence of umbilical bullae and the lack of ventral tubercles.

Remarks. *Holcodiscus caseyi* sp. nov. was collected from the middle part of the Lower Barremian, in the base of the marls with sphaerical weathering, above the beds with *Pseudothurmannia karakaschi* sp. nov. and *Acanthoptychoceras spinatocostatum* gen. et sp. nov.

Distribution. Lower Barremian.

Locality. The marls with sphaerical weathering, 1 km. to the south of the village of Dobrevtzi, Lovetsh district (North Bulgaria).

REFERENCES

- ANDERSON, F. M. 1938. Lower Cretaceous deposits in California and Oregon. *Geol. Soc. Amer. Spec. Paper*, **16**, 339 pp., 84 pl.
- ASTIER, J. E. 1851. Catalogue descriptif des Ancyloceras appartenant à l'étage Néocomien d'Escragnoles et des Basses-Alpes. *Ann. Soc. nation. d'agricult., d'hist. naturelle et des arts utiles de Lyon* (2), **3**, 1–27, pl. 1–9.
- BASSE, É. 1952. Ammonoidea. In J. PIVETEAU (ed.): *Traité de paléontologie*, **2**, 522–55, 581–688. Paris.
- CASEY, R. 1960. A monograph of the Ammonoidea of the Lower Greensand, Part I. *Palaeontogr. Soc.*, xxxiii+44 pp., pl. 1–10.
- 1961. *Idem.* Pt. II, 45–118, pl. 11–25. *Ibid.*
- COTTREAU, J. 1937. Types du prodrome de paléontologie universelle d'Orbigny. B. Néocomien Supérieur ou Urgonien. *Annales de Paléont.* **26**, fasc. 1–2, 53–84, 6 pl.
- DRUSHCHITZ, V. V. 1960. Ammonites. Pt. I. In V. V. MENNER (ed.): Atlas of the Lower Cretaceous fauna of the Northern Caucasus and Crimea (in Russian), 249–308, pl. 1–47. Moscow.
- KARAKASCH, N. I. 1907. Le Crétacé inférieur de la Crimée et sa faune. *Trav. Soc. impér. nat. St. Pétersb., Sect. géol. min.* **32**, livre 5, 1–482, pl. 1–28.
- LUPPOV, N. P. and MIKHAILOV, N. P. 1958. In JU. A. ORLOV (ed.): *Principles of palaeontology*. 6, Mollusca—Cephalopoda. II, Ammonoidea (Ceratites and Ammonites), Dibranchiata (in Russian), 359 pp., 71+7 pl., 160+8 figs. Moscow.
- MANOLOV, ZH. (=J.). 1960. On the presence of Barremian cephalopod facies in the environs of the villages of Yablanitsa, Dobrevtzi, and Batultsi near the town of Lovech, Northern Bulgaria. *Review Bulg. Geol. Soc.* **21**, Pt. 2, 96–100.
- MANOLOV, J. and RADEV, G. 1960. Presence of Cephalopod Barremian in the Salaš syncline (North-western Bulgaria). *Review Bulg. Geol. Soc.* **21**, Pt. 3, 90–92.
- NIKOLOV, T. 1960. La faune d'ammonites dans le Valanginien du Prébalcan Oriental. *Travaux géol. Bulgarie, Sér. Paléontologie*, **2**, 143–206, pl. 1–27.

- TZANKOV, V. 1935. Notes sur le genre *Holcodiscus*. *Annuaire Univ. Sofia, fac. phys., mathém.*, **31**, livre 3, 35–111, pl. 1–6.
- UHLIG, V. 1883. Die Cephalopodenfauna der Wernsdorfer Schichten. *Denkschr. d. k. Akad. Wiss, Wien, math.-naturw. Cl.* **46**, Abt. II 125 (1)—290 (166), pl. 1–32.
- WRIGHT, C. W. 1957. In W. J. ARKELL, B. KUMMEL, and C. W. WRIGHT: Mesozoic Ammonoidea. In R. C. MOORE (ed.): *Treatise on Invertebrate Paleontology*, Part L, Mollusca 4, Cephalopoda, Ammonoidea; L80–L490. Geol. Soc. America-Univ. Kansas Press.

J. R. MANOLOV
Geological Institute,
Bulgarian Academy of Sciences

Manuscript received 25 September 1961

SOME WENLOCKIAN FENESTRATE BRYOZOA

by T. G. MILLER

ABSTRACT. *Fenestella rigidula* M'Coy 1850 and *F. lineata* Shrubsole 1880 are considered to be conspecific. Their zooecial chambers are shown to contain structures comparable with the diaphragms of the Trepostomata, and a new genus, *Archaeofenestella*, is erected to contain them. One new species and two new subspecies are described: *Archaeofenestella rigidula polynodosa*, *Fenestella pseudosubantiqua*, and *F. pseudosubantiqua catrionae*. Elias's (1956) suggestion of the presence, in the English Wenlockian, of d'Orbigny's genus *Reteporina* from the Devonian is confirmed. A new genus, *Neoretaporina*, is proposed for certain Carboniferous species described by Nekhoroshev. Finally the polyphyletic nature of the genus *Fenestella* is suggested.

SINCE the validation by the International Commission on Zoological Nomenclature of the generic name *Fenestella* as applied to the well-known Palaeozoic cryptostome bryozoan (*Bull. Zoo. Nom.* 1962), and the designation of a neotype, *Fenestella subantiqua* d'Orbigny 1850, by Elias (1956), I have had the opportunity of examining material from the same locality and horizon in the Holcroft Collection of the Department of Geology in the University of Birmingham, together with type specimens of M'Coy and Shrubsole in the Sedgwick Museum at Cambridge. This study permits certain additions to and modifications of Elias's preliminary assessment of the Wenlockian fenestrate bryozoan assemblage at Dudley.

The lithostratigraphic unit from which this material was collected is the Wenlock Limestone, which occurs at the celebrated collecting locality known as The Wren's Nest, Dudley, near Birmingham. The horizon, in terms of the standard British Silurian succession, is considered (Das Gupta 1933; Butler 1939) to lie at or about the top of the '*Cyrtograptus huldgreni* Zone'. This is probably within the Upper Wenlockian stage VI of Bouček (1953)—i.e. above the zone of *Cyrtograptus rigidus*.

A summary account of some Dudley Wenlockian material in various British collections was included in a review of Palaeozoic Bryozoa published by Nekhoroshev in 1930. This constitutes the only reference to the rich and varied bryozoan assemblage of the Dudley Wenlockian between Shrubsole's 'revision' of 1880 and Elias's of 1956.

Discussion of 'fenestellid' species. In his 1956 paper Elias discussed in detail (1) *Fenestella subantiqua* d'Orbigny; (2) *F. rigidula* M'Coy and *F. lineata* Shrubsole; and (3) *F. reticulata* Lonsdale. It will be convenient to refer to these briefly in the same order.

1. *Fenestella subantiqua* d'Orbigny 1852. It is interesting to note that the Holcroft Collection at Birmingham—which contains large numbers of well-preserved fenestrate bryozoan fragments from The Wren's Nest, Dudley, representing several genera, e.g. *Fenestella*, *Reteporina*, *Semicoscium*, and *Unitrypa*—does not seem to include an undoubted example of *Fenestella subantiqua* as redescribed by Elias. It is true that, failing the possibility of reference to Lonsdale's holotype, and in view of the extreme fineness with which interspecific discriminations are now made in the fenestrate Bryozoa, it is impossible to be certain to which of the available forms Lonsdale's description referred. This limitation was recognized by Elias (1956, p. 318) when he wrote: '... one may

question whether the selected topotypes truly belong to the species illustrated by Lonsdale. If not, then no specimens from Dudley examined in various collections by Bassler, Duncan, Miller or myself are referable to *F. subantiqua*, and *this species must be extremely rare at Dudley.*' (My italics.) The situation is now clarified in that the neotype material selected by Elias must be taken as the point of reference for any subsequent attribution to *F. subantiqua*.

No. 35 in the Holcroft Collection has gross mesh-dimensions close to those of *F. subantiqua* d'Orbigny emend. Elias, and in certain states of preservation might be confused with that species. In detail, however, it is found that there are differences of specific importance, and I accordingly describe this form below (p. 544) as *Fenestella pseudo-subantiqua* sp. nov., together with a new subspecies, *F. pseudosubantiqua catrionae*.

2. *F. rigidula* M'Coy and *F. lineata* Shrubsole. Examination of the type specimens of these species shows that, contrary to Elias's conclusions (1956, pp. 324-9), but in agreement with those of Nekhoroshev (1930), they are conspecific, and Shrubsole's species must therefore be suppressed.

In thin sections cut in the plane of the zoarial expansion an exceedingly important distinguishing feature is seen, namely, the presence, within the zooecial chambers, and occasionally also between them and the median wall, of numerous gently curved and inclined walls or septa passing across from side to side or from side to end (Pl. 77, fig. 4, and text-fig. 1). These structures recall the diaphragms of the Trepostomata, and particularly those of the family Phylloporinidae, which has been assigned tentatively to the Trepostomata by Bassler (1953, p. 116) as '... intermediate between Cryptostomata, which it [the family assemblage] resembles in zoarial form, and Trepostomata, which it matches in internal structure'.

Although externally the zoarial mesh of *F. rigidula* is indistinguishable from a 'normal' fenestellid, the presence of internal structures possibly homologous with the diaphragms of the Trepostomata makes it necessary to separate forms in which this morphological feature is developed. I accordingly erect (below, p. 542) the new genus *Archaeofenestella* to accommodate such forms.

3. *F. reticulata* Lonsdale. There remains what is perhaps the most interesting of all the Dudley fenestellids, the form described by Elias (1956, p. 329) as *Fenestella reticulata* Lonsdale. As Elias points out, there seems little doubt that Shrubsole (1880, p. 249) was wrong to erect a new species, *F. reteporata*, distinct from Lonsdale's *F. reticulata*. On the other hand, Nekhoroshev (1930) may have come nearer the truth in supposing that the form described by Lonsdale as *Gorgonia assimilis* is the common large-meshed Dudley fenestellid, in which case the form might seem to be attributable to *Fenestella assimilis* (Lonsdale).

However, there are certain features of the species which make it doubtful whether any attribution to the genus *Fenestella* is correct. This doubt was expressed by Elias (1956, p. 329) when he noted that both Lonsdale and Shrubsole show, in their figures of *F. reticulata* and *F. reteporata* respectively, occasional apertures 'in some carinate dissepiments'; and concludes that 'the occasional lateral contacts of its branches place it close to *Reteporina* (= ?*Semicoscinium*)'.

Examination of thin sections of examples of this form from the Dudley Wenlockian (H:26 and H:10) shows that some of the so-called 'dissepiments' are parts of normal zooecia-bearing branches, in which deflection of growth-direction has apparently led to

branch anastomosis. In other cases only half a 'dissepiment' contains cells, while the other half completes an inter-branch linkage with the massive calcareous tissue of a normal dissepiment. When an 'abortive' branch-division forms part of a 'pseudo-dissepiment', the resulting structure is irregular in shape, the cell-bearing part usually projecting into the fenestrule, so that the fenestrule is roughly heart-shaped. In a single zoarium, or zoarial fragment, every gradation can be seen, from cases of extremely short, wide dissepiments at points where branches almost touch, to comparatively long dissepiments, without cells. In the latter case there is often enlargement of the zooecial chambers opposite the point of insertion of the dissepiment in the branch, and abnormally constricted cells project from the branch into the dissepiment.

The obverse of the branches shows, instead of a fenestellid 'carina', a steep-sided but apically rounded axial surface above the zooecial apertures, and no 'carinal' nodes. The line of separation between the main skeletal material and the external 'sclerenchymal' investment is not sharp. The external investment itself contains, or is partly constructed of, a mass of small, isolated tubular (or possibly rod-like) bodies, arranged more or less radially with respect to the branch and 'dissepiment' cross-sections, and normal to the fenestrule sides.

These characters make it impossible to assign the form under discussion to the genus *Fenestella* Lonsdale 1839.

Nekhoroshev (1956, pp. 173-83) has discussed the genus *Reteporina* at considerable length. Bassler (1953, p. 126) described it as 'poorly known; may be senior synonym of *Semicosciniium*'. Some of Nekhoroshev's figures (e.g. pl. 27, figs. 1, 2) of *Reteporina altaica e.* and *R. altaica major*, from the Lower Carboniferous of the Altai, are at first sight similar in general appearance to Lonsdale's species, although in detail the dimensions are of course different. The resemblance is less marked in the outline drawings of thin sections (e.g. pl. 28, figs. 1-10). Nowhere in this series of drawings does Nekhoroshev show a true anastomosis of branches. Although in fig. 8a he shows branches almost touching each other, there is no case of a row of zooecial chambers passing uninterruptedly from one branch to another. D'Orbigny's diagnosis (quoted by Nekhoroshev 1956, p. 173) explicitly states that anastomoses are present: '. . . branches largement anastomosées de manière a ne laisser entre elles que des oscules oblongs, réguliers, placés par lignes divergentes'.

It must be concluded, therefore, that the Dudley Wenlockian '*Fenestella*' *reticulata* should properly be assigned to *Reteporina* d'Orbigny 1849, erected for a Devonian example; and that Nekhoroshev's Carboniferous species must be ascribed to a separate genus, *Neoretaporina* (which I define below, p. 547), morphologically intermediate between *Reteporina* and *Fenestella*, and probably related to *Levifenestella* Miller 1961b.

SYSTEMATIC DESCRIPTIONS

Specimens from the Sedgwick Museum, Cambridge, are prefixed SM; those from the Department of Geology, University of Birmingham, are prefixed BU.

Order CRYPTOSTOMATA Shrubsole and Vine 1882

Family FENESTELLIDAE King 1850

Genus ARCHAEOFENESTELLA gen. nov.

Type species: Fenestella rigidula M'Coy (1850, p. 288), Silurian, England.

Diagnosis. Zoarium of branches and dissepiments arranged to form a reticulate 'fenestellid' mesh. Branches with a straight internal median wall separating two rows of zooecial chambers opening on the obverse of the zoarium, and externally with a prominent median carina which bears nodes. Zooecial chambers rectangular or rhomboidal in base shape, divided internally by transverse diaphragm-like walls in the posterior part of the chamber.

Discussion. The genus is distinguished from *Fenestella* by the presence of diaphragm-like dividing walls within the zooecial chambers (and occasionally between them), and by the straightness of the median wall dividing the branches, which allows the zooecial chambers on each side to follow each other without alternation with their neighbours on the other side of the wall. In all other respects, and particularly in the gross form of the zoarial expansion, there seems to be no difference from *Fenestella*. However, the internal zooecial septa, which recall the internal structure of the zooecia in *Subretepora*, and which are not present in any other genus of the Fenestellidae, must reflect some fundamental distinguishing feature in the zooid. The presence of apparently similar structures in members of the mainly Ordovician family Phylloporinidae suggests that the structure should be regarded as 'primitive' in terms of bryozoan phylogeny.

Archaeofenestella rigidula (M'Coy)

Plate 77, figs. 1, 4; text-fig. 1

- Fenestella rigidula* M'Coy 1850, p. 288.
Fenestella rigidula M'Coy; M'Coy 1855, p. 50.
Fenestella rigidula M'Coy; Shrubsole 1880, p. 248.
Fenestella lineata Shrubsole 1880, p. 249.
Fenestella rigidula M'Coy; Nekhoroshev 1930, p. 185.
Fenestella rigidula M'Coy; Elias 1956, p. 327.

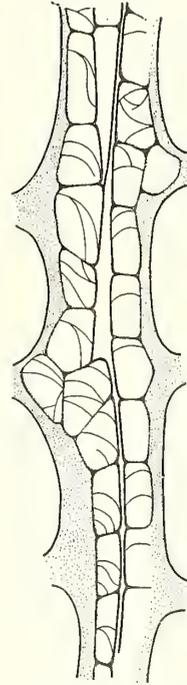
Material:

1. *A. rigidula* (M'Coy), holotype, SM. A:10111, Wenlock Limestone, Dudley, Staffordshire (*sic.*).
2. *Fenestella lineata* Shrubsole, holotype, SM. A:10210, Wenlock Limestone, Dudley, Worcestershire.
3. Topotypes BU. H:39 and H:40, Wenlock Limestone, Wren's Nest, Dudley, Worcestershire.

Micrometric formulae:

	B/10	D/10	Z/5	N/5	B _w	ZD	ZB
SM. A:10111	20-22	15-17	26-28	16-25	0.25	0.10	rh.
SM. A:10210	20-28	13-16	24-30	17-22	0.25	0.10	rh.
BU. H:39	22	18	30	?	0.25	0.10	rh.
BU. H:40	21	14-15	28-30	12-14	0.25	0.10	rh.

[B/10—no. of branches in 10 mm. across the zoarium; D/10—no. of dissepiments in 10 mm. along the branches; Z/5, N/5—no. of zooecial apertures and carinal nodes in 5 mm. along branches; B_w—width



TEXT-FIG. 1. Semi-diagrammatic drawing of branch structure in *Archaeofenestella* showing septal traces within the zooecial chambers. (From a thin section of *A. rigidula*; notional magnification $\times 45$.)

of branches in mm.; ZD—diameter of zooeical apertures in mm.; ZB—shape of main part of zooeical chamber in plane of zoarial expansion; rh.—rhomboidal; rect.—rectangular.]

Description. Normal reticulate fenestellid mesh of bifurcating branches and transverse dissepiments. Branches markedly straight and parallel, bearing rather large ‘collared’ zooeical apertures, less than their own diameter apart. Occasionally an abnormally large cell-aperture is placed opposite the end of a dissepiment. Reverse of branches with prominent longitudinal ribs. In thin section in the plane of the expansion the zooeical chambers are seen to be set in two rows within the branches, the rows separated by a straight central dividing wall, each cell-base having the shape of a parallelogram. The cells are divided internally by transverse, gently curved septa, usually two, but in some cases up to four in a cell (text-fig. 1; Pl. 77, fig. 4). In both branches and dissepiments scattered ‘tubules’ occur. These lie generally normal to the axis of the branch or dissepiment.

Archaeofenestella rigidula polynodosa subsp. nov.

Material: Syntypes BU. H:24 (ii), and H:45, Wenlock Limestone, Dudley, Worcestershire.

Micrometric formulae:

BU. H:24 (ii), H:45.	22–24	16–18	26–29	26–30	0.15–0.25	0.10–0.13	rh.
<i>F. lineata</i> Elias 1956	18–24	12–15	26–27	25–27	?	?	?
<i>A. rigidula</i> M’Coy	20–22	15–17	26–28	16–25	0.25	0.10	rh.

Discussion. This form is exceedingly close to *A. rigidula* (M’Coy) except in the somewhat greater density of carinal nodes. It may be the form described by Elias (1956, p. 324) as *Fenestella lineata* Shrubsole.

Genus FENESTELLA Lonsdale 1839

Fenestella pseudosubantiqua sp. nov.

Plate 77, fig. 3

Material: Holotype BU. H:35, Wenlock Limestone, Dudley, Worcestershire.

EXPLANATION OF PLATE 77

All specimens from Wenlock Limestone, Dudley, Worcestershire.

Fig. 1. *Archaeofenestella rigidula* (M’Coy). Holotype SM. A:10111. Part of obverse of zoarial expansion in which zooeical septa have been exposed by weathering, $\times 25$.

Fig. 2. *Reteporina reticulata* (Lonsdale). BU. H:26. Polished and etched surface showing arrangement of zooeical chambers within the branches, and ‘abortive’ branch-divisions forming pseudo-dissepiments, $\times 14$.

Fig. 3. *Fenestella pseudosubantiqua* sp. nov. Holotype BU. H:35. Part of reverse of zoarial expansion. The upper half of the fragment has been removed to show (as dark spots) the impressions of the prominent widely-spaced carinal nodes, $\times 8$.

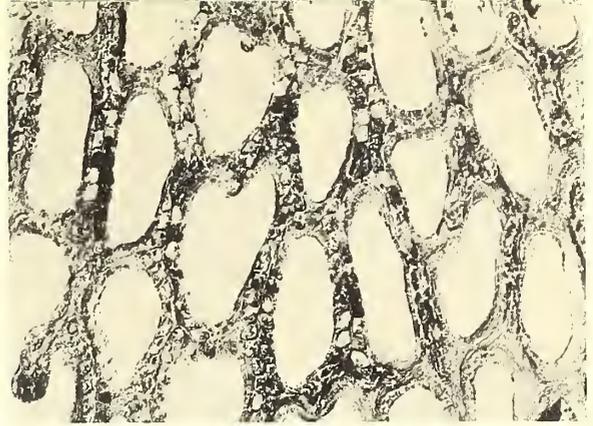
Fig. 4. *Archaeofenestella rigidula* (M’Coy). SM. A:10210 (labelled *Fenestella lineata* Shrubsole—holotype). Thin section in plane of zoarial expansion showing rhomboidal zooeical base-shape and internal transverse septa, $\times 20$.

Fig. 5. *Reteporina reticulata* (Lonsdale). BU. H:10. Part of reverse of zoarial expansion, $\times 8$.

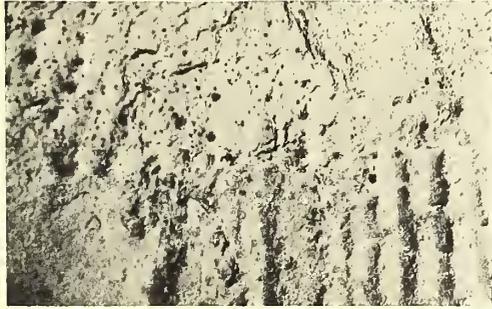
Fig. 6. *Reteporina reticulata* (Lonsdale). BU. H:26. Thin section of branch showing zooeical chambers and median wall, $\times 70$.



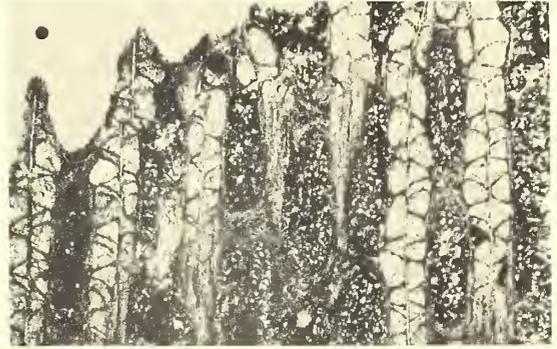
1



2



3



4



5



6

Micrometric formulae:

Holotype BU. H:35	16-18	9	20-29	8-11	0.15-0.20	0.10	rh.
cf. <i>F. subantiqua</i> d'Orbigny 1852,	16-19	9-11	25-26	c. 25-26	?	?	?
emend. Elias 1956							

Description. Normal, regular fenestellid mesh of slender, slightly flexuous branches with transverse dissepiments. The gross dimensions of the zoarial elements closely resemble those of *F. subantiqua* d'Orbigny as redescribed by Elias (1956), except for the presence in the new species of relatively stout straight-sided cylindrical carinal nodes widely spaced along the carina.

Fenestella pseudosubantiqua catrionae subsp. nov.

Material: Holotype BU. H:24 (i), Wenlock Limestone, Dudley, Worcestershire.

Micrometric formula:

Holotype BU. H:24 (i) | 16-20 | 13-16 || 26-28 | 7-10 || 0.20-0.25 | 0.10 || rh.

Discussion. This form differs from *F. pseudosubantiqua* in having slightly straighter, stouter, branches, and almost square rather than oblong fenestrules.

Genus RETEPORINA d'Orbigny 1849 emended

Type species: *Reteporina prisca* (Goldfuss 1826), Middle Devonian, Germany.

Emended diagnosis. Zoarium of irregularly flexuous, relatively stout, non-carinate, occasionally anastomosing branches with some transverse dissepiments. Fenestrules correspondingly large, elongated and irregular. Zoecial chambers with rectangular base-shape and small apertures directed towards one side of the zoarial expansion only. Investing tissue compounded of densely packed minute rods or 'tubules' in a fibrous calcareous 'matrix'.

Discussion. There seems to be no question of the possible identity of this genus with *Semicoscinium* Prout 1859 (as suggested tentatively by Bassler 1953, p. 126), since the latter genus is distinguished by the prominent expansion of the upper part of a well-developed median carina on the obverse of its branches. In *Reteporina* the branches, although rising to a rounded crest, have no distinct carina.

Reteporina reticulata (Lonsdale)

Plate 77, figs. 2, 5, 6; text-fig. 2

Retepora reticulata Lonsdale 1839, p. 678.

Gorgonia assimilis Lonsdale 1839, p. 680.

Fenestella reteporeta Shrubsole 1880, p. 249.

Fenestella assimilis (Lonsdale); Nekhoroshev 1930, p. 184.

Fenestella reticulata Lonsdale; Elias 1956, p. 329.

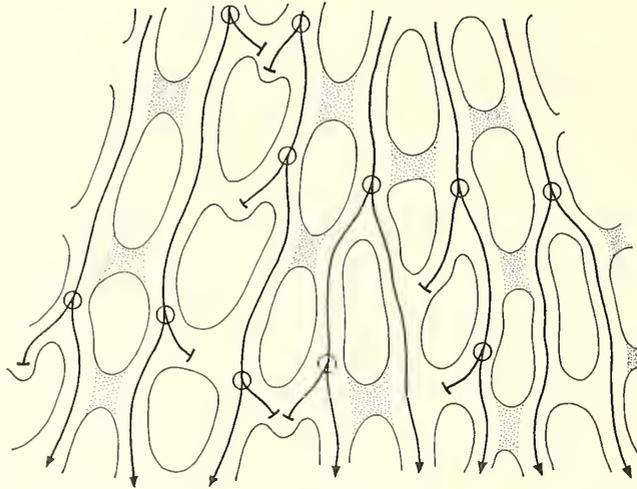
Material: Specimens BU. H:10 and H:26, Wenlock Limestone, Dudley, Worcestershire.

Micrometric formula:

Specimens BU. H:10 and H:26 | 10-12 | 4-5 || 19-23 | 0 || 0.3-0.5 | 0.125 || rect.

Description. Irregular to subreticulate mesh of stout flexuous bifurcating and anastomos-

ing cell-bearing branches occasionally joined by oblique or transverse dissepiments which may also bear cells either throughout their length, or in part only. The branches do not carry, on the obverse, a distinct carina, but their sides rise fairly steeply to a rounded crest. There are no carinal nodes. Each branch is divided by a central, slightly flexuous longitudinal wall into two parts occupied by a regular line of zoecial cells. The cells have rectangular bases and relatively small apertures emerging at the end of long vestibules. The appearance of true dissepiments is sometimes achieved by the effect



TEXT-FIG. 2. Diagram of branch-division structure in relation to dissepiments and pseudo-dissepiments in *Reteporina*. The branch growth-direction is indicated by heavy arrowed lines, and terminations of 'abortive' branches by cross-bars. Dissepiments are stippled. (Notional magnification $\times 15$.)

of bifurcating branches which on approaching neighbouring branches have become united to them by an outgrowth of investing tissue. Part of the 'pseudo-dissepiment' is cell-bearing in such a case, and part not. In other cases true dissepiments have developed where the bending of adjacent branches has almost brought them into contact. In yet other cases one branch appears to have grown straight into another without interruption of cell arrangement. Fenestrules sometimes irregularly heart-shaped near cell-bearing pseudo-dissepiments resulting from abortive branch division. The zoecial chambers or cells occasionally contain a single, obliquely transverse, septum.

Discussion. Nekhoroshev (1956, pp. 173-85) has described a well-developed assemblage, in the Lower Carboniferous rocks of the Altai, as *Reteporina altaica* vars. *a*, *b*, *c*, *d*, *e*, and *major*, and *R. minima*. Although all these forms show the characteristic reteporinoid flexuosity of branches, none of them appears, from Nekhoroshev's photographs and drawings, to have truly anastomosing branches or cell-bearing dissepiments. Instead, wide non-celluliferous dissepiments are developed wherever branch bending brings two neighbouring branches almost into contact. Moreover, in some of the varieties, particularly var. *a*, the number of zoecial apertures is reduced to only three or four to a fenestrule; while in others, for example *c*, *d*, and *e*, a distinct carina can be seen on the branches, with a suggestion (in var. *e*) of carinal nodes. It seems unlikely,

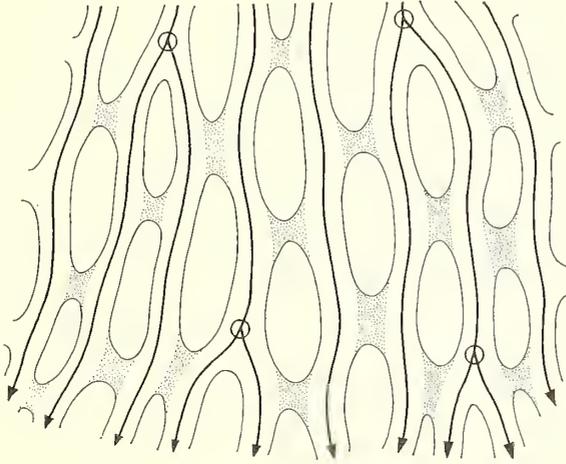
therefore, that Nekhoroshev's species can properly be assigned to *Reteporina*, although they are sufficiently distinct from species of *Fenestella* to be excluded from that genus. I therefore propose to transfer these Russian species to a new genus, *Neoretaporina*.

Genus NEORETEPORINA gen. nov.

Text-fig. 3

Type species: Reteporina altaica Nekhoroshev (1956, p. 177, pls. 26–28), Lower Carboniferous, Russia.

Diagnosis. Like *Reteporina*, but with a more regular meshwork, without cell-bearing dissepiments and true anastomosis of branches, and with an incipient carina on the obverse of the branches, but no carinal nodes.



TEXT-FIG. 3. Diagram of branch structure in relation to dissepiments in *Neoretaporina*. The branch growth-direction is indicated by heavy arrowed lines. Dissepiments are stippled. (Composite drawing after Nekhoroshev 1956, pl. 28, figs. 1–7; notional magnification $\times 15$.)

CONCLUSION

The presence, in English Silurian strata, of the genus *Reteporina*, together with a 'primitive' representative of the main fenestellid stock, here distinguished as *Archaeofenestella*, and apparently 'normal' members of the genus *Fenestella*, has some bearing on currently accepted notions of the phylogeny of the Fenestellidae.

Nekhoroshev (1928, p. 505, fig. 9) suggested the more or less 'explosive' derivation of six fenestellid genera from a main *Fenestella* stock during the Silurian period. These genera were *Polypora*, *Helicopora*, *Ptiloporella*, *Fenestralia*, *Semicoscium*, and *Hemistrypa*. The main *Fenestella* stock was shown as associated rather tentatively with the development in early Ordovician times of *Chasmatopora* (now ascribed to *Subretepora*), a little-known Phylloporinid genus.

There seems little doubt that members of the family Fenestellidae could be derived on purely morphological grounds from several members of the Phylloporinidae, e.g.

Chasmatoporella, *Phylloporina*, *Subretepora*, *Sardesonina*, &c. It also seems necessary to regard the genus *Fenestella* itself as polyphyletic.

If Lower Carboniferous assemblages of species of *Fenestella* are examined as representatives of the time of maximum proliferation of the genus, it is clear that certain broad groupings can be made. For example, there is a rather well-defined group of forms (*F. polyporata* (Phillips), *F. longa* Nekhoroshev, *F. regalis* Ulrich, *F. oblongata* Koenig, are examples of it) characterized by relatively stout, flexuous branches arranged in a meshwork in which the fenestrules are noticeably long and somewhat irregular in shape, and having relatively small zooecial apertures, which thus appear rather closely packed along the fenestrule sides. At another extreme there is a group characterized by a markedly regular, straight-branched, fine meshwork, with small fenestrules and rather large zooecial apertures, of which *F. bicellulata* Etheridge is an example (*F. tenax*, formerly regarded as typical of this group, is now ascribed to Etheridge's species, see Miller 1961a).

The presence of diaphragm-like structures within the zooecial chambers of *Archaeofenestella* is considered a 'primitive' feature. The Ordovician genus *Subretepora* d'Orbigny 1849 has a zoarium constructed of subreticulate anastomosing branches, each of which bears two or more rows of zooecial chambers containing diaphragms, the apertures being separated by irregularly placed acanthopores (nodes). Such a form may be regarded as a possible ancestor for *Archaeofenestella*, to which it might give rise by achieving more precise reticulation of the zoarium by straightening of the branches and the development of non-celluliferous dissepiments; and the reduction of the number of cell rows to two in a branch. By reduction of the internal walls or 'diaphragms' to the vestigial 'hemiseptum' of many Carboniferous fenestellid species it is possible to envisage *Archaeofenestella* as ancestral to just such a species-group within the genus *Fenestella* as that represented by *F. bicellulata* Etheridge.

Similarly, a reteporinid ancestor, also by straightening of branches (although to a lesser extent), with corresponding progressive development of true dissepiments (already present in *Reteporina*), might give rise to fenestellids of the *F. regalis* group, in which there is a carina with nodes, or to members of the genus *Levifenestella* Miller 1961b, in which there is only an incipient carina and no nodes.

Finally, the main body of carinate fenestellid meshworks could well have arisen from a genus like *Moorephyloporina* Bassler, in which the branches in an anastomosing mesh have two rows of circular zooecial apertures separated by a threadlike keel bearing minute perforated nodes.

Acknowledgements. I am indebted to the Curator of the Sedgwick Museum, Cambridge, Mr. A. G. Brighton; and to the Curator of the Holcroft Collection of the University of Birmingham, Mr. R. S. Coope, and Professor F. W. Shotton, F.R.S., for the loan of various specimens.

REFERENCES

- BASSLER, R. S. 1953. In *Treatise on Invertebrate Palaeontology* (R. C. Moore, Ed.), part G: 'Bryozoa' pp. xiii+253. Univ. of Kansas Press and Geol. Soc. Amer.
- BOUČEK, B. 1953. Biostratigraphy, development and correlation of the Zekovic and Motol beds of the Silurian of Bohemia. *Sbornik Ústřed. Úst. Geol. svazek* 20, 421-73. (Nakl. Česko. akad. věd Praha.)

- BUTLER, A. J. 1939. The stratigraphy of the Wenlock Limestone of Dudley. *Quart. J. geol. Soc. Lond.* **95**, 37-74.
- DAS GUPTA, T. 1933. The Zone of *Monograptus vulgaris* in the Welsh Borderland and North Wales. *Proc. Liverpool geol. Soc.* **16**, 109-15.
- ELIAS, M. K. 1956. Revision of *Fenestella subantiqua* and related Silurian fenestellids. *J. Paleont.* **30** (2), 314-32.
- LONSDALE, W. 1839. *Corals*. In Murchison, R. I., *Silurian System*, **2**, 675-94.
- M'COY, F. 1850. On some new genera and species of Silurian Radiata . . . *Ann. Mag. nat. Hist.* (2nd ser.) **6**, 270-90.
- 1851-5. *Systematic description of the British Palaeozoic fossils in the Geological Museum of the University of Cambridge*. London and Cambridge.
- MILLER, T. G. 1961a. Type specimens of the genus *Fenestella* from the Lower Carboniferous of Great Britain. *Palaeontology*, **4**, 221-42.
- 1961b. New Irish Tournaisian Fenestellids. *Geol. Mag.* **98**, 493-500.
- NEKHOROSHEV, V. P. 1928. History of development of Bryozoa from the family Fenestellidae. *Bull. Com. géol. Leningrad*, **47** (5), 479-518.
- 1930. On certain Palaeozoic Bryozoa in the British Museum (Nat. Hist.). *Geol. Mag.* **67**, 178-89.
- 1956. Lower Carboniferous Bryozoa of the Siberian Altai. *Trudy vses. nauch. issled. geol. Inst.*, N.S., **13**, 419 pp.
- d'ORBIGNY, A. 1850-2. *Prodrome de Paléontologie Stratigraphique*. Paris.

T. G. MILLER
Department of Geology,
University of Keele,
Keele, Staffordshire

Manuscript received 1 December 1961

LOWER CARBONIFEROUS MICROFLORAS OF SPITSBERGEN

by G. PLAYFORD

ABSTRACT. Dispersed microspores recovered from the Culm succession (Lower Carboniferous) of Spitsbergen are described in detail and an assessment is made of their value in the elucidation of problems of stratigraphical correlation. The majority of the samples studied are from the Billefjorden Sandstones (i.e. the Culm sequence of Central Vestspitsbergen), which consist typically of sandstones, together with subordinate carbonaceous shales and siltstones and minor coal seams. Detailed collections from three of the most complete sections of the Billefjorden Sandstones, at Birger Johnsonfjellet, Triungen, and Citadellet, present a comprehensive picture of the microfloral succession. As such, they serve as valuable local reference columns with which numerous additional samples, from a variety of localities and horizons in Spitsbergen and Bjørnøya, may be correlated upon microfloral evidence. Two distinct, successive, microfloral assemblages are distinguishable within the otherwise sparsely fossiliferous Billefjorden Sandstones. The presence of numerous species recorded previously from various horizons of the Russian Lower Carboniferous and of the Mississippian of Canada facilitates international correlation. In terms of the standard European stages, the age of the Billefjorden Sandstones is shown to range from Tournaisian to Upper Viséan or lowest Namurian; in terms of North American (Mississippian) nomenclature, the series ranges in age from Kinderhook to lower or middle Chester. This paper includes the systematic descriptions of 115 microspore species. One new genus (*Radialetes*) and thirty-nine new species are proposed. Another genus (*Diatomozonotriletes*) is validated and emended. Three probably new species are described but not specifically named due to their insufficient representation. The remaining seventy-three species are all referable to previously described types. Consideration is given to relevant problems in dispersed-spore taxonomy, botanical relationships, and to differences in microspore composition of various lithological types.

[*Editor's note.* This paper will be printed in two parts, the second in *Palaeontology*, Vol 5. Part 4]

PART ONE

In October 1958 the writer commenced a study, at the Sedgwick Museum, Cambridge, of the spores contained in samples from the Culm succession (Lower Carboniferous) of Spitsbergen. This research was undertaken at the joint suggestion of Messrs. N. F. Hughes and W. B. Harland. An initial palynological study by Mr. Hughes and Mrs. Margaret Mortimer of some samples then available had disclosed the presence of prolific microfloras of potential stratigraphical value.

A preliminary paper (Hughes and Playford 1961) incorporated early results of the investigation; it was based upon the microfloral study of three representative samples of the Billefjorden Sandstones, which is the name given to the Culm development in Central Vestspitsbergen (Forbes, Harland, and Hughes 1958). One of the samples (B685), a sandstone from Citadellet, contained a diverse and well-preserved microflora which suggested a Tournaisian age; corroborative spore evidence for such an age is provided by numerous other samples, recorded herein, from Citadellet and from other localities. The other two samples, S59a (from the north side of Wordiekammen) and B609 (from the south side of Ebbadalcn), contained a different and demonstratively younger (Viséan or lowest Namurian) microflora, which is represented in the majority of samples examined subsequently by the present writer.

The large bulk of the samples upon which the present study is based had been col-

lected by members of Cambridge Spitsbergen Expeditions organized from the Sedgwick Museum. In particular, the detailed collections made in 1959 from the Billefjorden Sandstones have proved especially valuable. The purpose of this study was twofold. Firstly, to describe systematically the microspores present in the Culm succession of Spitsbergen. Secondly, to assess the correlative value of the microfloras, both within and outside Spitsbergen. As will be shown subsequently, external correlation of the Billefjorden Sandstones is facilitated by the close similarity of the microfloras contained therein, with previously described microfloras from the Lower Carboniferous of the U.S.S.R. and from certain horizons of the Canadian Mississippian. Hence, on the basis of microfloral evidence, dating of the Spitsbergen Culm with reference to the standard European Lower Carboniferous stages is a necessarily indirect process, since no spore floras have yet been recorded from the type areas of these stages. Thus, where 'Tournaisian', 'Viséan', and 'Upper Viséan/lowest Namurian' are specified herein with regard to the age of the Spitsbergen Culm, it is emphasized that their validity in that context is dependent directly upon the precision with which the Russian and Canadian sequences may be correlated with that of north-western Europe. This subject will be discussed more fully subsequently. It is important to note here that as a result of recommendations accepted at the XXIst International Geological Congress (*vide* Mr. W. B. Harland) it is likely that the terms 'Lower', 'Middle', and 'Upper' Carboniferous will in the future be used only with reference to the Russian succession; and furthermore that new stage names (presumably approximate equivalents of Tournaisian, Viséan, and Namurian A-B) are expected to be proposed by Russian stratigraphers for the subdivisions of their Lower Carboniferous. In the western European Carboniferous, the names 'Dinantian' and 'Silesian' are to be used as the two primary subdivisions of the Carboniferous; the former including the Tournaisian and Viséan, and the latter including the Namurian, Westphalian, and Stephanian. The Mississippian and Pennsylvanian nomenclature as applied to the North American succession is to remain unchanged. These proposals have obvious relevance in connexion with the international correlation of the Spitsbergen Culm, but have not as yet been detailed in publication. For the present purpose, the term 'Lower Carboniferous' is conveniently used in a general sense to embrace Tournaisian, Viséan, and Lower Namurian, corresponding thus approximately to 'Mississippian', and to its Scottish connotation.

Acknowledgements. The writer wishes to express his sincere gratitude to Mr. N. F. Hughes for constant advice and encouragement during the progress of this study. The investigation was made possible by the field-work of members of various Cambridge Spitsbergen Expeditions. In particular, the writer is indebted to Mr. W. B. Harland, who organized most of these Expeditions and who, jointly with Mr. Hughes, suggested this study; to Dr. D. J. Gobbett for his painstaking palynological sampling; and to Mr. P. F. Friend for help in the compilation of text-fig. 1. Grateful acknowledgement is made to Professor O. M. B. Bulman, F.R.S., for the use of the research facilities of the Sedgwick Museum, Cambridge, where the study was carried out. The writer also wishes to record his gratitude to Miss Mary Dettmann and Dr. D. M. Churchill for helpful discussions; and to Mrs. Margaret Mortimer who prepared some of the samples. Special thanks are due to Mr. A. Barlow for considerable assistance with the photography.

Through the courtesy of Drs. M. A. Butterworth and A. H. V. Smith, of the National Coal Board, the writer was able to examine the Scottish Lower Carboniferous spores which had been described in 1958 by Dr. Butterworth and Dr. R. W. Williams. Professor O. H. Selling, of the Naturhistoriska Riksmuseet, Stockholm, kindly allowed the writer to obtain palynological samples from the Nathorst Collection of Culm plant material.

This study was carried out during the tenure of a Robert and Maude Gledden Research Fellowship from the University of Western Australia (1958-60), and subsequently (1960-1) of an Overseas Post-graduate Studentship awarded by the Australian Commonwealth Scientific and Industrial Research Organization. The writer acknowledges gratefully both these sources of financial assistance.

REFERENCES

- AISENERG, D. E., BRAZHNIKOVA, N. E., NOVIK, K. A., ROTAY, A. P., and SHULGA, P. L. 1960. Carboniferous stratigraphy of the Donetz Basin. *C.R. 4th Congr. Strat. Geol. Carb.*, Heerlen (1958), **1**, 1-12.
- ALPERN, B. 1958. Description de quelques microspores du Permo-Carbonifère français. *Rev. Micropaléont.* **1**, 75-86.
- ANTEVS, E. and NATHORST, A. G. 1917. Kohlenführender Kulm auf der Bären-Insel. *Geol. Fören. Stockh. Förh.* **39**, 649-63.
- ARTÜZ, S. 1957. Die Spores dispersae der Türkischen Steinkohle vom Zonguldak-Gebiet. *İstanbul Üniv. Fen Fak. Mecm.*, ser. B, cilt **22**, sayı 4, 239-63.
- 1959. Zonguldak bölgesindeki Alimolla, Sulu ve Büyük kömür damarlarının sporolojik etüdü. *İstanbul Üniv. Fen Fak. Monograf.*, sayı **15**, 1-73.
- BALME, B. E. 1957. Spores and pollen grains from the Mesozoic of Western Australia. *C.S.I.R.O. Aust., Coal Res. Sect.*, T.C. **25**, 1-48.
- 1960. Notes on some Carboniferous microfloras from Western Australia. *C.R. 4th Congr. Strat. Geol. Carb.*, Heerlen (1958), **1**, 25-31.
- and HASSELL, C. W. 1962. Upper Devonian spores from the Canning Basin, Western Australia. *Micropaleontology*, **8**, 1-28.
- BHARDWAJ, D. C. 1957. The palynological investigations of the Saar coals (Part I—Morphology of Spores dispersae). *Palaeontographica*, **B101**, 73-125.
- 1959. On *Porostrobos zeileri* Nathorst and its spores with remarks on the systematic position of *P. bennholdi* Bode and the phylogeny of *Densosporites* Berry. *Palaeobotanist*, **7**, 67-75.
- BIRKENMAJER, K. 1960. Course of the geological investigations of the Hornsund area, Vestspitsbergen, in 1957-1958; in Geological results of the Polish 1957-1958 Spitsbergen expedition (K. Birkenmajer, Editor) Part I. *Studia Geol. Polon.* **4**, 7-35.
- BLUDOROV, A. P. and TUZOVA, L. S. 1956. Coal measures of the Lower Carboniferous of Tartary. *Dokl. Akad. Nauk S.S.S.R.* **111**, 663-6 [in Russian].
- BOLKHOVITINA, N. A. 1956. Atlas of the spores and pollen grains in Jurassic and Lower Cretaceous coals of the Viliusk Basin. *Tr. Inst. Geol., Akad. Nauk S.S.S.R.* **2**, 1-132 [in Russian].
- 1959. Spore-pollen complexes of the Mesozoic deposits of the Viliusk Basin and their stratigraphical significance. *Ibid.* **24**, 1-185 [in Russian].
- BUTTERWORTH, M. A. and MILLOTT, J. O'N. 1960. Microspore distribution in the coalfields of Britain. *Proc. Int. Committee for Coal Petrol.* **3**, 157-63.
- and WILLIAMS, R. W. 1958. The small spore floras of coals in the Limestone Coal Group and Upper Limestone Group of the Lower Carboniferous of Scotland. *Trans. Roy. Soc. Edinb.* **63**, 353-92.
- BYVSHEVA, T. V. 1957. A spore-pollen description of the terrigenous rock complex of the Lower Carboniferous of the Melekess and Busuluk deep wells. *Dokl. Akad. Nauk S.S.S.R.* **116**, 1009-11 [in Russian].
- 1960. Spore-pollen complexes of the terrigenous part of the Lower Carboniferous of the Volga-Ural region. *Ibid.* **131**, 146-9 [in Russian].
- CHALONER, W. G. 1953a. A new species of *Lepidostrobus* containing unusual spores. *Geol. Mag.* **90**, 97-110.
- 1953b. On the megaspores of four species of *Lepidostrobus*. *Ann. Bot. Lond.*, n.s., **17**, 263-93.
- 1954. Notes on the spores of two British Carboniferous lycopods. *Ann. Mag. Nat. Hist.* **7**, 81-91.
- 1958a. A Carboniferous *Selaginellites* with *Densosporites* microspores. *Palaeontology*, **1**, 245-53.
- 1958b. *Polysporia mirabilis* Newberry, a fossil lycopod cone. *J. Paleont.* **32**, 199-209.
- CHIBRIKOVA, E. V. 1959. Spores of the Devonian and older deposits of Bashkir. *Akad. Nauk S.S.S.R., Materials on Palaeont. and Strat. of Devonian and older Deposits of Bashkir*, 3-116 [in Russian].

- CHURCHILL, D. M. 1960. Living and fossil unicellular algae and aplanospores. *Nature*, **186**, 493–4.
- COOKSON, I. C., and DETTMANN, M. E. 1959. On *Schizosporis*, a new form genus from Australian Cretaceous deposits. *Micropaleontology*, **5**, 213–16.
- COOPER, R. A. 1958. British Mesozoic microspores and pollen grains, a systematic and stratigraphic study. *Palaeontographica*, **B103**, 75–179.
- DINELEY, D. L. 1958. Review of the Carboniferous and Permian rocks of the west coast of Vestspitsbergen. *Norsk Geol. Tidsskr.* **38**, 197–219.
- DYBOVÁ, S. and JACHOWICZ, A. 1957. Microspores of the Upper Silesian Coal Measures. *Inst. Geol. Prace*, **23**, 1–328.
- ELIAS, M. K. 1960. Marine Carboniferous of N. America and Europe. *C.R. 4th Congr. Strat. Geol. Carb.*, Heerlen (1958), **1**, 151–61.
- ERDTMAN, G. 1952. *Pollen morphology and plant taxonomy. Angiosperms*. Waltham, Mass.
- 1957. *Pollen and spore morphology|plant taxonomy; Gymnospermae, Pteridophyta, Bryophyta*. Stockholm.
- FELIX, J. 1894. Studien über fossile Pilze. *Z. Deutsch. Geol. Ges.* **46**, 269–80.
- FORBES, C. L., HARLAND, W. B., and HUGHES, N. F. 1958. Palaeontological evidence for the age of the Carboniferous and Permian rocks of Central Vestspitsbergen. *Geol. Mag.* **95**, 465–90.
- GEE, E. R., HARLAND, W. B., and MCWHAE, J. R. H. 1952. Geology of Central Vestspitsbergen: Part I. Review of the geology of Spitsbergen, with special reference to Central Vestspitsbergen; Part II. Carboniferous to Lower Permian of Billefjorden. *Trans. Roy. Soc. Edinb.* **62**, 299–356.
- GUENNEL, G. K. 1952. Fossil spores of the Alleghenian coals in Indiana. *Rept. Progr. Indiana Geol. Surv.* **4**, 1–40.
- 1958. Miospore analysis of the Pottsville coals of Indiana. *Bull. Indiana Geol. Surv.* **13**, 1–101.
- HACQUEBARD, P. A. 1957. Plant spores in coal from the Horton Group (Mississippian) of Nova Scotia. *Micropaleontology*, **3**, 301–24.
- and BARSS, M. S. 1957. A Carboniferous spore assemblage, in coal from the South Nahanni River area, Northwest Territories. *Bull. Geol. Surv. Canada*, **40**, 1–63.
- HARKER, P. 1961. Summary account of Carboniferous and Permian formations, southwestern district of Mackenzie. *Paper Geol. Surv. Canada*, **61-1**, 1–9.
- HARRIS, W. F. 1955. A manual of the spores of New Zealand Pteridophyta. *Bull. New Zealand Dept. Sci. Indust. Res.* **116**, 1–186.
- HEER, O. 1871. Fossile Flora der Bären Insel. *Kongl. Svenska Vetensk. Akad. Handl.* **9**, 1–51.
- HIGGINS, A. C. 1961. Some Namurian conodonts from North Staffordshire. *Geol. Mag.* **98**, 210–24.
- HOFFMEISTER, W. S., STAPLIN, F. L., and MALLOY, R. E. 1955a. Geologic range of Paleozoic plant spores in North America. *Micropaleontology*, **1**, 9–27.
- — — 1955b. Mississippian plant spores from the Hardinsburg formation of Illinois and Kentucky. *J. Paleont.* **29**, 372–99.
- HORN, G. and ORVIN, A. K. 1928. Geology of Bear Island. *Skrifter om Svalbard og Ishavet*, **15**, 1–152.
- HORST, U. 1955. Die Sporae dispersae des Namurs von Westoberschlesien und Mährisch-Ostrau. *Palaeontographica*, **B 98**, 137–236.
- HOSKINS, J. H. and ABBOTT, M. L. 1956. *Selaginellites crassinctus*, a new species from the Desmoinesian series of Kansas. *Amer. J. Bot.* **43**, 36–46.
- HUGHES, N. F. 1961. Fossil evidence and angiosperm ancestry. *Sci. Progr.* **49**, 84–102.
- and PLAYFORD, G. 1961. Palynological reconnaissance of the Lower Carboniferous of Spitsbergen. *Micropaleontology*, **7**, 27–44.
- IMGRUND, R. 1960. Sporae dispersae des Kaipingbeckens, ihre paläontologische und stratigraphische Bearbeitung im Hinblick auf eine Parallelisierung mit dem Ruhrkarbon und dem Pennsylvanian von Illinois. *Geol. Jahrb.* **77**, 143–204.
- ISHCHENKO, A. M. 1952. Atlas of the microspores and pollen of the Middle Carboniferous of the western part of the Donetz Basin. *Izd. Akad. Nauk Ukrainian S.S.R., Inst. Geol. Nauk*, 1–83 [in Russian].
- 1956. Spores and pollen of the Lower Carboniferous deposits of the western extension of the Donetz Basin and their stratigraphical importance. *Akad. Nauk Ukrainian S.S.R., Tr. Inst. Geol. Nauk Ser. Strat. Palaeont.* **11**, 1–185 [in Russian].
- 1958. Sporo-pollen analysis of the Lower Carboniferous sediments of the Dnieper–Donetz Basin. *Ibid.* **17**, 1–188 [in Russian].

- JACHOWICZ, A. 1958. Stratigraphical problems in the Upper Silesian productive Carboniferous in view of microspore investigations. *Kwart. Geol.* **2**, 483–506.
- KEDO, G. I. 1957. On the stratigraphy and spore-pollen complexes of the lower horizons of the Carboniferous in the B.S.S.R. *Dokl. Akad. Nauk S.S.S.R.* **115**, 1165–8 [in Russian].
- 1958. Characteristic spores and pollen of the lower horizons of the Carboniferous in the B.S.S.R. *Tr. Inst. Geol. Nauk Akad. Nauk B.S.S.R.* **1**, 44–56 [in Russian].
- 1959. Importance of spore-pollen analyses in the stratigraphy of the continental deposits of the lower horizons of the Carboniferous in the B.S.S.R. *Voprosy biostratigrafii kontinental'nykh tolshch, Gosgeoltekhizdat, Moscow*, 157–65 [in Russian].
- KNOX, E. M. 1948. The microspores in coals of the Limestone Group in Scotland. *Trans. Inst. Min. Engrs., Lond.* **107**, 155–63.
- 1950. The spores of *Lycopodium*, *Phylloglossum*, *Selaginella* and *Isoetes* and their value in the study of microfossils of Palaeozoic age. *Trans. Bot. Soc. Edinb.* **35**, 209–357.
- KOSANKE, R. M. 1950. Pennsylvanian spores of Illinois and their use in correlation. *Bull. Ill. State Geol. Surv.* **74**, 1–128.
- 1955. *Mazostachys*—a new calamite fructification. *Rept. Inv. Ill. State Geol. Surv.* **180**, 1–37.
- LESCHIK, G. 1955. Die Keuperflora von Neuwelt bei Basel. II. Die Iso- und Mikrosporen. *Abh. Schweiz. Paläont.* **72**, 1–70.
- LIBROVITCH, L. S. 1958. Système Carbonifère in: *Structure Géologique de l'U.R.S.S., t. 1—Stratigraphie, fasc. 3—Paléozoïque*, Moscow 1958 (French translation: Centre national de la recherche scientifique, Paris; 1959, 321 pp.).
- LOGINOVA, A. M. 1959. On the stratigraphy of the Yasnopolyansky substage of the Saratov-Stalingrad Volga area. *Bull. Soc. des Naturalistes de Moscou, sect. Géol.* **34**, 95–102 [in Russian].
- LOVE, L. G. 1960. Assemblages of small spores from the Lower Oil-shale Group of Scotland. *Proc. Roy. Soc. Edinb.* **67**, 99–126.
- LUBER, A. A. 1935. Les types pétrographiques de charbons fossiles du Spitsbergen. *Chimie combustible solide*, **6**, 186–95 [in Russian].
- 1955. Atlas of the spores and pollen grains of the Palaeozoic deposits of Kazakhstan. *Tr. Akad. Nauk Kazach. S.S.R., Alma-Ata*, 1–126 [in Russian].
- and WALTZ, I. E. 1938. Classification and stratigraphical value of spores of some Carboniferous coal deposits in the U.S.S.R. *Trans. Central Geol. Prosp. Inst.* **105**, 1–45 [in Russian].
- 1941. Atlas of microspores and pollen grains of the Palaeozoic of the U.S.S.R. *Tr. All-Union Geol. Sci. Res. Inst. (V.S.E.G.E.I.)*, **139**, 1–107 [in Russian].
- MAMAY, S. H. 1954. Two new plant genera of Pennsylvanian age from Kansas coal balls. *Prof. Paper U.S. Geol. Surv.* **254-D**, 81–95.
- MCGREGOR, D. C. 1960. Devonian spores from Melville Island, Canadian Arctic Archipelago. *Palaeontology*, **3**, 26–44.
- MCWHAE, J. R. H. 1953. The major fault zone of Central Vestspitsbergen. *Quart. J. Geol. Soc. Lond.* **108**, 209–32.
- MOORE, R. C. 1937. Comparison of the Carboniferous and early Permian rocks of North America and Europe. *C.R. 2nd. Congr. Strat. Carb., Heerlen (1935)*, **2**, 641–76.
- NATHORST, A. G. 1894. Zur paläozoischen Flora der arktischen Zone. *Kongl. Svenska Vetensk. Akad. Handl.* **26**, 5–80.
- 1899. Über die oberdevonische Flora (die 'Ursaflora') der Bären-Insel (Vorl. Mitt.). *Bull. Geol. Inst. Univ. Uppsala*, **4**, 152–6.
- 1902. Zur oberdevonischen Flora der Bären-Insel. *Kongl. Svenska Vetensk. Akad. Handl.* **36**, 5–60.
- 1910. Beiträge zur Geologie der Bären-Insel, Spitzbergens und des König-Karl-Landes. *Bull. Geol. Inst. Univ. Uppsala*, **10**, 261–416.
- 1914. Nachträge zur paläozoischen Flora Spitzbergens. *Zur fossilien Flora der Polarländer, Teil 1, Lief 4*. Stockholm.
- 1920. Zum Kulmflora Spitzbergens. *Ibid.*, Teil 2, Lief 1. Stockholm.
- NAUMOVA, S. N. 1939. Spores and pollen of the coals of the U.S.S.R. *Rept. Int. Geol. Congr., 17th Session, U.S.S.R.* **1**, 353–64.
- 1950. Pollen of angiosperm type from Lower Carboniferous deposits. *Izv. Akad. Nauk S.S.S.R., Geol. Ser.* **3**, 103–13 [in Russian].

- NAUMOVA, S. N. 1953. Sporo-pollen complexes of the Upper Devonian of the Russian Platform and their stratigraphical value. *Tr. Inst. Geol. Nauk Akad. Nauk S.S.S.R.* **143** (Geol. Ser. no. 60), 1–204 [in Russian].
- NEVES, R. 1958. Upper Carboniferous plant spore assemblages from the *Gastrioceras subrenatum* horizon, North Staffordshire. *Geol. Mag.* **95**, 1–19.
- 1961. Namurian plant spores from the Southern Pennines, England. *Palaeontology*, **4**, 247–79.
- NILSSON, T. 1958. Über das Vorkommen eines mesozoischen Sapropelgesteins in Schonen. *Lunds Universitets Årsskrift*, N.F., Avd. 2, **52**, 5–112.
- ORVIN, A. K. 1940. Outline of the geological history of Spitsbergen. *Skrifter om Svalbard og Ishavet*, **78**, 1–57.
- PATTON, W. J. H. 1958. Mississippian succession in South Nahanni River area, Northwest Territories; in Jurassic and Carboniferous of Western Canada, *Amer. Assoc. Petrol. Geol., Allen Mem. Vol.*, 309–26.
- POTONIÉ, R. 1956. Synopsis der Gattungen der Sporae dispersae. I. Teil: Sporites. *Beih. Geol. Jahrb.* **23**, 1–103.
- 1958. Synopsis der Gattungen der Sporae dispersae. II. Teil: Sporites (Nachträge), Saccites, Aletes, Praecolpates, Polyplificates, Monocolpates. *Ibid.* **31**, 1–114.
- 1960. Synopsis der Gattungen der Sporae dispersae. III. Teil: Nachträge Sporites, Fortsetzung Pollenites. Mit Generalregister zu Teil I–III. *Ibid.* **39**, 1–189.
- and KREMP, G. 1954. Die Gattungen der paläozoischen Sporae dispersae und ihre Stratigraphie. *Geol. Jahrb.* **69**, 111–94.
- 1955. Die Sporae dispersae des Ruhrkarbons, ihre Morphographie und Stratigraphie mit Ausblicken auf Arten anderer Gebiete und Zeitabschnitte; Teil I. *Palaeontographica*, **B98**, 1–136.
- 1956a. *Idem*; Teil II. *Ibid.* **B99**, 85–191.
- 1956b. *Idem*; Teil III. *Ibid.* **B100**, 65–121.
- RADFORTH, N. W. and MCGREGOR, D. C. 1954. Some plant microfossils important to pre-Carboniferous stratigraphy and contributing to our knowledge of early floras. *Canad. J. Bot.* **32**, 601–21.
- 1956. Antiquity of form in Canadian plant microfossils. *Trans. Roy. Soc. Canada*, **50**, 27–33.
- RAISTRICK, A. 1934. The correlation of coal seams by microspore content. Pt. I: The seams of Northumberland. *Trans. Inst. Min. Engrs., Lond.* **88**, 142–53.
- REINSCH, P. F. 1884. *Micropalaeophytologia formationis carboniferae; Vol. 1—Continens Trileteas et Stelideas*. Erlangen.
- REMY, W. and R. 1957. Durch Mazeration fertiler Farne des Paläozoikums gewonnene Sporen. *Paläont. Z.* **31**, 55–65.
- RICHARDSON, J. B. 1960. Spores from the Middle Old Red Sandstone of Cromarty, Scotland. *Palaeontology*, **3**, 45–63.
- SCHEMEL, M. P. 1950. Carboniferous plant spores from Daggett County, Utah. *J. Paleont.* **24**, 232–44.
- SCHOPE, J. M., WILSON, L. R., and BENTALL, R. 1944. An annotated synopsis of Paleozoic fossil spores and the definition of generic groups. *Rept. Inv. Ill. State Geol. Surv.* **91**, 1–72.
- SCOTT, R. A., BAGHOORN, E. S., and LEOPOLD, E. B. 1960. How old are the angiosperms? *Amer. J. Sci.* **258A**, 284–99.
- SEN, J. 1958. Notes on the spores of four Carboniferous lycopods. *Micropaleontology*, **4**, 159–62.
- SIEDLECKI, S. 1960. Culm beds of the S.W. coast of Hornsund, Vestspitsbergen. *Studia Geol. Polon.* **4**, 93–102.
- SMITH, A. H. V. 1960. Structure of the spore wall in certain miospores belonging to the series Cingulati Pot. and Klaus 1954. *Palaeontology*, **3**, 82–85.
- SOMERS, G. 1952. A preliminary study of the fossil spore content of the lower Jubilee seam of the Sydney coalfield, Nova Scotia. *Publ. Nova Scotia Found.*, Halifax, 1–30.
- STAPLIN, F. L. 1960. Upper Mississippian plant spores from the Golata formation, Alberta, Canada. *Palaeontographica*, **B107**, 1–40.
- STEPANOV, D. L. 1959. Carboniferous system and its main stratigraphical subdivisions. *Izv. Akad. Nauk S.S.S.R., Geol. Ser.* **11**, 52–65 [in Russian].
- SULLIVAN, H. J. 1958. The microspore genus *Simozonotriletes*. *Palaeontology*, **1**, 125–38.
- TETERIUK, V. K. 1956. Angiosperms in the Lower Carboniferous sediments of the western extension of the Donetz Basin. *Dokl. Akad. Nauk S.S.S.R.* **109**, 1032–4 [in Russian].

- TETERIUK, V. K. 1958. On the finding of open-pored pollen grains of Palaeozoic angiosperms. *Dokl. Akad. Nauk S.S.S.R.* **118**, 1034-5 [in Russian].
- WALTON, J. 1957. On *Protopytis* (Göppert): with a description of a fertile specimen *Protopytis scotica* sp. nov. from the Calciferous Sandstone Series of Dunbartonshire. *Trans. Roy. Soc. Edinb.* **63**, 333-40.
- WELLER, J. M. *et al.* 1948. Correlation of the Mississippian formations of North America. *Bull. Geol. Soc. Amer.* **59**, 91-196.
- WILSON, L. R. 1958. Photographic illustrations of fossil spore types from Iowa. *Oklah. Geol. Notes*, **18**, 99-101.
- 1960. *Florinites pelucidus* and *Endosporites ornatus* with observations on their morphology. *Ibid.* **20**, 29-33.
- and COE, E. A. 1940. Descriptions of some unassigned plant microfossils from the Des Moines series of Iowa. *Amer. Midl. Nat.* **23**, 182-86.
- and HOFFMEISTER, W. S. 1956. Plant microfossils of the Croweburg coal. *Circ. Oklah. Geol. Surv.* **32**, 1-57.

STRATIGRAPHY

The Lower Carboniferous (Culm) succession of Spitsbergen consists principally of sandstones, together with carbonaceous shales and siltstones and minor lenses of coal. It represents a typical non-marine (deltaic and lacustrine) sequence, showing marked local changes in thickness and notable lateral and vertical lithological variation. The formation rests unconformably upon folded Middle Devonian or older rocks, and (in Central Vestspitsbergen) passes upwards by concordant transition into the Lower Gypsiferous Series, the lower unit of the Campbellryggen Group which is considered to be of Middle Carboniferous age (Gee, Harland, and McWhae 1952, p. 342; Forbes, Harland, and Hughes 1958, p. 486).

The term 'Culm' has been consistently applied (Nathorst 1910, Orvin 1940, Gee *et al.* 1952, and others) to the Lower Carboniferous continental succession of Svalbard, despite the fact that the deposits are quite dissimilar from the typical Culm (Kulm) deep-water facies of south-west England and Germany. More recently, Forbes *et al.* (1958) proposed the name Billefjorden Sandstones for the characteristic development, in Central Vestspitsbergen, of this distinctive plant-bearing series, whilst retaining Culm 'for general use in Svalbard in the sense of Nathorst 1910'.

Plant macrofossils occur at many horizons and have been generally regarded as indicative of a Lower Carboniferous age. As listed by Forbes *et al.* (1958, pp. 468-9), the macroflora of the Billefjorden Sandstones consists predominantly of representatives of *Lepidodendron* and of the Sublepidodendron group, together with some macrophyllous leaves (*Cardiopteridium*, *Sphenopteridium*, *Adiantites*) which are probably mostly pteridospermous. On the basis of this palaeontological evidence Forbes and his co-authors concluded that sedimentation occurred during a large portion of Lower Carboniferous time.

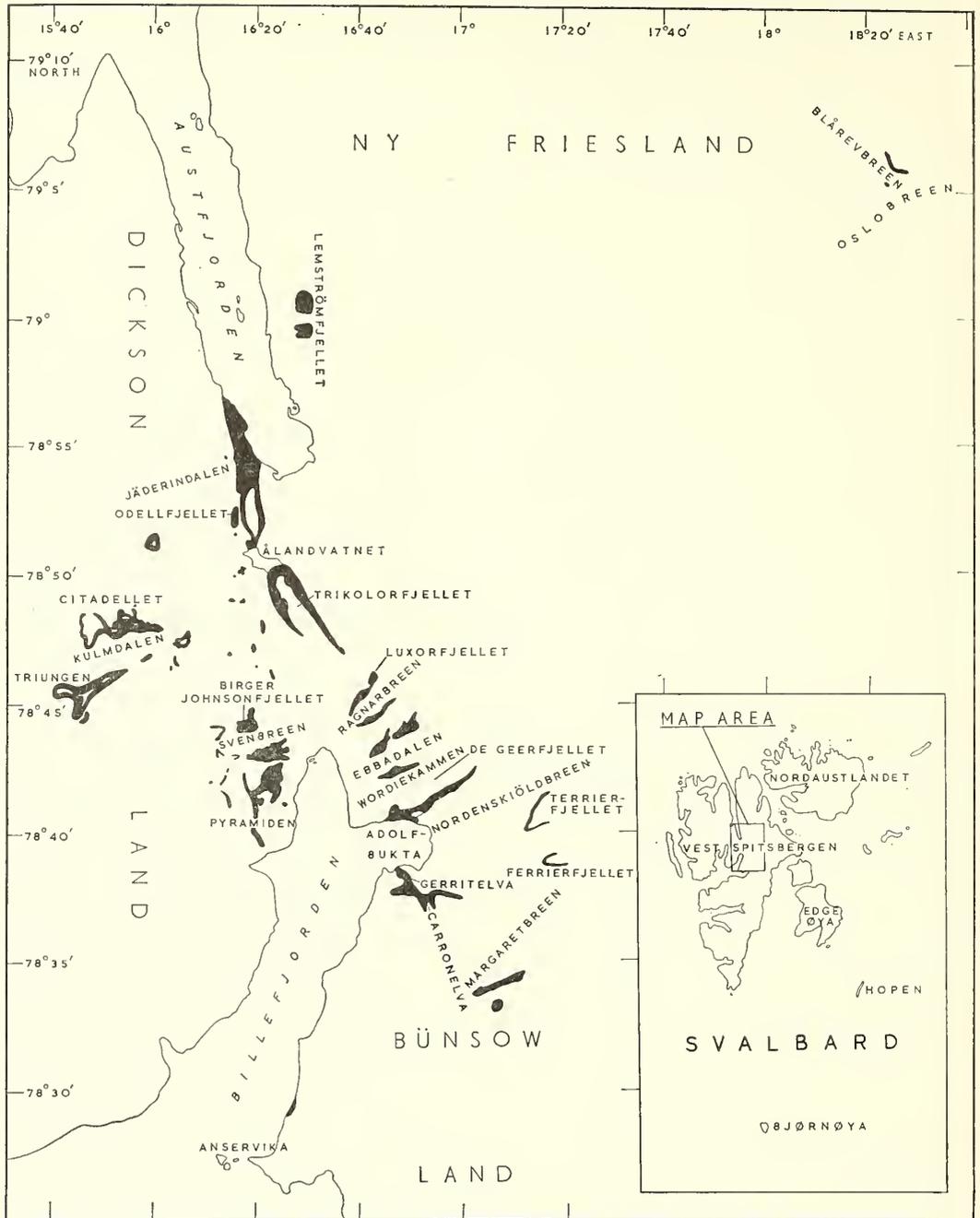
According to Gee *et al.* (1952, p. 312), late Palaeozoic deposition commenced over much of Svalbard in early Carboniferous times in a general submergence, following a period of extensive faulting, uplift, and erosion during the Upper Devonian. The irregular development of the Culm sediments strongly suggests their accumulation on a landscape of considerable relief. A graphic example is recorded by McWhae (1953, pp. 220-1) who describes a prominent buttress of pre-Downtonian (Hecla Hoek) basement over which Culm rocks are draped spectacularly in both the Ragnarbreen and

Ebbadalen areas. McWhae interprets this feature as a fault scrap (his hypothetical fault H) which must have been prominent in early Carboniferous time and had therefore resulted from (west block down) movement late in the Upper Devonian. This conjectural fault is traceable as a conspicuous basement step extending 'in a remarkably straight line from the east side of Wijdefjorden to the north-east corner of Adolfbukta at the foot of Nordenskiöldbreen' (McWhae 1953, p. 220).

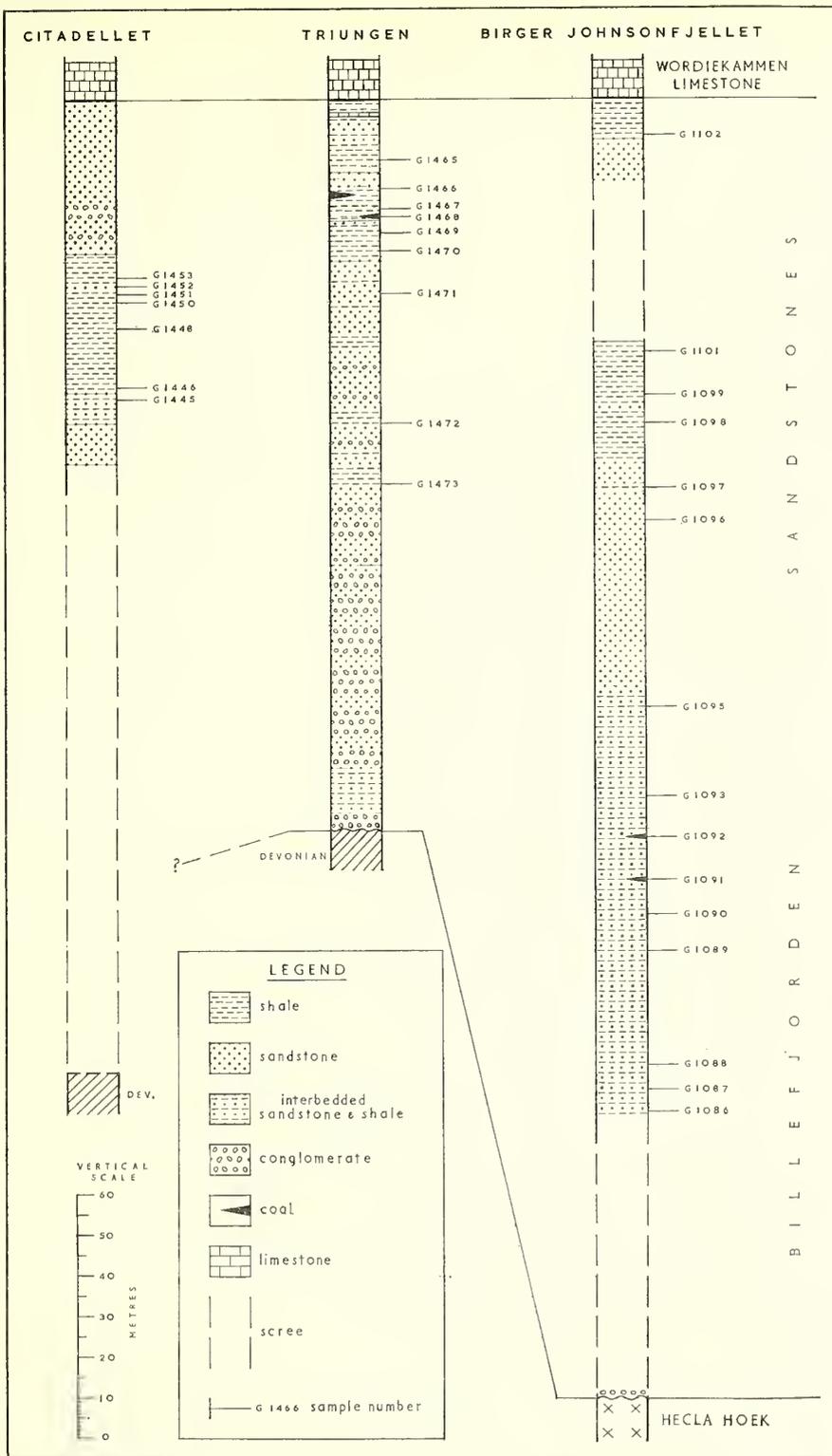
As shown in text-fig. 1 of Forbes *et al.* (1958), Lower Carboniferous deposits are exposed in Spitsbergen, principally in the central and extreme western parts of Vestspitsbergen; apparently isolated developments are also known in eastern Ny Friesland, Vestspitsbergen. Text-fig. 1, showing Culm outcrops in Central Vestspitsbergen, was compiled mainly from a comprehensive geological map prepared by Mr. P. F. Friend and based upon the field-work of Cambridge Spitsbergen Expeditions. The samples, constituting the basis of this study, were collected from the majority of localities indicated on text-fig. 1; for simplification of reference the only place-names included are those relevant to the outcrop positions. Contemporary exposures of the Billefjorden Sandstones represent remnants of a once more or less continuous development of strata in a depositional basin which, as noted by McWhae (1953, p. 212) and Forbes *et al.* (1958, p. 468), ran roughly north-south, approximately through the position of Wijdefjorden and Billefjorden. Relatively small exposures in eastern Ny Friesland, at Blårevbreen (text-fig. 1) and near Lomfjorden (see Forbes *et al.* 1958, text-fig. 1) may perhaps have been part of this continuous development in central Vestspitsbergen, which taken as a whole was 'possibly originally isolated from the deposits in western Spitsbergen' (Forbes *et al.* 1958, p. 468).

Three well-exposed and representative sections of the Billefjorden Sandstones, at Citadellet, Triungen, and Birger Johnsonfjellet, were collected for palynological purposes by Dr. D. J. Gobbett in 1959. Text-fig. 2, based upon Gobbett's detailed field notes, illustrates the succession at these localities together with the precise position of the samples which form an important basis for the present study. At Triungen and Birger Johnsonfjellet, the Billefjorden Sandstones rest unconformably upon the Devonian and Hecla Hoek rocks respectively; at Citadellet, the base of the Billefjorden Sandstones is scree-covered. The Lower Carboniferous sequence of all three localities is overlain disconformably by the Wordiekammen Limestones (Upper Carboniferous). Of other Culm samples examined from Citadellet and Triungen, B685 (studied by Hughes and Playford 1961) and B687 are from unspecified horizons at Citadellet; and G1461 was collected 23 metres stratigraphically below the base of the Wordiekammen Limestones in a section exposed about a quarter of a mile east of the Triungen section illustrated in text-fig. 2.

Many of the samples examined had been collected from various localities on the east side of Billefjorden, but as noted by Gee *et al.* (1952, p. 335) most of the Culm exposures in this area are largely covered by scree. On the south side of Ebbadalen, numerous samples (B604, B609, F531, F774, G332, G334, G366, G382) are from a thin coaly seam (and associated shales and siltstones) occurring 620 feet above the base of a Culm section measuring 840 feet in total thickness (McWhae 1953, fig. 6, stratigraphical column H); the microflora of B609 was recorded by Hughes and Playford (1961). Two samples (B706, W860) were collected from a similar succession exposed on the north flank of Ebbadalen; both are close to the local base of the Billefjorden Sandstones, which here



TEXT-FIG. 1. Map of part of Vestspitsbergen showing distribution of Lower Carboniferous, Culm, sediments (in heavy black); samples have been examined palynologically from the majority of localities indicated.



TEXT-FIG. 2. Stratigraphical columns of the Billefjorden Sandstones as exposed at Citadellet, Triungen, and Birger Johnsonfjellet, Vestspitsbergen (compiled from field notes of Dr. D. J. Gobbett).

conspicuously overlap the pre-Downtonian buttress mentioned previously. Farther north, 500 feet of Billefjorden Sandstones crop out on the north side of Ragnarbreen; sample R38 was collected approximately 90 feet above base. The formation is poorly exposed on De Geerfjellet, where a thickness of 'probably more than 700 feet' is reported by Gee *et al.* (1952, p. 335; pl. 2, stratigraphical column A); samples G636 and T269 are from a limited outcrop of interbedded shales and sandstones occurring in the bed of a small stream some distance west of column A cited above. Sample S59a was obtained from the north side of Wordiekammen, approximately 620 feet above the base of the Billefjorden Sandstones, which here attain a thickness of about 850 feet; the microflora of this sample was described by Hughes and Playford (1961). Sample W217 is from an outcrop on the north shore of Adolfbukta, about 400 yards west of Nordenskiöldbreen.

To the east of Adolfbukta, good exposures of the Culm are recorded by McWhae (unpublished data) at Terrierfjellet and Ferrierfjellet, with respective thicknesses of 325 feet and 175 feet. Several coal seams are included within a predominantly sandstone lithology, but unfortunately sampling was not undertaken.

Extending south-east from the south side of Adolfbukta, the Billefjorden Sandstones are exposed discontinuously in the vicinity of Gerritelva and Carronelva. According to Gee *et al.* (1952, p. 335; pl. 2, stratigraphical column E) the thickness at the latter locality is over 640 feet. None of the samples from Gerritelva (353, 390, 391) or from Carronelva (G1080) is from a specified horizon.

Two streams on the east and west sides of Margaretbreen, northern Bünsow Land, disclose respectively about 48 metres and 62 metres of Billefjorden Sandstones, consisting of interbedded sandstones and shales (D. J. Gobbett, field notes). Base is not exposed at either locality. Samples G1339 and G1344 are from the eastern and western sections respectively; G1339 is from a horizon about 30 metres stratigraphically below that represented by G1344.

A small coastal inlier of Billefjorden Sandstones occurs to the north of Anservika, western Bünsow Land. This was studied in detail by members of the 1949 Expedition. As stated by Gee *et al.* (1952, p. 336), correlation of these beds is uncertain owing to major dislocation of the area. Seven samples examined by the writer (R5, F20, D120, G1283, G1280, G1278, G1276) had all been collected from the 22-foot bed of 'carbonaceous sandstone with shaly partings and indeterminate leaf remains' occurring 32 feet above sea-level (Gee *et al.* 1952, p. 336). The total thickness of Culm exposed in the Anservika section is 316 feet, and its base lies somewhere below sea-level.

Coal-measure facies in the Culm are being mined by the Russians at Pyramiden, north-west Billefjorden, and as noted by Gee *et al.* (1952, p. 335) the strata are notably thinner here (about 80 metres) than on the east side of Billefjorden; no Pyramiden samples have been examined by the present writer. To the immediate north, at Birger Johnsonfjellet, the Culm increases in thickness to approximately 320 metres (see text-fig. 2). One sample examined (E363) is from Svenbreen, which is situated between Birger Johnsonfjellet and Pyramiden; it was obtained from just above the unconformable contact between the Billefjorden Sandstones and the Hecla Hoek.

Scattered Culm samples have come from exposures occurring between the south-western coast of Austfjorden and the north end of Ålandvatnet. From the latter locality, samples B616 and B619 are from a 50-foot section of Culm lying unconformably upon pre-Downtonian rocks (B. Moore, field notes). According to Moore, a faulted outlier

of Culm, resting unconformably upon pre-Downtonian rocks, occurs on the north summit ridge of Odellfjellet. Although not precisely located stratigraphically, samples B624 and B680 were collected respectively from near the top and bottom of this exposure which is some 170 metres thick; another sample (H267) collected earlier by Mr. W. B. Harland is probably from near the top of the exposure. Forbes *et al.* (1958, p. 468) quote a minimum of 500 metres as the comprehensive thickness of Billefjorden Sandstones in the Odellfjellet area. Numerous samples collected from around the south-west shore of Austfjorden failed to yield determinable microfloras.

Forbes *et al.* (1958, p. 468) mention the presence of at least 300 metres of Billefjorden Sandstones at Lemströmfjellet, immediately east of Austfjorden. Of samples examined from this locality, a recognizable microfloral assemblage was recovered from sample B443.

A remote exposure of Culm rocks occurs at Blårevbreen, a tributary of Oslobreen, in eastern Ny Friesland. Sample M365 was collected in 1952 by Mr. M. B. Bayly and samples Q55 and Q56 in 1959 by Mr. J. L. Fortescue from the poorly exposed Culm section, 30 metres thick, which rests unconformably upon Hecla Hoek rocks and is overlain (? disconformably) by massive, crag-forming, coral-bearing limestones, which are probably attributable to the Cyathophyllum Limestones.

Culm strata are developed along the western seaboard of Vestspitsbergen as a relatively narrow belt extending discontinuously southwards from Brøggerhalvøya, on the south side of Kongsfjorden, to the south-west side of Hornsund. Although no palynologically useful samples have been examined from this region by the writer, it is relevant to give some consideration here to this important development of the Spitsbergen Lower Carboniferous.

Whereas in Central Vestspitsbergen the Upper Palaeozoic rocks appear relatively undisturbed (apart from some rejuvenation in the Tertiary of mainly Devonian fractures), the western coast of Vestspitsbergen has been subjected to considerable earth-movements in the Tertiary causing strong folding, and in places overthrusting, of Palaeozoic and Mesozoic strata (Orvin 1940, pp. 42 *et seq.*). Thick sequences of Lower Carboniferous rocks are exposed at a number of localities, where they rest unconformably upon folded Hecla Hoek and are overlain, usually conformably, by ? Middle Carboniferous red beds. For the most part the Culm dips steeply to the east, locally becoming overturned (see Orvin 1940, pl. III).

An important section of Culm, 1,000 metres in thickness, on the north side of Bellsund, has yielded abundant plant material which was described by Nathorst (1914, 1920). Three clearly defined successive floras were distinguished (Nathorst 1920) as follows:

3. Diabasbucht flora with *Cardiopteridium nanum*, &c.
2. Hagerup Haus flora with *Sphenopteridium norbergii*, &c.
1. Camp Miller flora with *Adiantites bellidulus*, &c.

Forbes *et al.* (1958, p. 480) commented that the 'Hagerup Haus flora may be of approximately the same age as that of the shales at Pyramiden and Linnéelva'.

Other well-known exposures of Lower Carboniferous terrestrial beds occur at St. Jonsfjorden (325 metres in thickness, according to Dineley 1958), Trygghamna (700–800 m., Dineley 1958), Festningen (*c.* 700 m., Orvin 1940), Reinodden (*c.* 700 m.,

Orvin 1940), Ahlstrandodden (200 m., Orvin 1940), and at south-west Hornsund (930 m., Siedlecki 1960). Plant macrofossils have been reported from some localities; Nathorst (1914) lists collections from Örretelven (Festningen section), Ingeborgfjell (north Bellsund), Midterhuken (east Bellsund), and from Robertdalen (Reinodden section).

Macrofloras collected up to the present time do not permit more than a broad correlation between the Culm sequences of Central and of Western Vestspitsbergen (see Forbes *et al.* 1958, p. 480). On the other hand, palynological investigation of the latter may well provide a precise means of correlation with the Billefjorden Sandstones sequence with which the present study is primarily concerned. Through the courtesy of Professor O. H. Selling, of the Paleobotaniska Avdelningen, Naturhistoriska Riksmuseet, Stockholm, the present writer obtained fragments from plant-bearing Culm material collected in Western Vestspitsbergen by Swedish expeditions during the late nineteenth century and early twentieth century. These samples come from many of the localities listed by Nathorst (1914, 1920), viz. Diabasbukta, Hagerup Haus, Camp Miller, Ingeborgfjell, Örretelven, Midterhuken, and Robertdalen; unfortunately none yielded spores of any description. Perhaps it may be that the microfloras failed to survive the intensive Tertiary tectonism of Western Spitsbergen outlined above. In this connexion, the results should prove significant of a palynological investigation (Birkenmajer 1960, p. 30 footnote) being undertaken on samples from a Culm coal seam exposed at Sergejev-fjellet, south-west Hornsund (see Siedlecki 1960, p. 98).

Upper Palaeozoic rocks are exposed extensively on Bjørnøya (Bear Island), the southernmost island of Svalbard, situated some 120 nautical miles south of Spitsbergen. An admirable account of the geology of this island is contained in the 1928 publication of Horn and Orvin. In contrast to Spitsbergen, Bjørnøya is especially notable for the presence of a widespread terrestrial, plant-bearing deposit, the Ursa Sandstone, which was laid down apparently continuously during Upper Devonian and Lower Carboniferous times.

In 1902 Nathorst described his well-known Upper Devonian *Archaeopteris* flora from Austervåg (south of Engelskelva) and from five other localities, all on the east coast of Bjørnøya. Earlier, Heer (1871) had described a collection of plant macrofossils from a coastal section, the precise locality of which seems uncertain (see Forbes *et al.* 1958, p. 478) but is either to the immediate north or south of the mouth of Engelskelva. This collection included some Lower Carboniferous forms (e.g. *Lepidodendron veltlieimi* Sternb., *Stigmaria ficoides* (Sternb.)) recognized as such by Heer, and in addition some probable Devonian floral elements. Confirmation of the existence of Lower Carboniferous strata on Bjørnøya came later from Antevs and Nathorst (1917), who reported the penetration of Culm strata, including a thin coal seam, in a borehole situated at the western outlet of Laksvatnet in the northern part of the island. The flora of these rocks included *Sphenopteris bifida* L. & H., *Adiantites* cf. *bellidulus* Heer, *Cardiopteridium* cf. *spetsbergense* Nath., and *Stigmaria ficoides* (Sternb.), all of which are well known from the Spitsbergen Culm.

At Nordkapp, on the north-east coast, Horn and Orvin (1928, pp. 82–83; fig. 50) recorded a coal seam occurring on the down-thrown (east) side of a fault in Culm sandstone which is considerably disturbed by faulting in the general area. All but one (P702) of numerous palynological samples collected by the writer from this section failed to

yield a determinable microflora. Approximately 100 yards east of, and about 50 feet stratigraphically below, this coal seam, abundant plant fossils were observed in a 10-foot band of carbonaceous shaly siltstone and fine-grained sandstone. Fossils collected from this horizon comprise:

<i>Calamites</i> sp.	* <i>Knorria</i> '
* <i>Lepidodendron spetsbergense</i> Nathorst	<i>Stigmara ficoides</i> (Sternberg) Brongniart
<i>Lepidodendron ?heeri</i> Nathorst	<i>Cardiopteridium ?spetsbergense</i> Nathorst (pinnules)
<i>Lepidodendron</i> sp.	* <i>Carpolithus</i> sp.

In addition, one sample (P725), which bears macrofossils marked * above, contains an identifiable microflora.

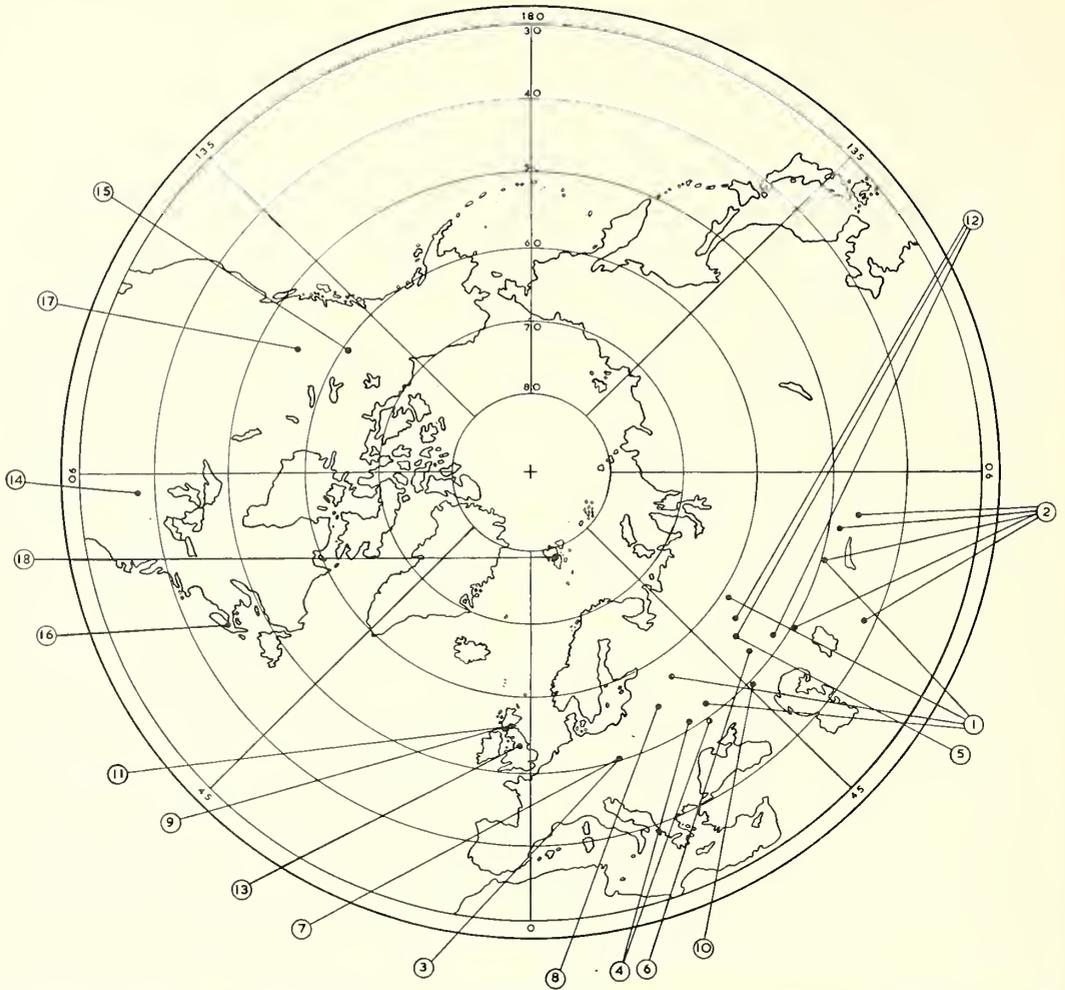
Numerous other samples collected from the majority of the Culm exposures on Bjørnøya are apparently devoid of spores; this may possibly be due to adverse weathering effects.

PREVIOUS INVESTIGATIONS OF LOWER CARBONIFEROUS MICROFLORAS

Until comparatively recently, palynological work on Carboniferous strata has been concerned mainly with the upper part of the System, due to the economic importance of coal seams contained therein, particularly in Great Britain and the United States. Thus microfloras, especially in coals, of Westphalian age are now known in considerable detail, and their useful application to problems of coal seam correlation has been demonstrated conclusively. With the widespread recognition of the unique value of fossil spores in the elucidation of general stratigraphical problems, an increasing amount of attention has been paid over the past few years to the microfloral content of other portions of the geological column. In the case of the Lower Carboniferous, a review of the steady stream of more recent palynological publications provides ample testimony that, in the Northern Hemisphere at least, precise correlation by palynological methods is possible between widely separated non-marine sequences of this age. A limiting factor is the all-important systematic aspect of palynology: it can scarcely be said that equilibrium has been reached in the taxonomy of fossil spores, but this is a not unexpected consequence of a relatively new and rapidly evolving science.

In the following paragraphs a brief review of published work on older Carboniferous microspore assemblages is presented. As far as possible, the fullest details are given concerning the stratigraphical position of such assemblages. This is deemed an essential preliminary to the assessment of the local and regional stratigraphical significance of a number of Spitsbergen spore species which are either identical with or closely related to certain elements of these previously recorded microfloras. Where it is known, detailed reference to extra-Spitsbergen occurrences of individual species is incorporated within the Systematic Section.

From text-fig. 3 it is apparent that Lower Carboniferous small-spore assemblages have been investigated from numerous, often widely separated localities. The stratigraphical interval covered by each individual author is recorded in text-fig. 4, and the geographical position of their described assemblages is shown on text-fig. 3. It is a convenient if perhaps precursory step at this stage to include the Spitsbergen sequence in text-fig. 4; microfloral evidence as to its placement will be adduced in a subsequent section of this paper.

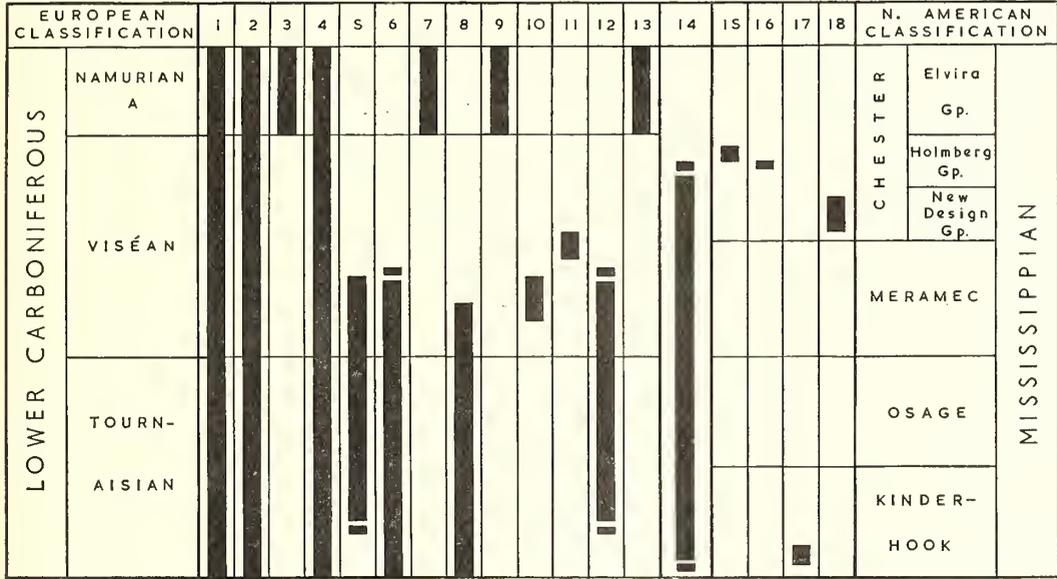


TEXT-FIG. 3. Localities from which Lower Carboniferous microspore assemblages have been described (or recorded) in the Northern Hemisphere. Index to authors—1, Luber and Waltz 1938, 1941; 2, Luber 1955; 3, Horst 1955; 4, Ishchenko 1956, 1958; 5, Bludorov and Tuzova 1956; 6, Byvsheva 1957; 7, Dybová and Jachowicz 1957; 8, Kedo 1957, 1958, 1959; 9, Butterworth and Williams 1958; 10, Loginova 1959; 11, Love 1960; 12, Byvsheva 1960; 13, Neves 1961; 14, Hoffmeister, Staplin, and Malloy 1955; 15, Hacquebard and Barsz 1957; 16, Hacquebard 1957; 17, Staplin 1960; 18, Hughes and Playford 1961, and present study.

The substantial, excellently illustrated publication of Reinsch (1884) is generally acclaimed as the most outstanding of earlier contributions to our knowledge of fossil microfloras. Most of the spores (both micro- and megaspores) had been recovered from coals of a number of localities, mainly in central Russia and also in Saxony. Unfortunately, Reinsch did not specify the age of the strata more precisely than 'Carboniferous', although it is evident from his illustrations that a considerable number of Lower Carboniferous types were represented. He believed that the organisms he found in the

Russian and Saxonian coals were of algal origin. Due to uncertainty regarding stratigraphical horizons and some localities, the work of Reinsch is not included on either text-figs. 3 or 4, but this is not intended to minimize or detract in any way from what must still be regarded as an essential reference for the worker on Lower Carboniferous microfloras.

In 1931 work was initiated by Russian palynologists on the spore content of Upper



TEXT-FIG. 4. Showing age and relative stratigraphical position of Lower Carboniferous microspore assemblages recorded from the Northern Hemisphere. Correlation of the European and North American subdivisions is based upon Weller *et al.* (1948). Broken limits of columns represent uncertainty regarding precise age limits. Index to authors—1, Luber and Waltz 1938, 1941; 2, Luber 1955; 3, Horst 1955; 4, Ishchenko 1956, 1958; 5, Bludorov and Tuzova 1956; 6, Byvsheva 1957; 7, Dybova and Jachowicz 1957; 8, Kedo 1957, 1958, 1959; 9, Butterworth and Williams 1958; 10, Loginova 1959; 11, Love 1960; 12, Byvsheva 1960; 13, Neves 1961; 14, Hughes and Playford 1961, and present study; 15, Hoffmeister, Staplin, and Malloy 1955; 16, Hacquebard and Barss 1957; 17, Hacquebard 1957; 18, Staplin 1960.

Palaeozoic strata, principally Carboniferous coals, of the U.S.S.R. This culminated in the important publication of Luber and Waltz (1938), which contains a systematic and stratigraphical account of spore complexes occurring in Russian coals of Tournaisian-Viséan and of Middle and Upper Carboniferous age. The bulk of the investigation was concerned with the microfloral content of Tournaisian, in part Viséan, coals of the Moscow Basin, Kizel district, Borovichi district, Selizharovo district, and Voronezh region; and of exclusively Viséan coals of the Karaganda Basin. The first five localities (all in European Russia) were characterized by a fairly uniform Lower Carboniferous microfloral suite dominated by cingulate spores. In contrast, more or less contemporary microfloras of the Karaganda Basin (Asiatic Russia) comprised mainly azonate forms having spinose-tuberculate sculpture. On this basis, Luber and Waltz (1938, p. 42) deduced 'the existence of a peculiar provincial flora in the Karaganda region, differing

from the European and characterized by strict endemism'. These authors also noted a marked difference between the specific composition of their Lower Carboniferous microflora as a whole, and that of the Middle-Upper Carboniferous assemblages.

A subsequent major publication (Luber and Waltz 1941) included the description of 262 species of microspores and pollen grains recovered from Russian strata (predominantly coals) ranging in age from Devonian to Permian. Forms characteristic of each geological subdivision were listed. Most of the Lower Carboniferous species instituted in the earlier paper (Luber and Waltz 1938) were refigured, but in addition many new species of the same age were described and illustrated. Both publications have proved invaluable references in connexion with the present study and have revealed a striking similarity between the Spitsbergen Culm microfloras recorded herein, and those of the Russian Lower Carboniferous.

Luber (1955) made a further study of Middle and Upper Palaeozoic spores of Kazakhstan (including the Karaganda Basin). A number of supra-specific taxa were instituted (e.g. *Filictriletes*, *Calamotriletes*, *Asterocalamotriletes*, *Lycopodizonotriletes*, &c.) all having implied botanical affinities. Her Lower Carboniferous forms contrast strongly with those of the European part of Russia, and indeed bear little resemblance to the Spitsbergen spores.

Two recent substantial publications of Ishchenko (1956, 1958) contain the results of an intensive palynological investigation of the Lower Carboniferous sediments of the vast Donetz Basin. The first is concerned with the western extension of the Basin, and the 1958 paper deals with the Dnieper-Donetz Basin. Many new spore species are described and stratigraphical ranges within the Lower Carboniferous of individual forms are documented in considerable detail, especially in the 1956 paper. The 1958 range charts are less precise within the confines of the Lower Carboniferous but extend downwards into the Famennian and upwards as high as the Moscovian. Numerous species were recorded as possessing limited vertical distribution. On the basis of these, and that of relative abundance studies, Ishchenko was able to delimit three distinct microfloral suites, characteristic respectively of the Tournaisian, Viséan, and Namurian stages. The successful application of these to correlative problems of boreholes within the basin was also reported by Ishchenko (1958). It will be shown subsequently that the Spitsbergen microfloras bear a close similarity in many respects with those described from the Russian Lower Carboniferous by Ishchenko, as also by Luber and Waltz. In particular, Ishchenko's precisely recorded vertical distribution studies find direct application in the external correlation of the Spitsbergen Lower Carboniferous succession.

A number of short Russian papers—Bludorov and Tuzova 1956; Byvsheva 1957, 1960; Kedo 1957, 1958, 1959; Loginova 1959—record the occurrence of many of Luber and Waltz's (1938, 1941) species in horizons of the Tournaisian and Viséan, as developed in various parts of the U.S.S.R. Bludorov and Tuzova (1956) were concerned with the Lower Carboniferous Coal Measures of Tartary; Byvsheva (1957) with terrestrial Lower Carboniferous from the Melekes and Busuluk deep wells; Kedo (1957, 1958, 1959) with the Lower Carboniferous of White Russia; Loginova (1959) with the Yasnopolyansky substage (Lower Viséan) of the Saratov-Stalingrad Volga area; and Byvsheva (1960) with the terrestrial Lower Carboniferous of the Volga-Ural region. None of these papers contains systematic spore descriptions. Their value is diminished

somewhat by their listed occurrence of a considerable number of species which are attributed to Naumova (and often appear to have stratigraphical significance) but whose description and illustration remain obscure.

Supposed angiosperm-type pollen grains have been reported by Naumova (1950) from the Lower Carboniferous of the Moscow Basin, and subsequently by Teteriuk (1956, 1958) from approximately contemporary strata of the Donetz Basin. Such forms (*Tetraporina*) are of rare occurrence in the Spitsbergen Culm and will be discussed in the Systematic Section below.

Apart from the Russian work mentioned above, palynological investigation of the European older Carboniferous has been concerned mostly with sediments of Namurian age. Indeed, very little is known as yet of the spore content of Tournaisian and Viséan strata of western Europe.

Microfloras of the Upper Silesian Coal Measures have been described by Horst (1955) and by Dybová and Jachowicz (1957). The age of these coal measures ranges from Lower Namurian A to Westphalian D. Horst's investigation was mainly on the Namurian A strata, whilst Dybová and Jachowicz made a comprehensive study of 156 coal seams occurring throughout the sequence.

In 1958 Butterworth and Williams presented a concise account of the spore assemblages recovered from coals of the Limestone Coal Group and the Upper Limestone Group (Namurian A) of the Scottish Lower Carboniferous. This amplified to some extent the earlier work of Knox (1948) on spores from the Limestone Coal Group. Many of the spores described by Butterworth and Williams compare closely with those identified from Upper Silesia by Horst (1955) and by Dybová and Jachowicz (1957).

A sequence of microspore zones has been proposed recently (Butterworth and Millott 1960) in the coalfields of Britain, ranging in age from Upper Viséan to at least Westphalian D. Each zone is defined by the presence of an index microspore species. Their Microspore Distribution Chart shows the stratigraphical extent of these respective zones, and incorporates also the ranges of microspore genera as evidenced by various coal microfloras.

Love (1960) recorded spore assemblages occurring in certain horizons of the Lower Oil-shale Group (Viséan) of Scotland. From his Table 2, a downward extension is evident of many of the Scottish Namurian species described by Butterworth and Williams (1958). Love considered that his assemblages may be equated to the *Campotriletes verrucosus* Zone of Butterworth and Millott (1960), which had been delineated in coals of the Scremerston Coal Group and Lower Limestone Group (Viséan) of Northumberland.

Neves (1961) has described selected spores from Namurian coals and shales occurring in the Southern Pennines region of central England. This work is of especial stratigraphical significance in that the strata investigated may be referred directly to the established Namurian sequence of goniatite stages.

Hoffmeister, Staplin, and Malloy (1955) contributed a major work on Upper Mississippian microfloras from Illinois and Kentucky, U.S.A. Their described assemblages are from coals and shales of the Hardinsburg formation, which is equivalent in age to part of the Homburg division of the Chester series. These authors emphasized the importance of examining spore assemblages from clastic sediments as well as from coal seams, in order to obtain a more comprehensive, less environmentally restricted picture of the contemporary flora.

Another North American microflora of Upper Mississippian age is recorded by Hacquebard and Barss (1957). This microflora is from a thin coal seam occurring within, and 650 feet above the base of, the Mattson formation of the South Nahanni River area, Northwest Territories, Canada. According to Patton (1958, p. 324 and fig. 6), who collected the single sample, its age is equivalent to that of the mid-Meramec series of the standard North American Mississippian. More recently, however, Harker (1961, p. 8) states that the Mattson formation must post-date the Meramec because it conformably overlies beds containing a convincingly lower Chester marine fauna. Thus, the coal concerned is of middle or perhaps upper Chester age. Many of the spores described by Hacquebard and Barss are represented in the Russian Lower Carboniferous, and also, as shown below, in upper horizons of the Spitsbergen Culm.

Hacquebard (1957) described small-spore floras present in two coals from the Horton group (Mississippian) of Nova Scotia, Canada. The age of these coals is not known precisely, but on macrofloral and general stratigraphical evidence is certainly low in the Mississippian (Hacquebard 1957, p. 302). Certain aspects of the Horton microflora are discernible in assemblages from the lower horizons of the Billefjorden Sandstones; this resemblance will be amplified subsequently.

An important recent contribution is that of Staplin (1960), who described an abundant microflora from the Golata formation (Upper Mississippian) of Alberta, Canada. Numerous species described by Staplin are recorded herein from the upper part of the Spitsbergen Lower Carboniferous. According to Staplin's text-fig. 1, the Golata formation is equivalent in age to the lower part of the Chester series, and is thus probably somewhat older than the coal investigated by Hacquebard and Barss (1957).

The first published record of Lower Carboniferous spores in the Southern Hemisphere is contained in a recent paper by Balme (1960), who in addition investigated sediments of Upper Carboniferous age. The microfloras were obtained from the Laurel Beds (Lower Carboniferous) and from the Anderson Formation (Upper Carboniferous) of the Fitzroy Basin, Western Australia. Spore identifications were almost entirely on a generic level, although specific morphological characters were listed briefly. Balme noted some similarities between his Lower Carboniferous assemblages and those of the United States and the U.S.S.R.

With regard to dispersed-spore studies of the Spitsbergen Lower Carboniferous the only publication prior to Hughes and Playford (1961) is that of Lubert (1935), who figured but did not describe or name several spores from the Culm of Pyramiden. She noted a general resemblance of the microflora with that of the Russian Lower Carboniferous; this was reiterated by Lubert and Waltz (1938, p. 42) and is confirmed abundantly in the present investigation.

Of particular interest is a recent reinvestigation (Bharadwaj 1959) of the fructification *Porostrobos zeileri* Nathorst, which had been collected in 1882 by Nathorst from Pyramiden, Spitsbergen. From this cone, Bharadwaj obtained spores conformable with the dispersed-spore genus *Densosporites*. It will be shown subsequently that these spores, as described and illustrated by Bharadwaj, closely resemble a type which occurs in many of the samples examined by the present writer.

With reference to text-fig. 4, it is necessary to give some consideration here to the correlation of the North American Mississippian succession with the standard Carboniferous stages of western Europe. The combined equivalence of the Kinderhook

series and the overlying Osage series with the Tournaisian appears to be well established on the basis of the diagnostic *Spirifer tornacensis* fauna (Moore 1937, p. 660). However, as noted by Weller *et al.* (1948, p. 108), precise delineation of the Viséan boundaries in North America presents some difficulty owing to the fact that certain ammonoid genera (notably *Beyrichoceras*, *Eumorphoceras*, and *Goniatites*), which are stage indices in western Europe, appear to have different ranges on the other side of the Atlantic. Lithostrotionid coral faunas testify to the Viséan age of the Meramec series, and the general correspondence of the Namurian with the upper Chester series seems well established (Weller *et al.* 1948; Elias 1960). However, the position of the Viséan–Namurian boundary in the North American succession has been subject to some conjecture owing to the much earlier North American occurrence (in lower Meramec beds) of *Eumorphoceras*, the European introduction of which marks the beginning of the Namurian. Weller *et al.* (1948, p. 108) summed up the situation as follows: ‘the Viséan–Namurian boundary may correspond with the division between the Chesterian and the Meramecian, or it may fall within the Chesterian’. The latter correlation, as given on their chart (and on text-fig. 4, herein), was considered the more likely in view of the mid-Chester occurrence (in Arkansas and Oklahoma) of *Goniatites* which is unknown in European strata of post-Viséan age. More recent goniatite and conodont evidence also supports the placement of the Viséan–Namurian boundary within the Chester, approximately at the base of the Elvira group (Elias 1960, p. 152; Higgins 1961, p. 221). On the other hand, from Russia Stepanov (1959, p. 64) equates the base of the Namurian with that of the Chester series, but does not cite any palaeontological or other evidence for this correlation.

As outlined above, microfloras described by various authors from the Russian Lower Carboniferous have much in common with those of the present study. The strata from which the Russian microfloras have been documented are almost always recorded as being dated in varying degrees of precision with reference to the western European stages. A critical examination of two recent Russian stratigraphical publications, Librovitch (1958) and Aisenverg *et al.* (1960), indicates that such dating is, in fact, based reliably upon extensive studies of marine faunas, especially those of the Russian Platform and the Donetz Basin. Thus although microfloras have not been recorded from the type areas of the Lower Carboniferous stages, these latter divisions may be delineable reliably, if indirectly, in the Spitsbergen succession, through the correlative medium of the Russian Lower Carboniferous.

PREPARATION AND EXAMINATION OF SAMPLES

The samples studied comprise a fairly wide variety of lithological types, ranging from coals to medium-grained sandstones, all of apparently continental origin. It is difficult to generalize with regard to the most productive rock type. Perhaps the most generally reliable was the carbonaceous shale or siltstone, but then this lithology had been collected abundantly and preferentially from the Spitsbergen Culm with palynological work in mind. A number of fine-grained sandstones yielded exceedingly diverse and well-preserved spore assemblages. With such a variety of lithological types at hand, it proved essential, as a prerequisite in planning subsequent maceration procedure, to examine each specimen individually and to record macroscopic observations. Broadly

speaking, the samples were separable in the first instance into two categories—highly carbonaceous sediments (mainly coals) and clastics with less carbonaceous material.

Initially, mechanical disintegration involved crushing of the sample—*c.* 5 grammes of clastic sediment or 2 grammes of coal—to a size of about 1 millimetre. To minimize risk of contamination crushing of each sample was done on several layers of clean newspaper placed on an iron block. The hammer was cleaned carefully before and after the sample had been ground.

Coals were macerated by means of Schulze solution (concentrated nitric acid and potassium chlorate). The time for adequate maceration of individual samples was variable, ranging from 3 to 15 hours. An alternative procedure using fuming nitric acid, for a maximum of 4 hours, yielded comparable spore concentrations, but in many cases individual species appeared overmacerated. Following maceration and washing, the residue was treated with 1 per cent. ammonium hydroxide; in some instances, additional treatment with as strong as 10 per cent. ammonium hydroxide was necessary in order to solubilize excessive amounts of oxidized material. This step was found by experience to be one of the more critical phases of the process; indiscriminate use of strong alkali following oxidation proved highly destructive in many preparations. If the residue contained a conspicuous amount of mineral matter it was allowed to stand overnight in cold, 50–60 per cent. hydrofluoric acid.

Clastic sediment samples were initially placed in nickel crucibles, to which 50–60 per cent. hydrofluoric acid was added and boiled for 30–45 minutes. The residue was washed thoroughly, and in some preparations a 5-minute treatment with warm, 20 per cent. hydrochloric acid was necessary to dissolve fluorides resulting from the HF treatment. Oxidation of the humic material was then carried out with Schulze solution. Maceration time was much less than for coals; it ranged from 10 minutes to 4 hours. Subsequent alkali treatment was not invariably required for satisfactory spore concentrations, but where necessary it was undertaken with caution as in coals above.

In the preparation of many coals and clastics, a 15–30 seconds' treatment with an ultrasonic disintegrator (1:1 end ratio steel probe vibrating at 20 kilocycles per second) proved highly effective in disaggregating clumps consisting of spores and other organic or mineralogical matter. In the case of coals, it was undertaken following the maceration step, and with clastics, immediately after the HF processing; disaggregation was accomplished in an aqueous medium containing a few drops of non-ionic detergent. Great care was necessary as excessive ultrasonic treatment was shown to cause considerable, often preferential, damage to the spores.

Fifty per cent. glycerine containing a few drops of phenol was added to the ultimate, thoroughly washed residues, which were then transferred for storage to small plastic-stoppered glass tubes. Adequate natural colour of the spores made staining unnecessary. Glycerine jelly was used for mounting of the residues. At least three slides were made from each residue, dependent upon its richness. In addition, over 200 spores were mounted singly, following the method described by Balme (1957, p. 13). Cover slips of all slides were sealed with gold size at least three days after mounting.

Initially, all slide preparations were scanned thoroughly at a magnification of $\times 120$, and preliminary determinations of, and morphological observations on, species present were recorded from high power ($\times 450$) magnification. The first samples examined systematically in this manner were those from the well-documented successions at

Birger Johnsonfjellet, Triungen, and Citadellet. These gave an overall picture of the sequence of microfloras represented in the Spitsbergen Lower Carboniferous. Subsequent counting (250 specimens from each preparation) under high power enabled a quantitative estimation of the microspore species present in most of the samples from the three successions; a few of the samples, however, yielded insufficiently concentrated and poorly preserved microfloras such that meaningful counting was precluded. Preparations of numerous samples from other localities were then examined, and comparisons could be drawn between their microfloral content and that of individual samples from the three reference successions mentioned above, with a view to local correlation within Spitsbergen. Detailed systematic descriptions set out below were undertaken only after all the productive samples had been examined. The oil-immersion objective was used extensively in the elucidation of spore morphology.

SYSTEMATIC DESCRIPTIONS OF DISPERSED SPORES

Preliminary remarks. The morphographical system initiated by Potonié and Kremp (1954), and subsequently amplified by these authors (Potonié and Kremp 1955, 1956a; Potonié 1956, 1958, 1960) is followed throughout. From the point of view of the stratigraphical palynologist, this entirely artificial scheme is undoubtedly the most satisfactory presented to date, as it represents a comprehensive, readily applied method for the classification of dispersed spores, many of which have uncertain botanical affinities, but often considerable stratigraphical significance. Knox (1950, pp. 308–9) stated the case for artificial classification as follows: 'A natural classification of fossil spores is at present practically impossible, since few of the spores so far described have been found in organic connection with the parent plant. It is thus necessary to formulate an artificial system using the various features which have been found to be of diagnostic value.' Within the artificial framework, the documented botanical affinities of the morphographical spore taxa should be indicated wherever known. These can be based reliably only upon studies of the spore content of fossil fructifications, whose fossil record can unfortunately never approach that of the wealth of dispersed spores available. Certainly, it seems erroneous to endeavour to relate fossil spores, particularly of Palaeozoic age, to modern plant groups on the basis of spore morphology alone. In the systematic section below, known botanical affinities are given of the various microspore genera represented in the Spitsbergen material.

The term microspore is here used in the broad sense of dispersed fossil 'small spores' of diameter less than 200μ , corresponding thus to 'miospore' which was introduced by Guennel (1952, p. 10) to embrace 'all fossil spores and spore-like bodies smaller than 0.20 mm., including homospores, true microspores, small megaspores, pollen grains, and pre-pollen'.

In the systematic section below, the writer has attempted to use only those descriptive terms which appear to find widespread acceptance among palynologists. Sculptural terms employed are mainly those defined by Harris (1955, pp. 18–21); as far as possible their use is amplified by detailed measurements of the size and spacing of individual sculptural elements in an attempt to obviate differing connotations which exist in the case of many of these terms.

Following Potonié and Kremp (1955), the terms intexine and exoexine are used to denote respectively the inner and outer layers of the spore wall (exine).

Nomenclature for equatorial structures (cingulum, auriculae, zona, corona, limbus) is applied in the defined sense of Potonié and Kremp (1955). In addition, the term patina of Butterworth and Williams (1958) is used. Mention will also be made (see the genus *Monilospora*) of the 'capsula-patella' terminology of Staplin (1960), the use of which appears superfluous.

The term laesurae is here applied to the proximal polar dihiscence apertures (see Erdtman 1952, p. 12) and is thus synonymous with 'commissure(s)' of Harris (1955, p. 25) and Couper (1958, p. 102) and with 'Y-mark' of Potonié and Kremp (1955, p. 10). In the present context 'lips' denotes a conspicuous modification, usually a marked increase in thickness, of the exoexine immediately adjacent to the laesurae (see Harris 1955, p. 13).

The amb is defined by Erdtman (1952, p. 459) as the outline of a spore or pollen grain viewed from the direction of the polar axis.

Unless otherwise stated, the measurements given in the descriptions which follow were obtained from specimens preserved in full polar view. In the case of triangular forms, the equatorial diameter was taken as the maximum median length, and for quadrangular forms, the maximum diagonal length was measured.

All microspore species are illustrated by means of photographs from unretouched negatives; in addition, some camera-lucida drawings are given. New species have been instituted only where at least fifteen adequately preserved specimens have been available. Particular care has been given to describing these and all other forms from the largest possible number of samples, especially in order to appreciate the aspect of any particular species in varying states of preservation. Definite assignment to previously described species has been made only where reasonably conclusive identity could be demonstrated by reference to original descriptions and illustrations of apparently well-preserved types. Conspecificity is often difficult to establish, particularly in the case of Russian forms, which are often inadequately described and illustrated only by drawings. Thus several new species are qualified by statements to the effect that they may be identical to certain previously instituted types.

A number of ostensibly discrete, previously described species are shown to be linked by a continuous and not extreme morphographical variation as observed consistently in the preparations of many samples. For example, *Murospora aurita* (Waltz) comb. nov., emend., demonstratively includes several forms originally instituted as separate species, which are considered here merely as infraspecific morphographical variations.

Many genera of Palaeozoic *sporae dispersae* are poorly circumscribed, mutually overlapping, and of doubtful validity. Thus the generic assignment of some of the species described herein may well prove debatable. However, controversy regarding generic assignment should not obscure the fundamental importance of concise description and illustration at specific level, an undoubted prerequisite for meaningful generic institutions as for the useful application of palynology to stratigraphical correlation.

All type and other figured specimens of the present study are referred to by the preparation/slide number, followed by the 'east-west' and 'north-south' mechanical stage readings, and then the Sedgwick Museum Specimen number (prefixed 'L'). The stage readings are from Leitz Dialux microscope no. 1 (serial no. 469843) in the Sedgwick Museum, Cambridge, where the material is deposited (specimen registration numbers L.939-L.1258). The registered numbers (L.880-L.938) have also been given to all type and other figured specimens of Hughes and Playford (1961).

Anteturma SPORONITES (R. Potonié) Ibrahim 1933

Genus CHAETOSPHAERITES Felix 1894

Type species (here designated). *C. bilychnis* Felix 1894, pp. 272–3; pl. 19, fig. 4.

Affinity. The type species, which is of Eocene age, was allied by Felix (1894, p. 273) to spores borne by several species of the recent *Chaetosphaeria*, a member of the fungal family Ascomycetaceae.

Chaetosphaerites pollenisimilis (Horst) Butterworth and Williams 1958

Plate 78, figs. 1, 2

1955 *Sporonites pollenisimilis* Horst, pp. 150–1; pl. 24, figs. 84–87.

1957 *Sporonites cylindricus* (Horst) Dybová and Jachowicz, pp. 56–57; pl. 1, figs. 1–4.

1958 *Chaetosphaerites pollenisimilis* (Horst) Butterworth and Williams, p. 359; pl. 1, figs. 1–3.

Description. In addition to the usual bicellular forms, occasional specimens possessing one or three translucent ‘heads’ were encountered. Measurement of thirty-five specimens gave a size range of 21–52 μ (mean 36 μ).

Previous records. *Chaetosphaerites pollenisimilis* (Horst) has been recorded previously from European strata of Namurian age (Horst 1955; Dybová and Jachowicz 1957; Butterworth and Williams 1958), from the Golata formation (Upper Mississippian) of Canada (Staplin 1960), and from one sample (S59a) of the Spitsbergen Lower Carboniferous (Hughes and Playford 1961). Butterworth and Millott (1960) indicate Viséan–Namurian distribution in British coals.

Anteturma SPORITES H. Potonié 1893

Turma TRILETES (Reinsch) Potonié and Kremp 1954

Subturma AZONOTRILETES Lubert 1935

Infraturma LAEVIGATI (Bennie and Kidston) R. Potonié 1956

Genus LEIOTRILETES (Naumova) Potonié and Kremp 1954

Type species. *L. sphaerotriangulus* (Loose) Potonié and Kremp 1954.

Discussion. The validity of this genus, as emended in 1954 by Potonié and Kremp and generally applied exclusively within the confines of Palaeozoic palynology, has been questioned by Staplin (1960, p. 14), who assigned simple, smooth, triangular, trilete spores of Mississippian age to the genus *Deltoidospora* Miner 1935, which is often ‘reserved’ for post-Palaeozoic spores. Contrary also to usual practice, Nilsson (1958, pp. 30–33) included within *Leiotriletes* similar spores occurring in Swedish Liassic sediments.

The present writer is in agreement with Staplin’s (1960) statement—‘the argument that there is a separation in time between Miner’s species and species referred to *Leiotriletes* has little validity where form genera are concerned’. However, the question seems far from resolved, particularly in view of Potonié’s (1960, pp. 26–27) lengthy discussion, and accordingly the Spitsbergen spores concerned are assigned herein to *Leiotriletes*.

The problem is not, of course, restricted to *Leiotriletes*, but concerns equally the relationship between such comparatively characterless form-genera as *Punctatisporites* and *Calamospora*, and their Mesozoic equivalents.

Affinity. Representatives of *Leiotriletes* have been reported recently by W. and R. Remy (1957) from

the fern fructifications *Oligocarpia gutbieri* Göppert, *Oligocarpia cliveri* H. Potonié, *Renaultia* sp., *Discopteris schumanni* Stur, and from a new genus and species of the Saar Carboniferous. According to Potonié (1960, p. 27) those from *Oligocarpia gutbieri* and from *O. cliveri* may be referred to, respectively, *Leiotriletes adnatus* (Kosanke) and *L. sphaerotriangulus* (Loose).

Leiotriletes inermis (Waltz) Ishchenko 1952

Plate 78, figs. 3, 4

- 1938 *Azonotriletes inermis* Waltz in Luber and Waltz, p. 11; pl. 1, fig. 3, pl. 5, fig. 58, and pl. A, fig. 2.
 1952 *Leiotriletes inermis* (Waltz) Ishchenko, p. 9; pl. 1, figs. 2, 3.
 1955 *Asterocalamotriletes inermis* (Waltz) Luber, p. 40; pl. 1, figs. 20, 21.
 1955 *Leiotriletes inermis* (Waltz) Potonié and Kremp, p. 37.

Description of specimens. Spores radial, trilete; amb subtriangular, sides convex to almost straight, apices rounded. Laesurae distinct, simple, straight, extending almost to smooth equatorial margin. Exine 1–2 μ thick, laevigate.

Dimensions (50 specimens). Equatorial diameter 28–57 μ (mean 43 μ).

Previous records. From the Lower Carboniferous of the U.S.S.R.; Ishchenko (1958) indicates distribution from Devonian to Bashkirian.

Leiotriletes subintortus (Waltz) Ishchenko 1952 var. *rotundatus* Waltz 1941

Plate 78, figs. 5, 6

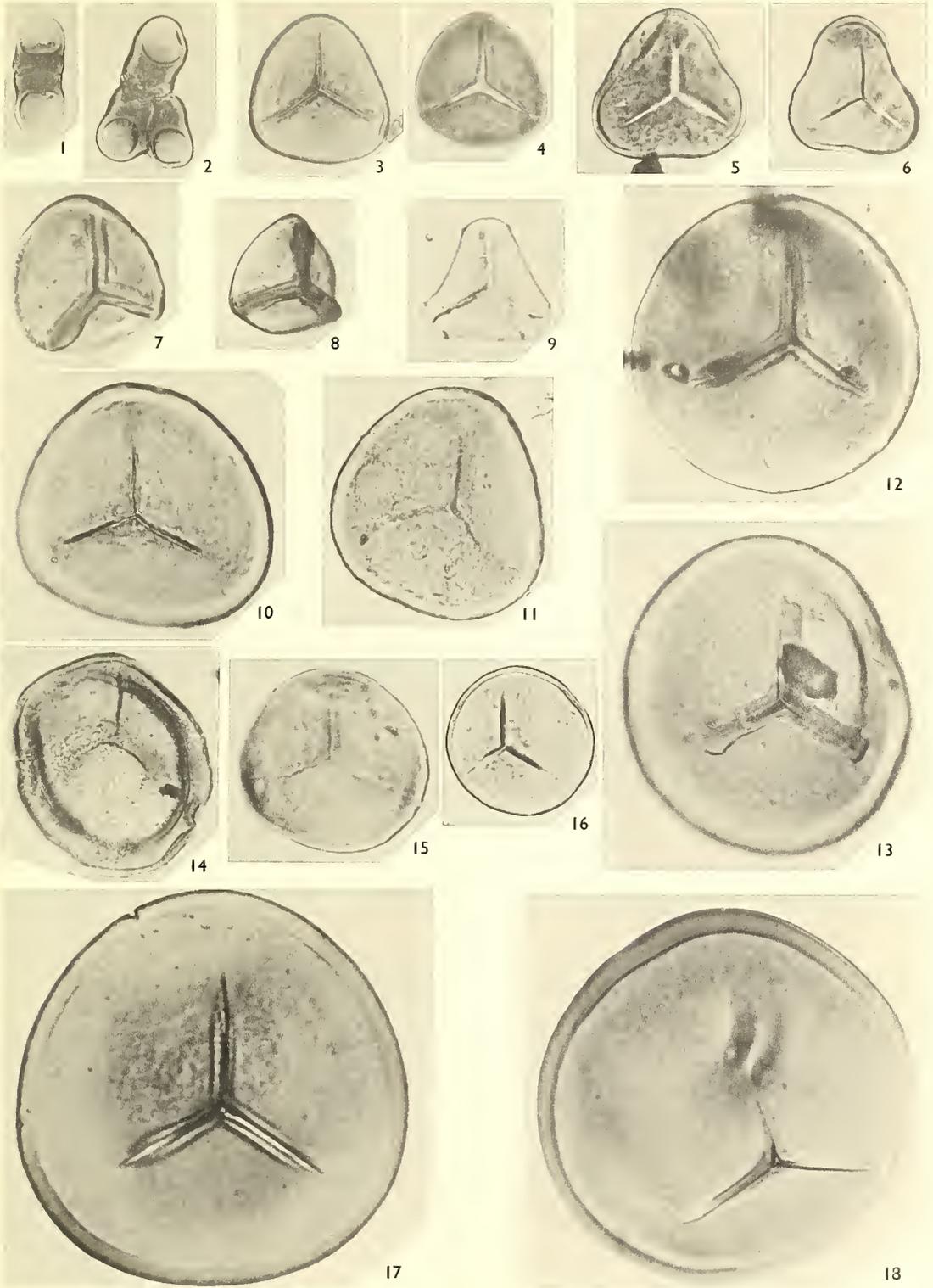
- 1941 *Azonotriletes subintortus* Waltz var. *rotundatus* Waltz in Luber and Waltz, pp. 13–14; pl. 2, fig. 15b.
 1952 *Leiotriletes subintortus* (Waltz) Ishchenko var. *rotundatus* Waltz; Ishchenko, p. 11; pl. 1, fig. 7.

Description of specimens. Spores radial, trilete; amb subtriangular with rounded apices

EXPLANATION OF PLATE 78

All figures $\times 500$, and from unretouched negatives.

- Figs. 1, 2. *Chaetosphaerites pollenisimilis* (Horst) Butterworth and Williams 1958. 1, Preparation P145C/2, 27.8 97.8 (L.939). 2, Preparation P145B/22, 36.1 103.2 (L.940).
 Figs. 3, 4. *Leiotriletes inermis* (Waltz) Ishchenko 1952. 3, Proximal surface; preparation M811/5, 38.3 100.9 (L.941). 4, Proximal surface; preparation P034/1, 35.8 103.8 (L.942).
 Figs. 5, 6. *L. subintortus* (Waltz) Ishchenko 1952 var. *rotundatus* Waltz 1941. 5, Proximal surface; preparation P163/6, 18.2 99.2 (L.943). 6, Proximal surface; preparation P163/7, 36.0 94.8 (L.944).
 Figs. 7, 8. *L. ornatus* Ishchenko 1956. 7, Proximal surface; preparation P163/5, 29.3 106.2 (L.946). 8, Proximal surface; preparation P163/6, 39.0 95.9 (L.945).
 Fig. 9. *L. curiosus* sp. nov. Holotype; proximal surface.
 Figs. 10, 11. *L. microgranulatus* sp. nov. 10, Proximal surface; preparation P181/4, 52.3 112.4 (L.948). 11, Holotype; distal surface.
 Figs. 12, 13. *Punctatisporites labiatus* sp. nov. 12, Holotype; proximal surface. 13, Proximal surface; preparation P163/5, 22.0 92.4 (L.957).
 Fig. 14. *P. parvivermiculatus* sp. nov. Holotype; distal surface.
 Figs. 15, 16. *P. glaber* (Naumova) comb. nov. 15, Proximal surface; preparation P148/1, 35.6 109.7 (L.952). 16, Proximal surface; preparation P163/5, 46.0 107.2 (L.953).
 Figs. 17, 18. *P. pseudobesius* sp. nov. 17, Proximal surface; preparation P149A/31, 36.3 105.0 (L.960). 18, Holotype; proximal surface.



PLAYFORD, Lower Carboniferous microspores

and concave sides. Laesurae distinct, straight, simple, extending almost to smooth equatorial margin. Exine 1–2 μ thick, laevigate.

Dimensions (45 specimens). Equatorial diameter 26–50 μ (mean 38 μ).

Comparison. *Granulatisporites adnatus* Kosanke 1950 has a definite contact area, but *G. adnatus?* in Wilson and Hoffmeister (1956, p. 16; pl. 2, fig. 9) lacks this feature and is probably conformable with *L. subintortus* var. *rotundatus*.

Previous records. Apparently widespread in the Russian Lower Carboniferous, with previous records from Luber and Waltz (1941) and Ishchenko (1952, 1956, 1958), whose work indicates a range from Tournaisian to Bashkirian for this variety.

Leiotriletes ornatus Ishchenko 1956

Plate 78, figs. 7, 8

1956 *Leiotriletes ornatus* Ishchenko, p. 22; pl. 2, figs. 18–21.

1960 Spore type 1 of Love, p. 122; pl. 2, fig. 9 and text-fig. 12.

Description of specimens. Spores radial, trilete; amb subtriangular with convex to almost straight sides. Laesurae distinct, straight, length approximately equal to spore radius; with prominent, dark, raised lips individually 2.5–4.5 μ wide. Exine 2–3.5 μ thick, laevigate or occasionally sparsely infrapunctate (oil immersion).

Dimensions (55 specimens). Equatorial diameter 32–63 μ (mean 46 μ).

Comparison. The two specimens described by Love (1960, p. 122) are undoubtedly representative of this species; the apparent 'equatorial thickening' has been observed in a number of the Spitsbergen specimens, and, as suggested by Love, is the result of exinal folding due to compression. Spore type C of Neves (1958, p. 12; pl. 2, fig. 6) has an 'equatorial flange' according to the description, and the lips have considerably greater development than those of *L. ornatus*. *Filicitriletes pyramidalis* (Luber in Luber and Waltz 1941, p. 54; pl. 12, fig. 182) Luber 1955 (p. 60; pl. 3, fig. 20) is larger than *L. ornatus* and appears to have only minor lip development.

Previous records. Ishchenko (1956) found this species to be restricted to Middle Viséan–Lower Namurian strata of the Western Donetz Basin. An interesting recent record is from the Pumpherstun Shell Bed (Viséan) of Scotland (Love 1960).

Leiotriletes microgranulatus sp. nov.

Plate 78, figs. 10, 11

Diagnosis. Spores radial, trilete; amb broadly roundly subtriangular. Simple, straight, distinct laesurae equal half to three-fifths of spore radius. Equatorial margin smooth. Exine 3–4.5 μ thick, finely and densely granulate ('peppery' appearance under oil immersion).

Dimensions (25 specimens). Equatorial diameter 58–86 μ (mean 70 μ).

Holotype. Preparation P176A/2, 23.5 95.2. L.947.

Locus typicus. Citadellet (sample G1451), Spitsbergen; Lower Carboniferous.

Description. Holotype subtriangular with slightly convex sides and broadly rounded apices, diameter $73\ \mu$; laesurae one-half spore radius; minutely granulate exine, $4\ \mu$ in thickness.

Comparison. *Leiotriletes convexus* (Kosanke 1950, pp. 20–21; pl. 3, fig. 6) Potonié and Kremp 1955 has similar sculpture but a thinner exine and longer laesurae.

Leiotriletes curiosus sp. nov.

Plate 78, fig. 9; text-fig. 5b

Diagnosis. Spores radial, trilete; amb subtriangular with straight to slightly concave sides and broad, bluntly rounded apices. Laesurae distinct, simple, straight or slightly undulating, length approximately four-fifths spore radius. Exine thin (less than $1\ \mu$), laevigate or faintly roughened (oil immersion). The (six) equatorial junctions between apical shoulders and interradial sides are each marked by a small, rounded, relatively broad-based granule.

Dimensions (25 specimens). Equatorial diameter, $28\text{--}40\ \mu$ (mean $35\ \mu$).

Holotype. Preparation P149B/1, 38·8 97·6. L.950.

Locus typicus. Triungen (sample G1470), Spitsbergen; Lower Carboniferous.

Description. Holotype $38\ \mu$; one laesura bordered by narrow folds simulating lips.

Remarks. On the basis of subtriangular shape and mainly smooth surface, this species is included within *Leiotriletes*, rather than in *Granulatisporites* which incorporates similarly shaped, but densely granulate spores.

Genus PUNCTATISPORITES (Ibrahim) Potonié and Kremp 1954

Type species. *P. punctatus* Ibrahim 1933.

Affinity. Psilopsida, Filicineae, Cycadofilicineae? (after Potonié and Kremp 1955, p. 42; 1956b, p. 81).

Punctatisporites glaber (Naumova) comb. nov.

Plate 78, figs. 15, 16

1938 *Azonotriletes glaber* (Naumova) Waltz in Luber and Waltz, p. 8; pl. 1, fig. 2 and pl. A, fig. 3.

1952 *Leiotriletes glaber* (Waltz) Ishchenko, pp. 13–14; pl. 2, figs. 15, 16.

1955 *Calamospora glabra* (Naumova) Potonié and Kremp, p. 47.

1955 *Punctatisporites nitidus* Hoffmeister, Staplin, and Malloy, pp. 393–4; pl. 36, fig. 4.

1955 *Punctatisporites? callosus* Hoffmeister, Staplin, and Malloy, p. 392; pl. 39, fig. 7.

1956 *Leiotriletes glaber* Naumova; Ishchenko, pp. 18–19; pl. 1, figs. 7, 8.

1958 *Punctatisporites* cf. *nitidus* Hoffmeister, Staplin, and Malloy; Butterworth and Williams, p. 361; pl. 1, figs. 7, 8.

1960 *Punctatisporites curviradiatus* Staplin, p. 7; pl. 1, figs. 17, 20.

Description of specimens. Spores radial, trilete; equatorial outline circular. Laesurae distinct, simple, straight, length one-third to two-thirds spore radius. Exine $1.5\text{--}2\ \mu$ thick, laevigate (corroded specimens finely punctate); rarely folded.

Dimensions (38 specimens). Equatorial diameter $32\text{--}70\ \mu$ (mean $52\ \mu$).

Remarks. The above synonymy does not attempt to be exhaustive. Several other species, for example *Punctatisporites planus* Hacquebard 1957 (p. 308; pl. 1, fig. 12), may well prove to be conspecific with *P. glaber*. The intention, however, is to emphasize the multitudinous nomenclature prevailing among such simple, circular, laevigate spores, and particularly those occurring in the Carboniferous System. As these forms are apparently of limited stratigraphical value there seems little point in attempting a rigorous subdivision (particularly on the basis of minute variations in such few and simple morphological characters), and certainly the validity of naming a spore according to its stratigraphical horizon is extremely doubtful. It is, of course, recognized that the dispersed spores included within *P. glaber* are probably representative of several different plants.

Staplin (1960, p. 7) in discussing his new species *Punctatisporites curvirodiatus* states that 'off-polar compression and resultant apparent curvature of two sutures distinguish this species from *P. nitidus* Hoffmeister, Staplin and Malloy'. This appears rather a questionable basis for specific distinction. The illustrations given by Waltz (*in* Luber and Waltz 1938 and 1941) of *P. glaber* include identical spores showing this same feature. Comparison with Staplin's (1960) species is often difficult owing to the fact that relative terms only are used in stating the thickness of the spore wall (e.g. 'moderate').

Punctatisporites glaber (Naumova) comb. nov. was assigned to the genus *Calamospora* by Potonić and Kremp (1955, p. 47); however, its relatively thick, rarely folded exine, together with fairly extensive laesurae, indicate more appropriate inclusion within *Punctatisporites*.

Previous records. Numerous previous records from the Carboniferous (see synonymy above). According to Ishchenko (1958) this species ranges from Devonian to Bashkirian.

Punctatisporites parvivermiculatus sp. nov.

Plate 78, fig. 14; text-fig. 5k

Diagnosis. Spores radial, trilete; amb circular to subcircular. Laesurae distinct, more or less straight, equal three-quarters or more of spore radius, sometimes with incipient lips. Exine 2–3 μ thick; sculpture infravermiculate with very fine, shallow, short, anastomosing grooves indenting the otherwise laevigate spore wall, constituting a highly imperfect negative microreticulum.

Dimensions (30 specimens). Equatorial diameter 58–88 μ (mean 74 μ).

Holotype. Preparation P169/1, 31.3 98.1. L.954.

Locus typicus. Birger Johnsonfjellet (sample G1036), Spitsbergen; Lower Carboniferous.

Description. Holotype subcircular, equatorial margin undulating due to folding, diameter 68 μ ; laesurae slightly curved due to compression, length approximately three-quarters spore radius; exine 3 μ in thickness, with peripheral arcuate folds. In many specimens the nature of the exinal sculpture is evident only under oil immersion. The grooves never attain the dimensions necessary to delimit definite positive processes, such as verrucae or grana.

Comparison. *Punctatisporites vermiculatus* Kosanke 1950 (p. 19; pl. 2, fig. 4) is similar,

but has a thicker exine deeply incised by a more extensively developed vermiculate sculpture. Potonié and Kremp (1955, p. 104) considered that *P. vermiculatus* may perhaps be referable to *Camptotriletes*. However, *P. parvivermiculatus* sp. nov. with its relatively minor sculpture is more appropriately included within *Punctatisporites*.

Punctatisporites labiatus sp. nov.

Plate 78, figs. 12, 13

Diagnosis. Spores radial, trilete; amb circular. Laesurae straight, length two-thirds to three-quarters spore radius; emphasized by prominent, smooth, slightly raised lips, individually 3–4 μ wide. Exine 3–4.5 μ thick; laevigate to indistinctly infragranulate.

Dimensions (20 specimens). Equatorial diameter 69–113 μ (mean 88 μ).

Holotype. Preparation P163/1, 30.0 97.3. L.956.

Locus typicus. Birger Johnsonfjellet (sample G1089), Spitsbergen; Lower Carboniferous.

Description. Holotype circular, diameter 94 μ ; laesurae equal three-quarters spore radius, rimmed by pronounced, dark lips 4 μ wide; exine 3 μ thick, laevigate, not folded. Other specimens occasionally show minor peripheral folding.

Comparison. This species resembles *Punctatisporites flavus* (Kosanke 1950, p. 41; pl. 9, fig. 2) Potonié and Kremp 1955, but differs in having longer laesurae, with more pronounced and regular lip development. *Azonotriletes microrugosus* (Ibrahim) forma *karagandensis* Lubert (in Lubert and Waltz 1938, p. 22; pl. 5, fig. 56) is smaller with incipient lips and thinner, folded exine.

Punctatisporites pseudobesus sp. nov.

Plate 78, figs. 17, 18

Diagnosis. Spores radial, trilete; amb circular, oval or broadly roundly subtriangular. Laesurae distinct, straight, length one-half to two-thirds spore radius. Exine perceptibly infragranulate (oil immersion), thickness 5.5–8 μ (average 7 μ); folding infrequent.

Dimensions (35 specimens). Equatorial diameter 97–157 μ (mean 125 μ).

Holotype. Preparation P149A/22, 31.8 101.3. L.959.

Locus typicus. Triungen (sample G1470), Spitsbergen; Lower Carboniferous.

Description. Holotype circular, 121 μ in diameter, laesurae about three-fifths spore radius, exine 7 μ thick.

Comparison. The closely allied species, *Punctatisporites obesus* (Loose) Potonié and Kremp (1955, p. 43; pl. 11, fig. 124), has a thinner spore wall (up to 5 μ), somewhat shorter laesurae, and a different size range.

Punctatisporites stabilis sp. nov.

Plate 79, figs. 1, 2

Diagnosis. Spores radial, trilete, originally spherical; amb circular, practically smooth.

Laesurae distinct, simple, straight or slightly curved, length approximately three-quarters spore radius. Exine $1.5\text{--}2.5\ \mu$ thick; with distinct, minute (less than $1\ \mu$ across), shallow punctations scattered on both proximal and distal hemispheres. Exinal folding rare.

Dimensions (45 specimens). Equatorial diameter $63\text{--}94\ \mu$ (mean $76\ \mu$).

Holotype. Preparation P158/7, 31.5 114.5. L.962.

Locus typicus. Birger Johnsonfjellet (sample G1092), Spitsbergen; Lower Carboniferous.

Description. Holotype $90\ \mu$; exine $2.5\ \mu$ in thickness; punctae fairly uniformly distributed, *c.* $4\ \mu$ apart, occasionally slightly elongate forming short grooves up to $2\ \mu$ long.

Comparison. *Azonotriletes punctulatus* Waltz var. *giganteus* Waltz (in Lubert and Waltz 1941, p. 14; pl. 2, fig. 16a) appears similar to *Punctatisporites stabilis* sp. nov., but differs in having an oval outline, shorter laesurae and generally larger size ($90\text{--}115\ \mu$); closer comparison is difficult owing to the brevity of Waltz's description. Another rather similar species, *Punctatisporites punctatus* Ibrahim 1933 (Potonié and Kremp 1955, p. 45; pl. 11, figs. 122, 123), is distinguishable from *P. stabilis* on the basis of its longer laesurae, broadly roundly triangular amb, and infrapunctate sculpture.

Genus CALAMOSPORA Schopf, Wilson, and Bentall 1944

Type species. *C. hartungiana* Schopf in Schopf, Wilson, and Bentall 1944.

Affinity. Sphenophyllaceae?, Calamariaceae, Noeggerathiales (after Potonié and Kremp 1954, p. 123). Spores conformable with *Calamospora* have been reported by Kosanke (1955) from his homosporous Calamarian species *Mazostachys pendulata*; and by W. and R. Remy (1957) from *Noeggerathiostrubus vicinalis* E. Weiss, *Discinites* sp. cf. *bohemicus* K. Feistmantel, and *Discinites* sp. Spores which appear to closely resemble *Calamospora* were recovered by Walton (1957) from his new species *Protopytis scotica*, a fertile shoot from the Calciferous Sandstone Series (Lower Carboniferous) of Dunbartonshire, Scotland. On the evidence of *P. scotica*, Walton considered that *Protopytis* had peridophytic reproduction and proposed a new group, the Protopytiales, to include the genus.

Calamospora microrugosa (Ibrahim) Schopf, Wilson, and Bentall 1944

Plate 79, figs. 3, 4

1932 *Sporonites microrugosus* Ibrahim in Potonié, Ibrahim, and Loose, p. 447; pl. 14, fig. 9.

1933 *Laevigati-sporites microrugosus* (Ibrahim) Ibrahim, p. 18; pl. 1, fig. 9.

1938 *Azonotriletes microrugosus* (Ibrahim) Waltz in Lubert and Waltz, p. 10; pl. 1, fig. 1 and pl. A, fig. 1.

1944 *Calamospora microrugosa* (Ibrahim) Schopf, Wilson, and Bentall, p. 52.

1952 *Leiotriletes microrugosus* (Ibrahim) Ishchenko, p. 15; pl. 2, fig. 19.

1955 *Calamotriletes microrugosus* (Waltz) Lubert, p. 36; pl. 1, figs. 1-3.

Description of specimens. Spores radial, trilete, originally spherical; amb circular to subcircular (modified by folding). Laesurae distinct, straight, length one-half to two-thirds spore radius, sometimes with faint, narrow, lip development. Equatorial margin smooth. Exine very thin (usually less than $1\ \mu$); laevigate or very minutely granulate (oil immersion), characteristically strongly plicated with folds of both major and minor proportions.

Dimensions (40 specimens). Equatorial diameter 62–104 μ (mean 82 μ).

Remarks. Spores similar to *Calamospora microrugosa* have been designated by a variety of specific names, many clearly synonymous, but until a direct comparison of the types is possible more precise assignment of the above specimens is precluded. As noted by Potonié and Kremp (1955, p. 49), *Calamospora liquida* Kosanke 1950 is undoubtedly very close to *C. microrugosa*. This is also the case with various spores described and illustrated by Ishchenko (1952, 1956, 1958) as *Leiotriletes platirugosus* (Waltz 1941) with three varieties, *L. vetustus* Ishchenko 1952, *L. mitus* Ishchenko 1952, and *L. immanis* Ishchenko 1952. The latter two species were considered synonymous with *C. liquida* Kosanke by Dybová and Jachowicz (1957, p. 63). Potonié and Kremp (1955), Lubert and Waltz (1938, 1941), Naumova (1953), Ishchenko (1952, &c.), Lubert (1955), Bolkhovitina (1956, 1959), Chibrikova (1959), and Imgrund (1960) have all recorded *C. microrugosa* as such. Naumova (1953) notes the vertical range as Cambrian to Cretaceous.

Previous records. *C. microrugosa* has been recorded by numerous authors from the Carboniferous (see above).

GENUS PHYLLOTHECOTRILETES Lubert 1955

Type species. *P. nigrifellus* (Lubert) Lubert 1955.

Affinity. Unknown.

Phyllothecotriletes rigidus sp. nov.

Plate 79, figs. 5, 6

Diagnosis. Spores radial, trilete; amb circular to subcircular. Laesurae distinct, typically

EXPLANATION OF PLATE 79

All figures $\times 500$, and from unretouched negatives.

Figs. 1, 2. *Punctatisporites stabilis* sp. nov. 1, Holotype; proximal surface. 2, Proximal surface; preparation P158/7, 24.6 96.8 (L.963).

Figs. 3, 4. *Calamospora microrugosa* (Ibrahim) Schopf, Wilson and Bentall 1944. 3, Proximal surface; preparation P181/4, 40.4 112.6 (L.965). 4, Proximal surface; preparation P148/18, 44.8 111.8 (L.966).

Figs. 5, 6. *Phyllothecotriletes rigidus* sp. nov. 5, Holotype; proximal surface. 6, Proximal surface; preparation P176A/3, 22.8 97.4 (L.968).

Fig. 7. *Waltzispora lobophora* (Waltz) Staplin 1960. Distal surface; preparation P145A/1, 40.2 105.8 (L.970).

Figs. 8–11. *W. albertensis* Staplin 1960. 8, Proximal surface; preparation P145C/2, 46.7 112.9 (L.971). 9, Distal surface; preparation P145C/1, 48.4 100.1 (L.972). 10, Proximal surface; preparation P145B/30, 38.8 101.9 (L.973). 11, Proximal surface; preparation P145C/2, 52.3 98.1 (L.974).

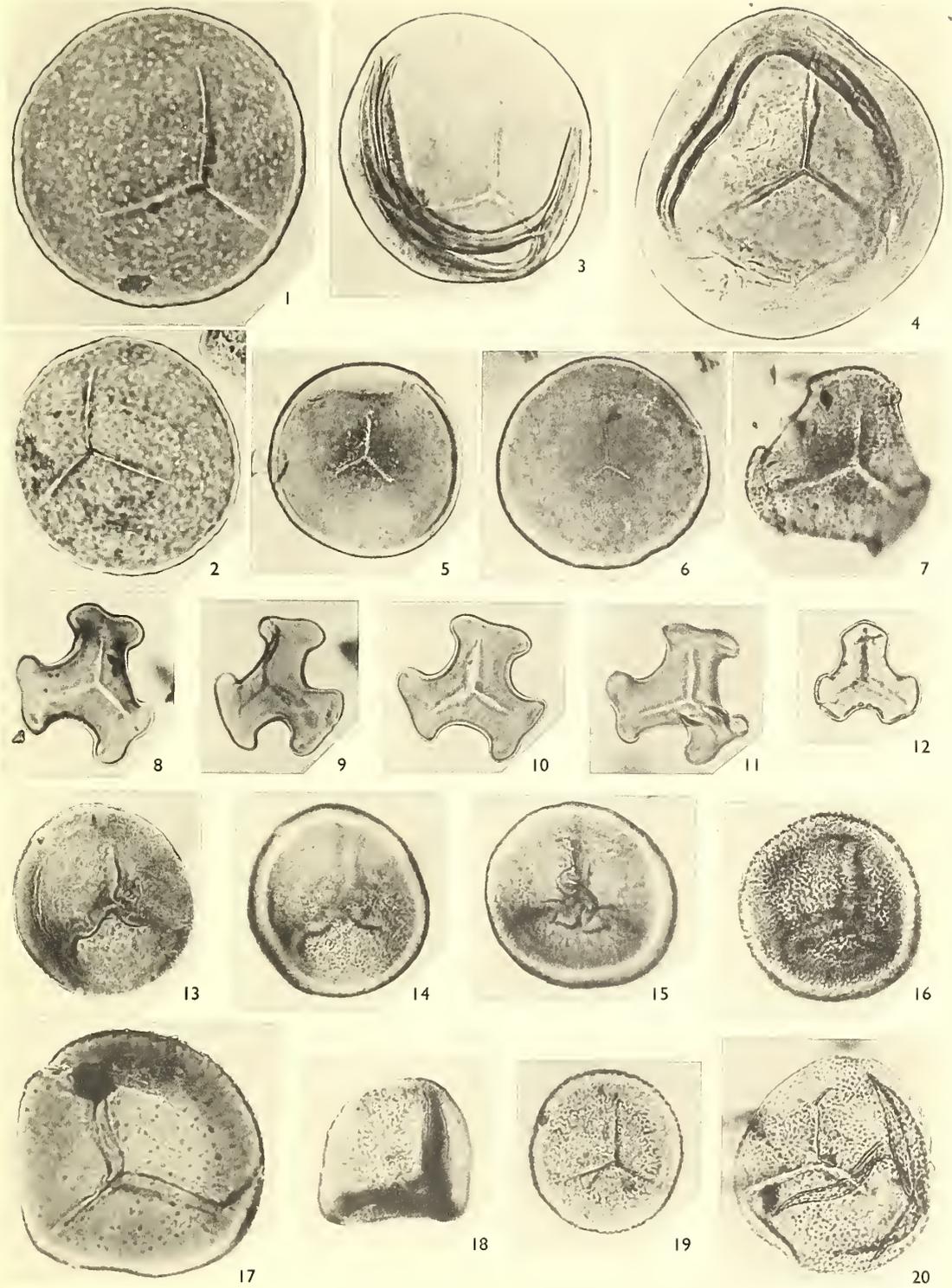
Fig. 12. *W. sagittata* sp. nov. Holotype; distal surface.

Figs. 13–16. *Cyclogranisporites flexuosus* sp. nov. 13, 14, Holotype; proximal and distal surfaces respectively. 15, Proximal surface; preparation P148/2, 45.8 94.0 (L.981). 16, Distal surface; preparation P148/33, 34.7 101.7 (L.982).

Fig. 17. *Lophotriletes coniferus* Hughes and Playford 1961. Proximal surface; preparation P175/7, 50.3 98.2 (L.993).

Fig. 18. *Granulatisporites planiusculus* (Lubert) comb. nov. Proximal surface; preparation P169/1, 33.9 113.5 (L.977).

Figs. 19, 20. *Cyclogranisporites lasius* (Waltz) comb. nov. 19, Proximal surface; preparation P175/2, 19.2 97.7 (L.978). 20, Proximal surface; preparation P145A/2, 22.4 112.2 (L.979).



PLAYFORD, Lower Carboniferous microspores

slightly sinuous; unequal in length, approximately one-third spore radius. Exine 2–4.5 μ thick, very finely granulate (oil immersion), folding minor—absent.

Dimensions (40 specimens). Equatorial diameter 57–77 μ (mean 66 μ).

Holotype. Preparation P172/3, 45.4 93.9. L.967.

Locus typicus. Citadelle (sample G1445), Spitsbergen; Lower Carboniferous.

Description. Holotype circular, 62 μ in diameter; exine 2.5 μ thick, very minutely granulate; laesurae \pm straight, approximately one-third spore radius, one slightly longer than others.

Comparison. *Phyllothecotriletes golatensis* Staplin 1960 (p. 9; pl. 1, fig. 27) is laevigate and has shorter laesurae; *P.?* *belloyensis* Staplin 1960 (p. 9; pl. 1, fig. 23) is smaller, and has longer laesurae together with distinct contact area.

Genus WALTZISPORA Staplin 1960

Type species. *W. lobophora* (Waltz) Staplin 1960.

Discussion. This distinctive genus embraces relatively simple, subtriangular, trilete spores having characteristically blunted and tangentially expanded radial extremities, and sculpture which, on presently known species, ranges from granulate to laevigate. It appears to have considerable stratigraphical significance within the Lower Carboniferous, as evidenced herein and from observations elsewhere.

Affinity. Unknown.

Waltzispora lobophora (Waltz) Staplin 1960

Plate 79, fig. 7

1884 Type 74 of Reinsch, p. 8; pl. 3, fig. 31.

1938 *Azonotriletes lobophorus* Waltz in Luber and Waltz, p. 12; pl. 1, fig. 5 and pl. A, fig. 8.

1941 *Azonotriletes lobophorus* Waltz var. *simplex* Waltz in Luber and Waltz, pp. 18–19; pl. 3, fig. 31.

1941 *Azonotriletes lobophorus* Waltz var. *submarginatus* Waltz in Luber and Waltz, pp. 18–19; pl. 3, fig. 32.

1956 *Triquitrites lobophorus* (Waltz) Potonié and Kremp, p. 87.

1960 *Waltzispora lobophora* (Waltz) Staplin, p. 18.

Description of specimens. Spores radial, trilete; amb subtriangular with concave to almost straight interrational margins, having conspicuous angular junctions with flatly rounded radial extremities, which thus constitute more or less prominent shoulders. Laesurae distinct, straight, length approximately four-fifths spore radius; sometimes with minor lip development in proximal polar region. Comprehensive granulate sculpture, particularly marked around distal pole, where grana are closely packed and comparatively large (up to 2.5 μ in basal diameter). Exine 1.5–2 μ thick.

Dimensions (20 specimens). Equatorial diameter 43–58 μ (mean 50 μ).

Remarks. The not extreme morphographical variation between specimens included within this species is clearly evident from the illustrations given by Reinsch (1884) and

by Lubert and Waltz (1938, and particularly 1941); it is confirmed by the Spitsbergen specimens recorded herein. In 1941 Waltz (*in* Lubert and Waltz, loc. cit.) distinguished two varieties of *Azonotriletes lobophorus*—var. *simplex* (identical to pl. 1, fig. 5 in Lubert and Waltz 1938) and var. *submarginatus*—which were not intended to be considered as discrete taxonomic units, but rather as extremes of infraspecific variation.

Comparison. If the absence of granules on the proximal surface is a constant feature of *Granulatisporites humerus* Staplin 1960 (p. 16; pl. 3, fig. 24) it may be considered as a species distinct from *W. lobophora* (Waltz). In any case, the inclusion of *G. humerus* within *Waltzisporea* is recommended on the basis of its close conformity to the type species in the diagnostic characters of equatorial outline and sculpture.

Previous records. This species was first reported by Reinsch (1884) from Russian (? Lower) Carboniferous rocks, and subsequently (Lubert and Waltz 1938, 1941) from the Lower Carboniferous of the Moscow Basin, and of the Selizharovo, Borovichi, and Kizel regions, U.S.S.R.

Waltzisporea albertensis Staplin 1960

Plate 79, figs. 8–11

1884 Type 78 of Reinsch p. 9; pl. 22, fig. 28A.

1957 cf. *Azonotriletes lobophorus* Waltz; Hacquebard and Barss, pp. 44–45; pl. 6, fig. 9.

1960 *Waltzisporea albertensis* Staplin, p. 18; pl. 4, figs. 2, 3.

Description of specimens. Spores radial, trilete. Amb concavely subtriangular, with prominent, blunted, radial extremities, which are conspicuously and more or less symmetrically expanded in a tangential direction; central parts of radial extremities often embayed (towards the polar axis). Laesurae more or less straight, length three-quarters to four-fifths spore radius; occasional minor development of lips. Exine 1.5–2 μ thick; essentially laevigate but may appear slightly roughened under oil immersion.

Dimensions (120 specimens). Equatorial diameter 23–37 μ (mean 29 μ).

Note that the discrepancy between the above size range and the measurements given by Hacquebard and Barss (1957) and Staplin (1960) is only apparent. Although not specified in their texts, it is evident from the plates that they have stated the 'angle to angle' measurement (Harris 1955, p. 14), whilst, as mentioned previously, the present writer takes the equatorial diameter of triangular forms as the maximum median length.

Remarks. The spores illustrated and described by Reinsch (1884) and Hacquebard and Barss (1957) as, respectively, type 78 and cf. *Azonotriletes lobophorus* Waltz 1938, are conformable in all respects with *W. albertensis* Staplin.

Previous records. This species has been recorded previously from the Russian (? Lower) Carboniferous (Reinsch 1884), and from the Upper Mississippian of Canada (Hacquebard and Barss 1957; Staplin 1960).

Waltzisporea sagittata sp. nov.

Plate 79, fig. 12; text-fig. 5c

1960 *Leiotriletes politus* (*non* Hoffmeister, Staplin, and Malloy 1955, p. 389; pl. 36, fig. 13) Love, pl. 1, fig. 1.

Diagnosis. Spores radial, trilete; amb subtriangular with concave interradial margins

and convex, somewhat pointed, radial extremities, which also show slight, but definite, tangential expansion. Laesurae simple, straight, length at least three-quarters spore radius. Equatorial margin smooth. Exine finely granulate to almost laevigate; up to $1\ \mu$ thick.

Dimensions (16 specimens). Equatorial diameter 24–35 μ (mean 29 μ).

Holotype. Preparation P180B/1, 54.4 105.8. L.975.

Locus typicus. Birger Johnsonfjellet (sample G1102), Spitsbergen; Lower Carboniferous.

Description. Holotype 27 μ ; proximal and distal surfaces with uniform sculpture of fairly widely spaced minute grana, which do not project at the equator; laesurae almost attain equatorial margin.

Comparison. *Waltzispora lobophora* (Waltz) Staplin 1960 is larger, more densely granulate, and the convexity of the radial extremities is less pronounced than in *W. sagittata* sp. nov. *Zonotriletes triplex* Andrejeva (in Luber and Waltz 1941, p. 18; pl. 3, fig. 33), which is almost certainly a comparatively thick-walled species of *Waltzispora*, is laevigate, has very deeply incised interradial margins, and ranges in size from 45 to 55 μ .

Remarks. The spore illustrated by Love (1960, pl. 1, fig. 1) as *Leiotriletes politus* (Hoffmeister, Staplin, and Malloy) appears identical to the Spitsbergen specimens described above, and seems to have little diagnostically in common with the description and illustration given by Hoffmeister, Staplin, and Malloy (1955, p. 389; pl. 36, fig. 13).

Although the photograph given by Butterworth and Williams (1958, pl. 1, fig. 15) is probably of a genuine representative of *Granulatisporites politus*, it is possible that *Waltzispora sagittata* sp. nov. is present in their Scottish material, but was considered by them as a variant of *G. politus*. This is suggested by the statement (Butterworth and Williams, loc. cit., p. 361) regarding 'the tendency for the rounded radial extremities to project laterally, thus giving an angular junction of radial and inter-radial areas', an attribute which suggested to them an analogy with a 'similar species', *Azonotriletes lobophorus* Waltz (which was subsequently designated as the type species of *Waltzispora*).

Previous records. From the Lower Oil-shale Group (Viséan) of Scotland (Love 1960).

Infraturma APICULATI (Bennie and Kidston) R. Potonié 1956

Subinfraturma GRANULATI Dybová and Jachowicz 1957

Genus GRANULATISPORITES (Ibrahim) Potonié and Kremp 1954

Type species. *G. granulatus* Ibrahim 1933.

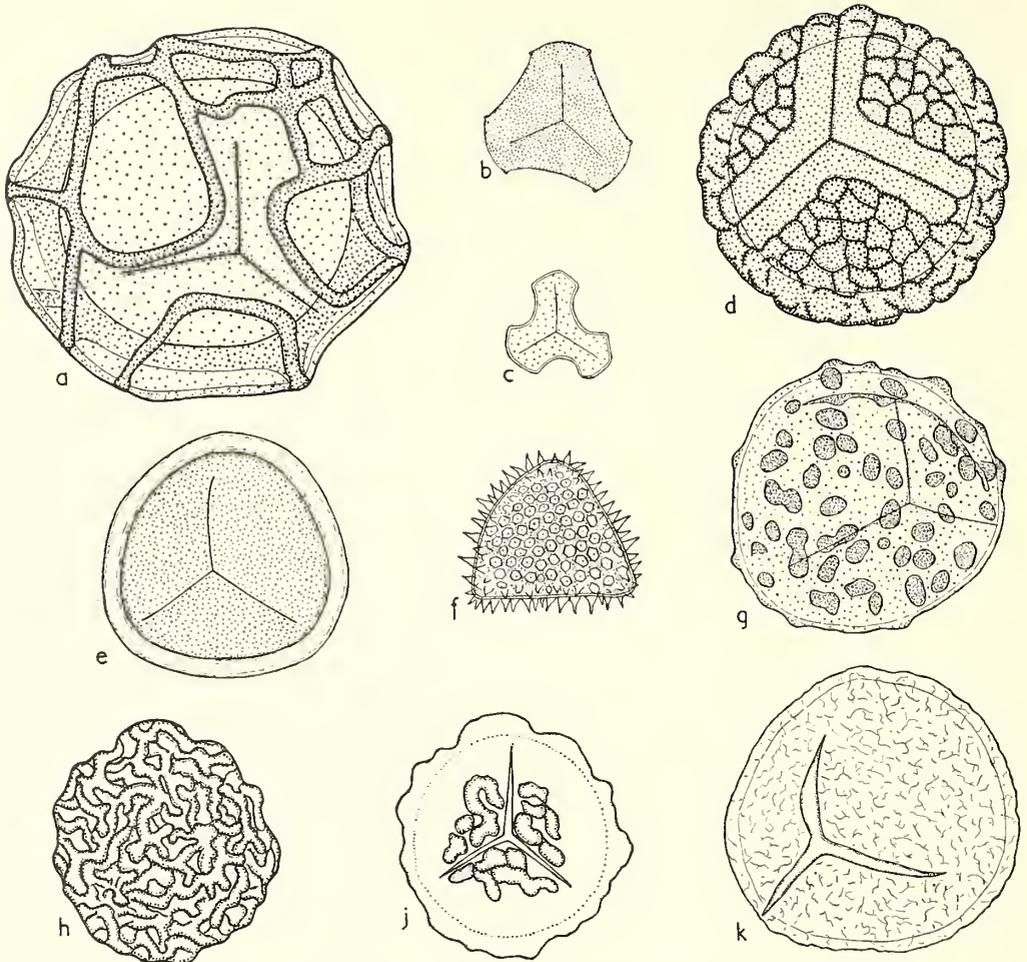
Affinity. Probably related to the Filices, and perhaps also to the Cycadofilicales (after Potonié and Kremp 1954, p. 126).

Granulatisporites planiusculus (Luber) comb. nov.

Plate 79, fig. 18

1955 *Filictriletes planiusculus* Luber, p. 60; pl. 3, fig. 71.

Description of specimens. Spores radial, trilete; amb convexly subtriangular. Laesurae distinct, straight, extending to equatorial margin; prominent, dark, elevated lips,



TEXT-FIG. 5. Camera-lucida drawings; all magnifications $\times 500$ unless otherwise specified. *a*, *Reticulatisporites variolatus* sp. nov.; proximal surface; preparation P166/3, 32.9 98.1 (L.1047). *b*, *Leiotriletes curiosus* sp. nov.; proximal surface; preparation P149A/1, 20.4 102.4 (L.951). *c*, *Waltzisporea sagittata* sp. nov.; proximal surface; preparation P180B/2, 42.1 94.5 (L.976). *d*, *Verrucosisporites eximius* sp. nov.; proximal surface; preparation P149/A40, 35.5 109.5 (L.992). *e*, *Stenozonotriletes perforatus* sp. nov.; proximal surface; preparation P147A/1, 48.6 96.7 (L.1078). *f*, *Anapiculatisporites serratus* sp. nov.; distal surface; preparation P149A/2, 24.3 98.9 (L.1003). *g*, *Verrucosisporites gobbettii* sp. nov.; proximal surface; preparation P148/2, 17.0 109.7 (L.988). *h*, *j*, *Convolutispora harlandii* sp. nov. ($\times 250$); distal and proximal surfaces respectively; preparation P148/12, 34.9 103.1 (L.1019). *k*, *Punctatisporites parvivermiculatus* sp. nov.; proximal surface; preparation P163/6, 36.9 105.1 (L.955).

individually $2-3 \mu$ wide. Exine $2.5-3 \mu$ thick; distinctive, finely areolate sculpture with fairly regular, negative microreticulum encompassing fine, irregular granules.

Dimensions (15 specimens). Equatorial diameter $51-71 \mu$ (mean 60μ).

Remarks. The species is included within *Granulatisporites* on the basis of its subtriangular

amb and areolate-granulate sculpture. *Filicitriletes* Lubert 1955 lacks type-species designation and in any case embraces the categories of several well-established genera (see Potonié 1958, p. 35).

Previous records. Lubert (1955) recorded this species from the Lower (C1) and Upper (C3) Carboniferous of Kazakhstan.

Genus CYCLOGRANISPORITES Potonié and Kremp 1954

Type species. *C. leopoldi* (Kremp) Potonié and Kremp 1954.

Affinity. W. and R. Remy (1957, p. 61; pl. 3, fig. 11 and pl. 4, figs. 1–3) refer to *Microreticulatisporites* the microspores of *Noeggerathiostrubus bohemicus* O. Feistmantel (Upper Westphalian B), which, however, seem more closely related to *Cyclogranisporites*. Potonié (1960, p. 34) has noted the resemblance between *Cyclogranisporites* and the spores recovered by W. and R. Remy (1957, pl. 3, figs. 1, 2) from *Acitheca* (al. *Pecopteris*) *longifolia* Brongniart.

Cyclogranisporites lasius (Waltz) comb. nov.

Plate 79, figs. 19, 20

1884 Type 524 of Reinsch, p. 52; pl. 32, fig. 211 and pl. 42, fig. 220.

1938 *Azonotriletes lasius* Waltz in Lubert and Waltz, p. 9; pl. 1, fig. 4 and pl. A, fig. 4.

1955 *Filicitriletes lasius* (Waltz) Lubert, p. 55; pl. 2, fig. 50.

Description of specimens. Spores radial, trilete; amb circular. Laesurae simple, straight, length approximately two-thirds spore radius. Exine densely and finely granulate; thickness 1–3 μ .

Dimensions (20 specimens). Equatorial diameter 50–88 μ (mean 68 μ).

Remarks. *Filicitriletes* Lubert 1955 was rejected correctly by Potonié (1958, p. 35) on the basis of its unsuitability as a generic unit, since it would embrace innumerable species already suitably placed in established genera. Potonié and Kremp (1955, p. 98) tentatively included *Azonotriletes lasius* Waltz within *Microreticulatisporites* (Knox) Potonié and Kremp. However, from the description given by Waltz (in Lubert and Waltz 1938), the circular outline coupled with comprehensive granulate sculpture clearly indicates a correct assignment to *Cyclogranisporites*.

Previous records. Lubert and Waltz (1938, 1941) and Lubert (1955) have reported this species from the Lower Carboniferous of European Russia and of western Kazakhstan.

Cyclogranisporites flexuosus sp. nov.

Plate 79, figs. 13–16

Diagnosis. Spores radial, trilete; amb circular or subcircular, occasionally broadly roundly subtriangular. Laesurae approximately two-thirds to three-quarters amb radius, often totally obscured by prominent, raised, sinuous lips; overall width of lips up to 6.5 μ (usually about 3 μ), often varying considerably in any one specimen. Exine 3–5.5 μ thick; distal hemisphere sculptured with densely distributed fine grana; proximal hemisphere frequently with conspicuous laevigate-infragranulate contact faces, otherwise very finely granulate overall.

Dimensions (65 specimens). Equatorial diameter 44–78 μ (mean 59 μ).

Holotype. Preparation P148/1, 40·8 94·9. L.980.

Locus typicus. Triungen (sample G1472), Spitsbergen; Lower Carboniferous.

Description. Holotype subcircular, diameter 62 μ ; laesurae just perceptible, approximately two-thirds spore radius, straight, with strong, dark, sinuous lips individually 3 μ wide. Exine 5 μ thick; apart from laevigate contact faces, exine finely but conspicuously granulate.

Comparison. This species differs from other described representatives of *Cyclogranisporites* in its distinctively lipped laesurae together with thick exine.

Subinfraturma VERRUCATI Dybová and Jachowicz 1957
GENUS VERRUCOSISPORITES (Ibrahim) Potonié and Kremp 1954

Type species. *V. verrucosus* Ibrahim 1932.

Discussion. This genus and *Convolutispora* Hoffmeister, Staplin, and Malloy are closely related morphographically. *Verrucosisporites* is characterized by closely spaced verrucae whilst the sculpture of *Convolutispora* consists typically of crowded, anastomosing rugulae. Some difficulty is experienced in the generic assignment of species, e.g. *Convolutispora clavata* (Ishchenko), which possess composite rugulate/verrucate sculpture; in such instances the decision must rest upon an assessment of the predominating type of sculpturing elements.

Affinity. W. and R. Remy (1957) have recovered spores conformable with *Verrucosisporites* from the Upper Carboniferous fern fructifications *Corynepteris silesiaca* R. and W. Remy, *Zygopteris* sp., and *Waldenburgia corynepteroides* Gothan.

Verrucosisporites gobbettii sp. nov.

Plate 80, figs. 1–4; text-fig. 5g

Diagnosis. Spores radial, trilete; amb circular to subcircular. Laesurae simple, straight, length two-thirds to three-quarters spore radius. Conspicuous sculpture of numerous, somewhat irregularly distributed verrucae, both discrete and coalescent, having circular to elliptical bases and broadly rounded apices; basal diameter of verrucae 4–12 μ (average 8 μ), height 2–3 μ . Surface between verrucae laevigate or very faintly infrapunctate; thickness of exine (excluding verrucae) 2 μ .

Dimensions (50 specimens). Equatorial diameter 55–89 μ (mean 72 μ).

Holotype. Preparation P148/42, 48·8 105·2. L.984.

Locus typicus. Triungen (sample G1472), Spitsbergen; Lower Carboniferous.

Description. Holotype circular, diameter 88 μ , amb undulating due to verrucae; laesurae distinct, equal three-quarters spore radius; one minor peripheral fold. Although comprehensive, the verrucate sculpture is, in most specimens, more pronounced on the distal hemisphere.

Comparison. *Verrucosisporites scrobiculatus* (Luber in Luber and Waltz 1938, p. 24;

pl. 5, fig. 70) Potonié and Kremp 1955 has more closely spaced, less broadly based projections, together with shorter laesurae. *V. baccatus* Staplin 1960 (p. 12; pl. 2, figs. 4, 10) has smaller sculpturing elements, shorter laesurae, and is additionally finely granulate.

The species is named for Dr. D. J. Gobbett of the Sedgwick Museum, Cambridge.

Verrucosisporites eximius sp. nov.

Plate 80, figs. 5–8; text-fig. 5d

Diagnosis. Spores radial, trilete, originally spherical; amb circular or subcircular. Laesurae distinct, straight, length three-quarters of, to almost equal to, amb radius; bordered by conspicuous, smooth lips extending 7–11 μ on either side. Exine strongly and comprehensively sculptured with large, flat-topped, closely packed, non-overlapping verrucae, which are separated by a continuous fine network of channels (up to 0.5 μ wide), i.e. constituting a negative microreticulum. Verrucae polygonal in surface view, 4–22 μ in longest diameter; normally smooth, but occasionally sparsely punctate (corroded specimens). Equatorial margin undulating. Exine very thick (5–8.5 μ , including sculpture).

Dimensions (30 specimens). Equatorial diameter 52–88 μ (mean 72 μ).

Holotype. Preparation P149A/36, 40.9 103.4. L.989.

Locus typicus. Triungen (sample G1470), Spitsbergen; Lower Carboniferous.

Description. Holotype 78 μ ; laesurae almost equal to spore radius; lips 8.5 μ wide, same height as polygonal verrucae; exine 7 μ in thickness. This species is characterized by its extremely thick, distinctively sculptured exine, together with pronounced development of lips.

Subinfraturma NODATI Dybová and Jachowicz 1957

Genus LOPHOTRILETES (Naumova) Potonié and Kremp 1954

Type species. *L. gibbosus* (Ibrahim) Potonié and Kremp 1954.

Affinity. Unknown.

Lophotriletes coniferus Hughes and Playford 1961

Plate 79, fig. 17

Dimensions (27 specimens). Equatorial diameter 69–105 μ (mean 89 μ).

Genus ANAPICULATISPORITES Potonié and Kremp 1954

Type species. *A. isselburgensis* Potonié and Kremp 1954.

Affinity. According to Potonié and Kremp (1955, p. 81) the genus may possibly be allied to the Filices.

Anapiculatisporites concinnus sp. nov.

Plate 80, figs. 9–12

Diagnosis. Spores radial, trilete; amb triangular with rounded apices and convex to

almost straight sides. Laesurae distinct, simple, more or less straight, length three-quarters to four-fifths spore radius. Proximal surface laevigate. Distal surface bearing scattered, small, uniform conii, $1-2\ \mu$ in length and $1-1.5\ \mu$ in basal diameter. Conii about $2-3\ \mu$ apart, fairly evenly distributed, but characteristically absent or markedly reduced in numbers at and around equatorial margin, particularly of interradial areas. Exine (excluding projections) about $1\ \mu$ thick; rarely folded. Equatorial margin mainly smooth with only a few projecting conii, and these generally in the vicinity of the triangular apices.

Dimensions (50 specimens). Equatorial diameter $23-44\ \mu$ (mean $32\ \mu$).

Holotype. Preparation P145C/1, 23.6 100.9. L.994.

Locus typicus. Triungen (sample G1466), Spitsbergen; Lower Carboniferous.

Description. Holotype $35\ \mu$; laesurae equal three-quarters spore radius; distal conii $1\ \mu$ broad at base, about $1.5\ \mu$ long, $2-4\ \mu$ apart, whole of proximal surface together with marginal interradial portions of distal surface entirely laevigate; twelve conii project from equator (four around each apex); margin otherwise smooth.

Comparison. This species is similar to *Granulatisporites? dumosus* Staplin 1960 (p. 16; pl. 3, figs. 15-17), which, however, differs principally in possessing spines that are 'largest along interradial portions of the equator' and 'reduced to granulations or absent at radial corners'; *G.? dumosus* should be assigned to *Anapiculatisporites*. In comparison with *Anapiculatisporites concinnus* sp. nov., *A. hispidus* Butterworth and Williams 1958 (p. 364; pl. 1, figs. 30, 31) has more prominent spinose ornamentation of different distribution, whilst *Azonotriletes cystostegius* Andrejeva (*in* Luber and Waltz 1941, p. 17; pl. 2, fig. 29) is sculptured with small, rounded tubercles. *Acanthotriletes microspinosus* (*non* Ibrahim) Ishchenko 1958 (pp. 46-47; pl. 3, fig. 39) may be conspecific, at least in part, with *Anapiculatisporites concinnus*.

EXPLANATION OF PLATE 80

All figures $\times 500$ unless otherwise specified; from unretouched negatives.

Figs. 1-4. *Verrucosisorites gobbettii* sp. nov. 1, Holotype; distal surface. 2, Sub-polar view; preparation P226/2, 47.6 102.2 (L.985). 3, Proximal surface; preparation P181/2, 41.2 104.9 (L. 986). 4, Distal surface; preparation P176B/1, 27.7 112.9 (L.987).

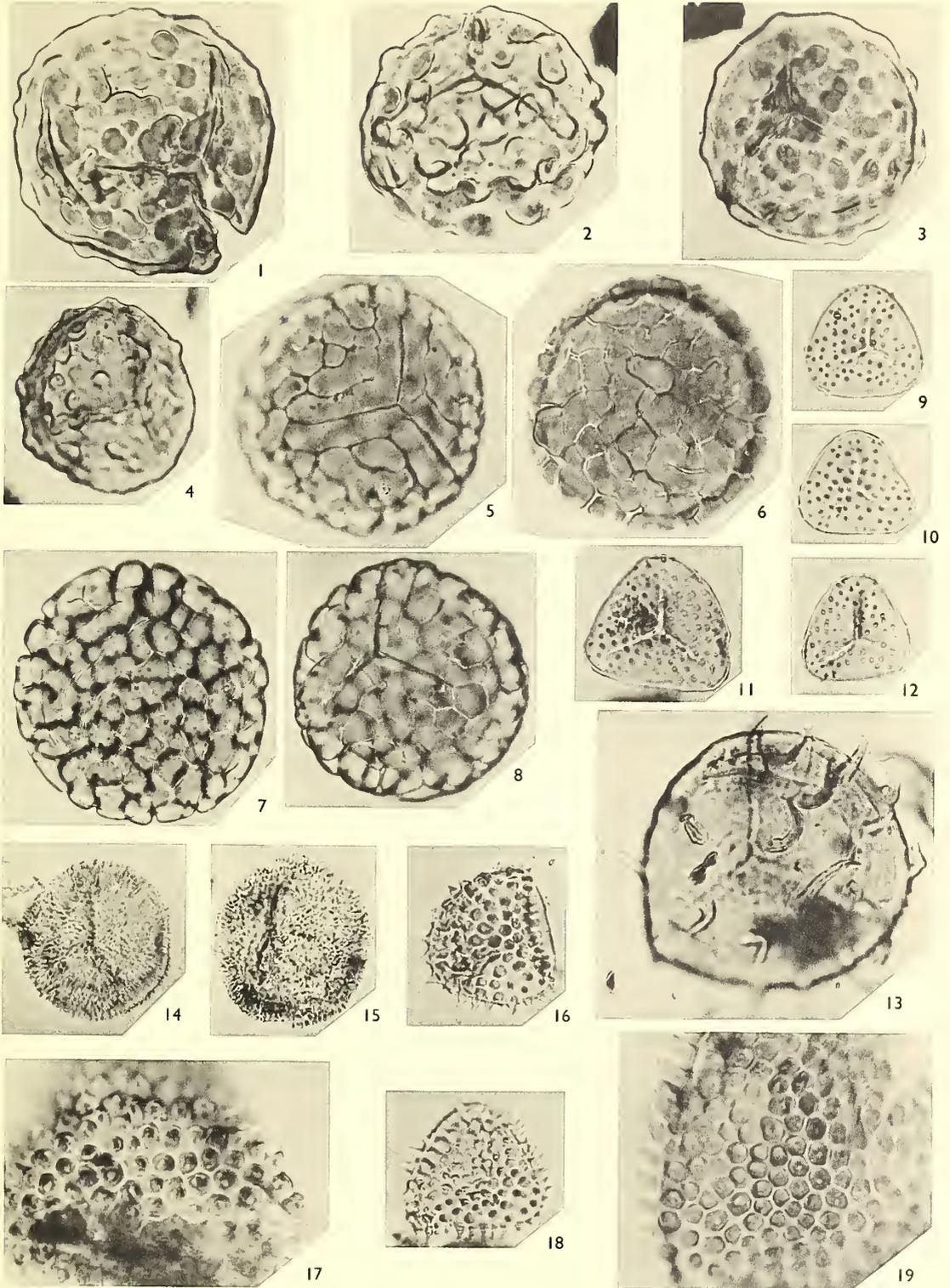
Figs. 5-8. *V. eximius* sp. nov. 5, 6, Holotype; proximal and distal surfaces respectively. 7, Sub-polar view; preparation P149A/11, 40.6 103.8 (L.990). 8, Proximal surface; preparation P149A/2, 46.8 106.3 (L.991).

Figs. 9-12. *Anapiculatisporites concinnus* sp. nov. 9, Holotype; distal surface. 10, Proximal surface; preparation P145B/37, 40.2 103.0 (L.995). 11, Proximal surface; preparation P164/3, 31.7 97.4 (L.997). 12, Distal surface; preparation P145B/2, 50.4 95.0 (L.996).

Fig. 13. *Hystricosporites* sp. Distal surface; preparation P164/1, 22.5 110.0 (L.1009).

Figs. 14, 15. *Acanthotriletes multisetus* (Luber) Potonić and Kremp 1955. 14, Proximal surface; preparation P175/2, 20.3 110.9 (L.1005). 15, Distal surface; preparation P163/1, 26.8 113.2 (L.1006).

Figs. 16-19. *Anapiculatisporites serratus* sp. nov. 16, Holotype; distal surface. 17, Closely spaced distal spinae having characteristic hexagonal bases, $\times 1,000$; preparation P145A/1, 44.8 108.4 (L.1000). 18, Distal surface; preparation P149A/2, 45.7 107.1 (L.1001). 19, Distal spinae, $\times 1,000$; preparation P145C/2, 40.2 113.3 (L.1002).



PLAYFORD, Lower Carboniferous microspores

Anapiculatisporites serratus sp. nov.

Plate 80, figs. 16–19; text-fig. 5f

1938 *Zonotriletes curiosus* (partim) Waltz in Luber and Waltz, pl. A, fig. 13 (non pl. 4, fig. 49).

Diagnosis. Spores radial, trilete; amb subtriangular with straight to slightly convex sides and rounded apices. Laesurae indistinct to perceptible, simple, straight, almost reaching to equatorial margin. Proximal surface laevigate. Distal surface strongly and uniformly sculptured with closely packed, broadly based, sharply tapering spines, which are also evident at the equator (projecting as a conspicuous pseudo-flange). Spines have characteristically hexagonal bases (diameter 2–4 μ) and range in length from 2.5 to 6 μ ; somewhat diminished in size and density around the triangular apices. Exine (excluding spinae) 1–1.5 μ thick.

Dimensions (15 specimens). Equatorial diameter (excluding spinae) 38–61 μ (mean 49 μ).

Holotype. Preparation P149A/3, 27.0 109.2. L.999.

Locus typicus. Triungen (sample G1470), Spitsbergen; Lower Carboniferous.

Description. Holotype 42 μ , convexly subtriangular. The species is characterized by its sculpture of strongly developed spines, which have distinctive hexagonal basal outlines (as seen in surface view) together with exclusively distal and equatorial distribution.

Remarks. The second spore figured in Luber and Waltz 1938 (pl. A, fig. 13) as *Zonotriletes curiosus* Waltz is almost certainly conspecific with *Anapiculatisporites serratus* sp. nov.; it undoubtedly represents a different species from the spore initially illustrated as *Zonotriletes curiosus* Waltz (in Luber and Waltz 1938, pl. 4, fig. 49) which, as reproduced in Luber and Waltz 1941 (pl. 5, fig. 79), has been utilized subsequently (Ishchenko 1956, 1958) as the reference type for *Z. curiosus*.

Comparison. *Procoronaspora williamsii* Staplin 1960 (p. 17; pl. 3, fig. 22) is smaller and has shorter laesurae; its spines are shorter at the distal pole, and do not possess the distinctive hexagonal bases of *Anapiculatisporites serratus*.

Genus APICULATISPORIS Potonié and Kremp 1956

Type species. *A. aculeatus* (Ibrahim) Potonié 1956.

Affinity. Unknown.

Apiculatisporis macrurus (Luber) Potonié and Kremp 1955

Plate 81, fig. 3

1938 *Azonotriletes macrurus* Luber in Luber and Waltz, p. 30; pl. 7, fig. 94.

1952 *Acanthotriletes macrurus* (Luber) Ishchenko, p. 28; pl. 6, fig. 65.

1955 *Apiculatisporites macrurus* (Luber) Potonié and Kremp, p. 77.

Description of specimens. Spores radial, trilete, originally spherical; amb circular to subcircular. Laesurae simple, length at least two-thirds spore radius; usually obscured by sculpture. Exine fairly thick, bearing prominent, somewhat variable, closely spaced

spines, which have more or less rounded apices, and are often fused at their bases; basal diameter of spines 3–6 μ , length 4.5–9 μ .

Dimensions (20 specimens). Equatorial diameter 50–65 μ (mean 59 μ).

Previous records. Reported previously from Russia only, as follows: from the Middle and Upper Carboniferous of the Donetz Basin (Luber and Waltz 1938, 1941; Ishchenko 1952); from Viséan–Namurian of the western extension of the Donetz Basin (Ishchenko 1956); and from Viséan–Bashkirian of the Dnieper–Donetz Basin (Ishchenko 1958).

Genus ACANTHOTRILETES (Naumova) Potonié and Kremp 1954

Type species. *A. ciliatus* (Knox) Potonié and Kremp 1954.

Affinity. W. and R. Remy (1957, p. 59; pl. 2, figs. 7–9) have recovered spores similar to *Acanthotriletes* from the Upper Carboniferous fern fructification *Sphyropteris* cf. *boehnischi* Stur.

Acanthotriletes multisetus (Luber) Potonié and Kremp 1955

Plate 80, figs. 14, 15

1938 *Azonotriletes multisetus* Luber in Luber and Waltz, p. 23; pl. 5, fig. 61.

1955 *Filicitriletes multisetus* (Luber) Luber, pp. 55–56; pl. 3, fig. 52.

1955 *Acanthotriletes multisetosus* (Luber) Potonié and Kremp, p. 84.

1957 *Acanthotriletes multisetus* (Luber) Kedo, p. 1167.

Description of specimens. Spores radial, trilete; equatorial outline circular to elliptical. Laesurae simple, obscure to perceptible, length approximately two-thirds spore radius. Exine thin (1–3 μ), commonly folded and torn; fine, dense sculpture of closely packed, minute projections which range from spinae to baculae and are evident at equator. Projections up to 1 μ in basal diameter and 2 μ in length, but usually considerably smaller.

Dimensions (30 specimens). Equatorial diameter 42–78 μ (mean 60 μ).

Comparison. *Cyclogranisporites amplus* McGregor 1960 (p. 26; pl. 11, fig. 8) is similar in general appearance, but larger and distinctly granulate.

Previous records. *Acanthotriletes multisetus* has been reported previously by Luber and Waltz (1938, 1941) and Luber (1955) from the Viséan of the Karaganda Basin; by Kedo (1957, 1958, 1959) from the Upper Tournaisian of White Russia; and recently by Love (1960) from the Lower Oil-shale Group (Viséan) of Scotland.

Acanthotriletes mirus Ishchenko 1956

Plate 81, figs. 1, 2

Description of specimens. Spores radial, trilete; amb circular to roundly subtriangular. Laesurae distinct, straight or slightly sinuous, length approximately equal to amb radius. Exine covered with numerous, evenly distributed, uniformly tapering spines, 4–8 μ high, 1.5–4 μ in basal diameter, and usually about 6 μ apart; remainder of surface somewhat rough in appearance (infrapunctate or infragranulate). Exine thickness (excluding spines) 2–3 μ .

Dimensions (12 specimens). Equatorial diameter 50–62 μ (mean 55 μ).

Previous records. Ishchenko (1956, stratigraphical range table 1) found this species to be restricted to Tournaisian strata of the Donetz Basin (western extension).

Genus HYSTRICOSPORITES McGregor 1960

Type species. *H. delectabilis* McGregor 1960.

Discussion. This genus was instituted by McGregor (1960, p. 31) to incorporate sub-circular spores possessing a proximal and distal sculpture of more or less uniformly tapering appendages bearing distinctive anchor-like apical terminations. As implied by McGregor, such spores would have undoubtedly found inclusion within the broad connotation of Naumova's (1953, p. 51) subgroup *Archaeotriletes*, which has since, however, been validated, emended, and thereby restricted by Potonié (1958, p. 30). McGregor discusses adequately the morphographical differences between *Archaeotriletes* (Naumova) Potonié 1958, *Nikitinisorites* Chaloner 1959, *Ancyrospora* Richardson 1960, and *Hystricosporites*, and they appear to represent clearly delineated generic units.

Affinity. Naumova (1953, pp. 8, 51) noted the resemblance between Devonian spores of her subgroup *Archaeotriletes*, and those of the present-day water fern *Azolla*. However, this similarity is probably only superficial (see McGregor 1960, p. 32).

Hystricosporites sp.

Plate 80, fig. 13

Description of specimens. Spores radial, trilete; amb broadly roundly subtriangular to subcircular. Laesurae distinct, length about three-quarters spore radius; accompanied by narrow, slightly elevated and convoluted, lips. Distal surface and equatorial region of proximal surface bear long, uniformly tapering processes, which have grapnel-like tips; length of processes 12–21 μ , basal diameter 4–6 μ . Exine 5–7 μ in thickness; micro-regularulate on proximal hemisphere, laevigate distally.

Dimensions (3 specimens). Equatorial diameter (excluding appendages) 88–119 μ .

Comparison. *Azonotriletes ancistrophorus* Luber (*in* Luber and Waltz 1941, p. 11; pl. 1, fig. 7; Luber 1955, p. 70; pl. 9, fig. 178), from the Upper Devonian and Lower Carboniferous of the U.S.S.R., is somewhat smaller (50–80 μ) and appears to lack a triradiate mark.

Remarks. The three spores described above, although insufficient to warrant the erection of a new species, represent an interesting new Lower Carboniferous occurrence of this distinctively sculptured group of spores, whose predominantly Devonian distribution is evident from Table 1 of McGregor (1960, p. 41). The only previous record from the Lower Carboniferous appears to be that of *Azonotriletes ancistrophorus* Luber, which occurs sparsely in Tournaisian strata of western Kazakhstan (Luber 1955).

Infraturma MURORNATI Potonié and Kremp 1954

Genus CONVOLUTISPORA Hoffmeister, Staplin, and Malloy 1955

Type species. *C. floridula* Hoffmeister, Staplin, and Malloy 1955.

Affinity. Unknown.

Convolutispora tuberculata (Waltz) Hoffmeister, Staplin, and Malloy 1955

Plate 81, figs. 4, 5

- 1938 *Azonotriletes tuberculatus* Waltz in Lubert and Waltz, p. 12; pl. 1, fig. 12, pl. 5, fig. 68, and pl. A, fig. 6.
 1955 *Verrucosiporites tuberculatus* (Waltz) Potonié and Kremp, p. 66.
 1955 *Filicitriletes tuberculatus* (Waltz) Lubert, p. 54; pl. 2, figs. 45, 46.
 1955 *Convolutispora tuberculata* (Waltz) Hoffmeister, Staplin, and Malloy, p. 384.
 1956 *Lophotriletes tuberculatus* (Waltz) Ishchenko, p. 40; pl. 6, figs. 75, 76.

Description of specimens. Spores radial, trilete, originally spherical; amb circular to subcircular. Laesurae simple, straight, length one-third to two-thirds spore radius, usually obscured by sculpture. Exine relatively thick, uniformly sculptured with low, more or less rounded, closely packed, anastomosing ridges or irregular rugulae-verrucae; lumina relatively insignificant, very irregular; muri roughly 1.5–4.5 μ high, 2–5 μ broad, highly variable. Equatorial margin undulating.

Dimensions (50 specimens). Equatorial diameter 40–82 μ (mean 60 μ). Previous authors have recorded the following as equatorial diameter of this species: Waltz (in Lubert and Waltz 1938), 50–90 μ ; Lubert (1955), 60 μ ; Ishchenko (1956, 1958), 45–50 μ .

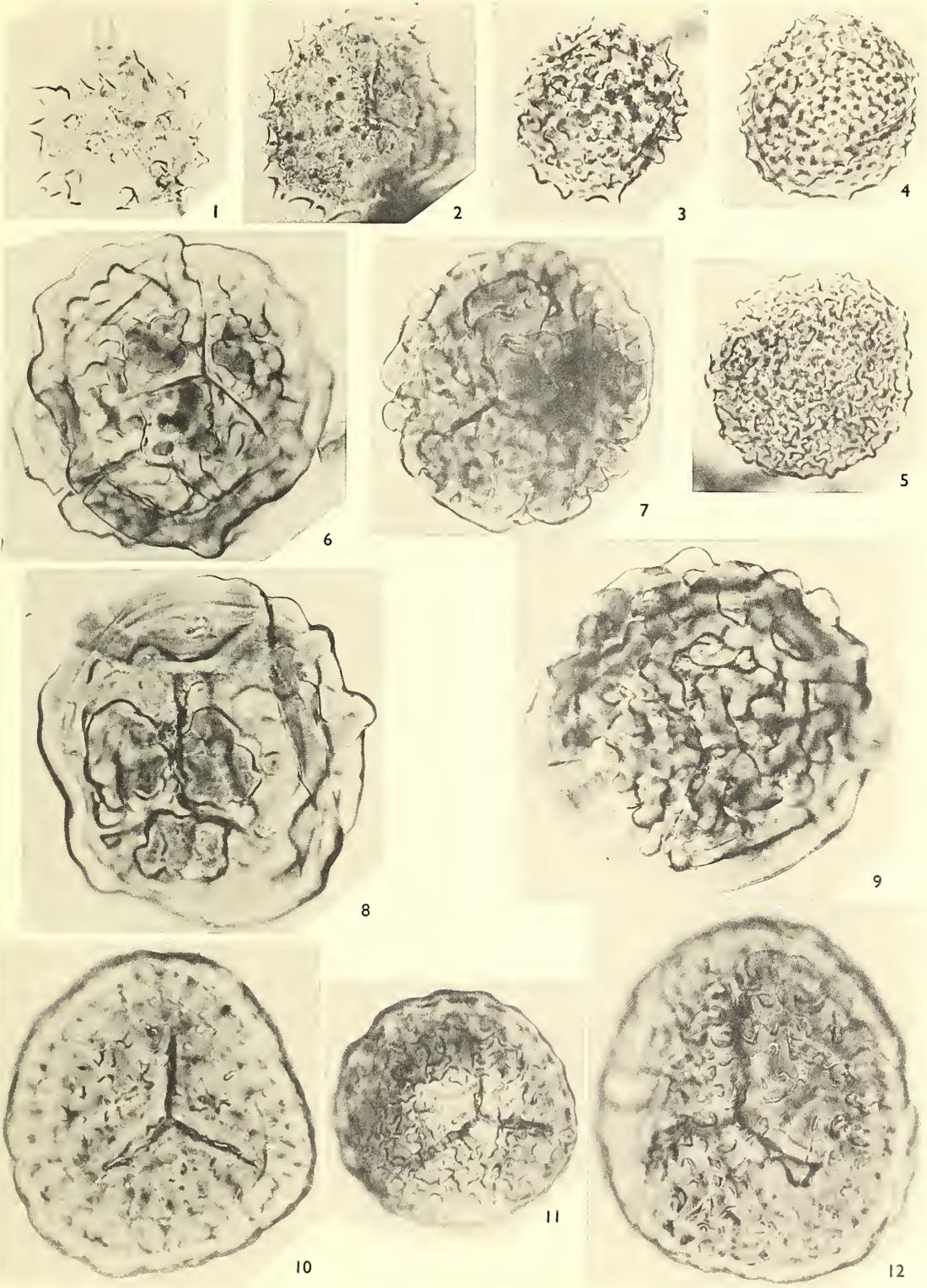
Comparison. The considerable variation, in both dimensions and sculpture, exhibited by this species was noted by Waltz (in Lubert and Waltz 1938) and although not precisely documented, is evident from her illustrations of *Azonotriletes tuberculatus*, and also from the specimens observed by the present writer. Two species described from North American strata of Mississippian age, *Convolutispora tessellata* Hoffmeister, Staplin, and Malloy 1955 (p. 385; pl. 38, fig. 9) and *C. punctatimura* Staplin 1960 (p. 12; pl. 2, figs. 12, 20, 21) appear to fall within this range of variation and are therefore probably synonymous with *C. tuberculata*.

Previous records. *Convolutispora tuberculata* has been reported by Lubert and Waltz (1938, 1941) from the Lower Carboniferous of the Moscow, Kizel, and Karaganda Basins, and the Voronezh region; by Lubert (1955) from the Lower Carboniferous of western Kazakhstan; and by Ishchenko (1956, 1958) from Upper Devonian–Namurian rocks of the Dnieper–Donetz Basin. Thus the Spitsbergen specimens described above are the first of this species reported definitely outside Russia.

EXPLANATION OF PLATE 81

All figures $\times 500$, and from unretouched negatives.

- Figs. 1, 2. *Acanthotriletes mirus* Ishchenko 1956. 1, Distal surface; preparation P226/4, 26.8 112.6 (L.1007). 2, Proximal surface; preparation P148/1, 46.1 101.5 (L.1008).
 Fig. 3. *Apiculatisporis macrurus* (Lubert) Potonié and Kremp 1955. Distal surface; preparation P163/1, 22.5 109.1 (L.1004).
 Figs. 4, 5. *Convolutispora tuberculata* (Waltz) Hoffmeister, Staplin, and Malloy 1955. 4, Sub-polar view; preparation P163/5, 18.4 110.7 (L.1011). 5, Distal surface; preparation P163/4, 34.3 103.2 (L.1012).
 Figs. 6–9. *C. harlandii* sp. nov. 6, Holotype; proximal surface. 7, Distal surface; preparation P148/15, 41.2 100.7 (L.1016). 8, Proximal surface; preparation P148/3, 38.7 100.5 (L.1017). 9, Distal surface; preparation P163/2, 21.2 113.8 (L.1018).
 Figs. 10–12. *C. crassa* sp. nov. 10, Proximal surface; preparation P148/1, 51.8 102.4 (L.1021). 11, Holotype; distal surface. 12, Distal surface; preparation P148/2, 44.8 92.9 (L.1022).



Convolutispora vermiformis Hughes and Playford 1961

Plate 82, figs. 5, 6

1957 *Convolutispora flexuosa* forma *minor* Hacquebard, p. 312; pl. 2, fig. 10.

Remarks. Spores recorded from Canada as *Convolutispora flexuosa* forma *minor* by Hacquebard (1957) and subsequently by McGregor (1960, p. 34; pl. 12, fig. 4) are considered identical to the Spitsbergen specimens which were described by Hughes and Playford (1961, p. 30; pl. 1, figs. 2-4) as *Convolutispora vermiformis*. As the spores almost definitely represent a distinct species, the latter name is retained in preference to the infraspecific taxon.

Dimensions (75 specimens). Equatorial diameter 47-86 μ (mean 66 μ). This corresponds closely to the size range of 47-81 μ noted by McGregor (1960) and includes the measurement (72 μ) stated by Hacquebard (1957).

Comparison. *Azonotriletes cancellothyris* Waltz (*in* Luber and Waltz 1941, p. 15; pl. 2, fig. 19) may be similar, but its description is too brief for precise comparison.

Previous records. Recorded previously from the Horton group (lowermost Mississippian) of Nova Scotia, Canada (Hacquebard 1957); from probable Upper Devonian of Melville Island, Canadian Arctic Archipelago (McGregor 1960); and from one sample (B685) of the Lower Carboniferous of Spitsbergen (Hughes and Playford 1961).

Convolutispora clavata (Ishchenko) Hughes and Playford 19611956 *Lophotriletes clavatus* Ishchenko, p. 43; pl. 6, fig. 82.1961 *Convolutispora clavata* (Ishchenko) Hughes and Playford, p. 31; pl. 1, figs. 7, 8.

Dimensions (30 specimens). Equatorial diameter 94-126 μ (mean 110 μ).

Previous records. Ishchenko (1956, 1958) described this species from Viséan sediments of the Donetz Basin (western extension) and of the Dnieper-Donetz Basin. Hughes and Playford (1961) reported its occurrence in the Spitsbergen Lower Carboniferous (sample S59a).

Convolutispora harlandii sp. nov.

Plate 81, figs. 6-9; text-figs. 5h, j

Diagnosis. Spores radial, trilete; amb circular to subcircular, undulating. Laesurae distinct, simple, straight, length approximately two-thirds to three-quarters amb radius. Exine very thick (8-12 μ , including muri). Distal hemisphere with pronounced, convolute sculpture comprising a complex, tangled network of strongly developed, smooth, ramifying, sinuous, rounded muri, which are closely packed and overlapping; width of muri 6-10.5 μ ; lumina where delimited, irregular, usually elongate, up to 22 μ in longest diameter. Contact faces marked by three, discrete, interrational clusters of several, large, flattened, often fused, muri or rugulae-verrucae, which usually have a highly irregular outline in polar view; proximal hemisphere otherwise laevigate.

Dimensions (66 specimens). Equatorial diameter 73-140 μ (mean 106 μ).

Holotype. Preparation P163/7, 58.3 100.2. L.1015.

Locus typicus. Birger Johnsonfjellet (sample G1089), Spitsbergen; Lower Carboniferous.

Description. Holotype circular, diameter $100\ \mu$; laesurae two-thirds amb radius; exine $12\ \mu$ thick; distal surface with crowded, anastomosing ridges $6.3\text{--}8.5\ \mu$ wide; sculpture of proximal hemisphere restricted to contact areas, consisting of three relatively small, subequal areas, individually roughly $21\ \mu \times 17\ \mu$, resulting from the fusion of two or three low, irregular rugulae-verrucae. In some specimens included within this species, the muri in the equatorial region form a more or less continuous band (up to $18\ \mu$ wide), which although simulating a cingulum is, in fact, part of the sculptural pattern of the distal hemisphere. This species is named for Mr. W. B. Harland, of the Sedgwick Museum, Cambridge.

Convolutispora crassa sp. nov.

Plate 81, figs. 10–12

Diagnosis. Spores radial, trilete; amb convexly subtriangular to circular, gently undulating. Laesurae simple, straight, length two-thirds to three-quarters spore radius. Exine very thick ($8.5\text{--}16\ \mu$, including muri); comprehensive sculpture of closely spaced, relatively low, smooth, sinuous, flat-topped, non-overlapping muri, which both anastomose and terminate freely, constituting an imperfect reticulum. Breadth of muri highly variable ($2\text{--}11\ \mu$), height $1.5\text{--}3.5\ \mu$. Lumina irregular, often elongate, up to $20\ \mu$ in longest diameter.

Dimensions (35 specimens). Equatorial diameter $61\text{--}115\ \mu$ (mean $85\ \mu$).

Holotype. Preparation P163/6, 37.3 99.3. L.1020.

Locus typicus. Birger Johnsonfjellet (sample G1089), Spitsbergen; Lower Carboniferous.

Description. Holotype $79\ \mu$, subcircular; laesurae approximately three-quarters amb radius; exine $10.5\ \mu$ thick; muri $2\text{--}10\ \mu$ wide, $2.5\ \mu$ high; lumina $3\text{--}16\ \mu$ in longest diameter. The species is characterized by its exceptionally thick exine, which exhibits a distinctive, imperfectly reticulate sculpture.

Comparison. *Convolutispora crassa* sp. nov. is probably conspecific with *Zonotriletes planotuberculatus* Waltz (in Lubert and Waltz 1941), but inadequate description (p. 21)

EXPLANATION OF PLATE 82

All figures $\times 500$, and from unretouched negatives.

Figs. 1–3. *Convolutispora labiata* sp. nov. 1, Holotype; proximal surface. 2, Proximal surface; preparation P158/7, 24.5 107.4 (L.1026). 3, Distal surface; preparation P158/10, 39.0 101.3 (L.1025).

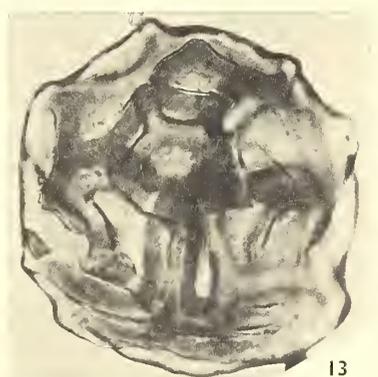
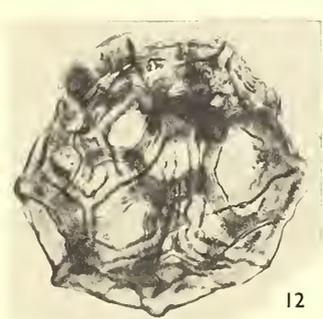
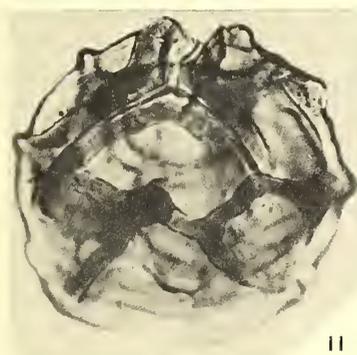
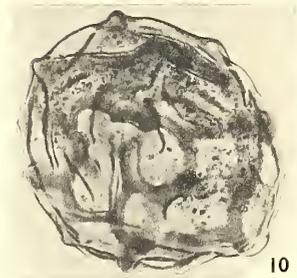
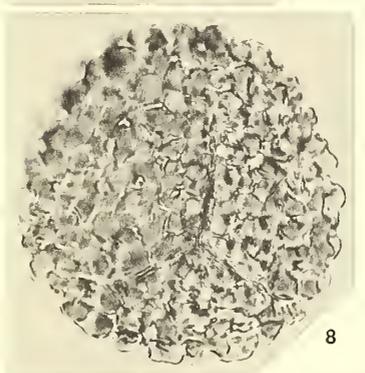
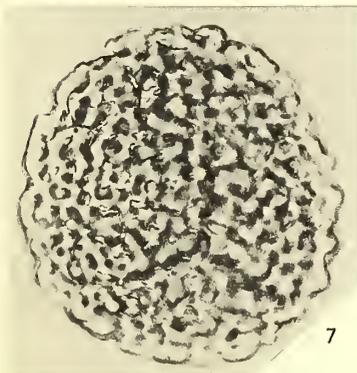
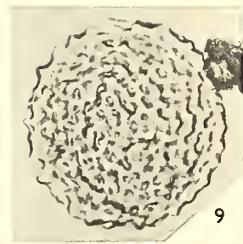
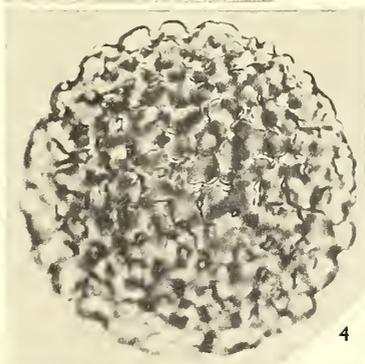
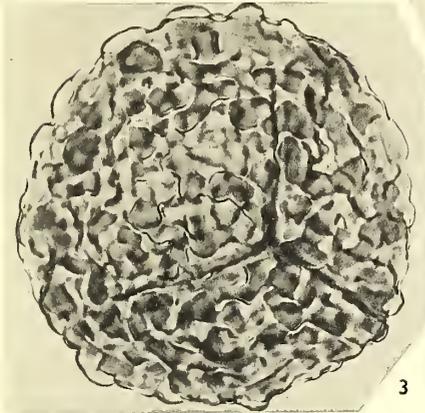
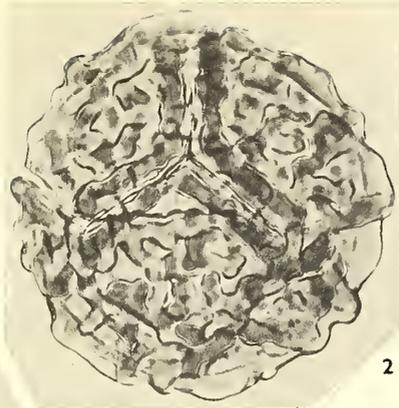
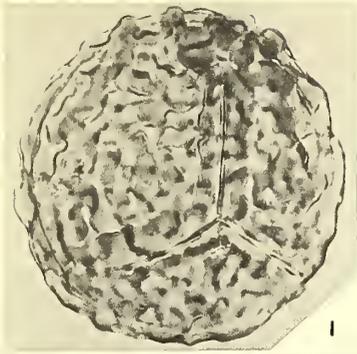
Figs. 4, 7, 8. *C. usitata* sp. nov. 4, Distal surface; preparation P149A/14, 39.9 102.6 (L.1029). 7, 8, Holotype; distal and proximal surfaces respectively.

Figs. 5, 6. *C. vermiformis* Hughes and Playford 1961. 5, Proximal surface; preparation P161B/3, 42.7 95.4 (L.1013). 6, Distal surface; preparation P163/4, 21.1 105.6 (L.1014).

Fig. 9. *Microreticulatisporites lunatus* Knox 1950. Distal surface; preparation P175/1, 32.4 92.9 (L.1031).

Fig. 10. *Reticulatisporites rudis* Staplin 1960. Proximal surface; preparation P145B/39, 38.5 103.7 (L.1036).

Figs. 11–13. *R. cancellatus* (Waltz) comb. nov. 11, Sub-polar view; preparation P163/8, 39.9 104.4 (L.1038). 12, Distal surface; preparation P139/3, 52.9 109.4 (L.1037). 13, Sub-polar view; preparation P163/4, 50.7 108.1 (L.1039).



and illustration (pl. 4, fig. 50) preclude an accurate comparison. Further, Waltz (loc. cit.) and subsequently Ishchenko, 1956 (who transferred the species to *Hymenozonotriletes* Naumova) did not mention a variation to subtriangular shape, and they apparently considered the species to be a zonate form, rather than one possessing an exceptionally thick spore wall. It should be added, however, that few Russian workers express adequately the distinction between a cingulum or zona, and a thick exine as seen in polar view (cf. discussion herein of *Stenozonotriletes*).

Previous records. The closely similar, if not identical, Russian species *Zonotriletes planotuberculatus* Waltz 1941 has been recorded by Luber and Waltz (1941) from the Lower Carboniferous of the Kizel region, and by Ishchenko (1956) who found it to be restricted to Tournaisian–Lower Viséan strata of the western Donetz Basin.

Convolutispora labiata sp. nov.

Plate 82, figs. 1–3

Diagnosis. Spores radial, trilete; amb circular to subcircular. Laesurae distinct, straight, length four-fifths of, to almost equal to, amb radius. Strongly developed, comprehensive sculpture of fairly closely spaced, rounded, smooth, sinuous muri, which both bifurcate and terminate freely. Width of muri irregular (range 3–12 μ), height 2–5 μ ; lumina rarely delimited. Prominent, more or less continuous lips result from radial alignment, and at least partial fusion, of muri in immediate vicinity of laesurae. Exine (including muri) 4.5–8 μ thick. Equatorial margin undulating.

Dimensions (20 specimens). Equatorial diameter 82–114 μ (mean 99 μ).

Holotype. Preparation P158/8, 36.0 103.3. L.1024.

Locus typicus. Birger Johnsonfjellet (sample G1092), Spitsbergen; Lower Carboniferous.

Description. Holotype 90 μ ; laesurae almost equal to spore radius, accompanied by mural lips (about 4 μ broad); convolute sculpture more strongly developed on distal surface but ridges remain non-overlapping; exine up to 6 μ thick.

Comparison. Although similar with respect to size and lip development, *Azonotriletes alveolatus* Waltz (in Luber and Waltz 1941, pp. 15–16; pl. 2, fig. 21) differs from *Convolutispora labiata* sp. nov. in having relatively narrow, uniform muri which coalesce to form a distinctly reticulate sculpture.

Convolutispora usitata sp. nov.

Plate 82, figs. 4, 7, 8

Diagnosis. Spores radial, trilete; originally spherical; amb circular or subcircular. Laesurae perceptible, simple, straight, length almost equal to spore radius. Exine 6–8 μ thick, including dense, comprehensive sculpture of broad, rounded, crowded, frequently anastomosing muri, 4–10 μ wide and 2–4 μ high; lumina highly irregular in shape and size, greatly subordinate to enclosing muri. Equatorial margin undulating to incised.

Dimensions (20 specimens). Equatorial diameter 84–112 μ (mean 100 μ).

Holotype. Preparation P149A/30, 36.7 102.5. L.1028.

Locus typicus. Triungen (sample G1470), Spitsbergen; Lower Carboniferous.

Description. Holotype diameter $91\ \mu$; laesurae $41\ \mu$ in length, discernible despite heavy exinal sculpture; exine $6.5\ \mu$ thick (including muri). The species possesses the typically 'convoluted' sculpture of the genus *Convolutispora*; its diagnostic features are large size, long laesurae, and strongly developed, ramifying muri.

Comparison. In comparison with *Convolutispora usitata* sp. nov., *C. cf. mellita* Hoffmeister, Staplin, and Malloy (Butterworth and Williams 1958, p. 372; pl. 2, figs. 20, 21) has shorter laesurae together with higher muri, which often fuse to form locally 'a thick, platy type of ornamentation'; *C. finis* Love 1960 (p. 115; pl. 1, fig. 7 and text-fig. 5) has much finer sculpture; and *C. clavata* (Ishchenko) Hughes and Playford 1961 (p. 31; pl. 1, figs. 7, 8) possesses shorter laesurae and less extensive, more verrucate sculpturing elements.

Genus MICRORETICULATISPORITES (Knox) Potonié and Kremp 1954

Type species. *M. lacunosus* (Ibrahim) Knox 1950.

Affinity. Unknown.

Microreticulatisporites lunatus Knox 1950

Plate 82, fig. 9

1948 Type 36K of Knox, fig. 41.

1950 *Microreticulatisporites lunatus* Knox, p. 320.

Description of specimens. Spores radial, trilete; amb circular, sinuous. Laesurae simple, straight, not always evident, length approximately equal to amb radius. Regular microreticulate sculpture of muri $1-2\ \mu$ wide and up to $1.5\ \mu$ high, enclosing rounded to polygonal lumina $2-4\ \mu$ in diameter. Exine (including muri) $2-3.5\ \mu$ thick.

Dimensions (36 specimens). Equatorial diameter $37-56\ \mu$ (mean $45\ \mu$). The mean corresponds with the single measurement given by Knox (1950, p. 320).

Previous records. From the Lower Carboniferous of Scotland (Knox 1948; Butterworth and Williams 1958).

Genus DICTYOTRILETES (Naumova) Potonié and Kremp 1954

Type species. *D. bireticulatus* (Ibrahim) Potonié and Kremp 1954.

Affinity. Unknown.

Dictyotriletes caperatus sp. nov.

Plate 83, figs. 3-5

Diagnosis. Spores radial, trilete; equatorial outline circular to subcircular. Laesurae distinct, straight, length three-fifths to two-thirds spore radius; often flanked by slightly raised, smooth, narrow lips about $2.5\ \mu$ wide, decreasing in width equatorially. Exine sculptured with very fine, narrow, sinuous muri, which are very low, thread-like, anastomosing or freely terminating to comprise an open-meshed reticulum imperfectum, inconspicuous in relation to overall proportions; lumina where delimited are of highly variable, usually irregular shape, ranging from 3 to $19\ \mu$ in diameter. Exine $3.5-6\ \mu$ thick; sometimes additionally infrapunctate or infragranulate.

Dimensions (40 specimens). Equatorial diameter 92–173 μ (mean 131 μ).

Holotype. Preparation P148/10, 37.9 104.1. L.1032.

Locus typicus. Triungen (sample G1472), Spitsbergen; Lower Carboniferous.

Description. Holotype 156 μ , amb elliptical due to compression; laesurae straight, approximately three-fifths spore radius, with smooth, narrow (3 μ) lips; exine finely, imperfectly reticulate, also infrapunctate; exine 4.5 μ thick, not folded. Some specimens show one or two major folds. Sculptural details are apparent only under oil.

Genus RETICULATISPORITES (Ibrahim) Potonié and Kremp 1954

Type species. *R. reticulatus* Ibrahim 1933.

Affinity. Spores conformable with *Reticulatisporites* have been recovered from *Sclerocelyplus oviformis* Mamay (1954, p. 82; pl. 21, figs. 7, 9). However, the systematic position of this Upper Carboniferous fructification is uncertain.

Reticulatisporites ruidis Staplin 1960

Plate 82, fig. 10

Description of specimens. Spores radial, trilete, originally spherical; amb circular to subcircular. Laesurae distinct, simple, length approximately two-thirds spore radius. Conspicuous reticulate sculpture of smooth, rounded muri (2 μ broad at base, 2 μ high) enclosing polygonal lumina (7–14 μ in longest diameter). Exine (excluding muri) very finely granulate, 1.5–2 μ thick.

Dimensions (20 specimens). Equatorial diameter 59–73 μ (mean 66 μ).

Previous records. From the Golata formation (Upper Mississippian) of Alberta, Canada (Staplin 1960).

Reticulatisporites cancellatus (Waltz) comb. nov.

Plate 82, figs. 11–13; Plate 83, figs. 1, 2

1884 ? Type 555 of Reinsch, p. 54; pl. 38, fig. 271.

1933 ? Type F6 of Raistrick, p. 5.

1938 *Azonotriletes cancellatus* Waltz in Luber and Waltz, p. 11; pl. 1, fig. 8 and pl. 5, fig. 73.

1955 *Sphenophyllotriletes cancellatus* (Waltz) Luber, pp. 41–42; pl. 4, figs. 78a, b, 79.

1955 *Dictyotriletes cancellatus* (Waltz) Potonié and Kremp, p. 108.

1956 *Dictyotriletes cancellatus* (Waltz) Ishchenko, p. 45; pl. 7, figs. 88, 89.

1957 *Dictyotriletes cancellatus* (Waltz) Naumova; Kedo, p. 1166.

1957 *Reticulatisporites varioreticulatus* Hacquebard and Barss, p. 17; pl. 2, figs. 15, 16.

In discussing their new species *Reticulatisporites varioreticulatus*, Hacquebard and Barss (1957, p. 17) state justifiably that 'it could be conspecific with *Azonotriletes cancellatus* Waltz 1938, but the brevity of the description precludes a definite assignment'. However, further description and illustration of this species given subsequent to Luber and Waltz (1938), by Luber (1955) and by Ishchenko (1956, 1958), clarifies and somewhat broadens the concept of *Azonotriletes cancellatus*, and as such includes *Reticulatisporites varioreticulatus*.

Potonié and Kremp (1955, p. 108) listed *A. cancellatus* as a species of *Dictyotriletes* (Naumova) Potonié and Kremp. However, the prominent reticulate sculpture which is

often evident at the equator in the form of bastion-like projections (cf. Luber 1955, pl. 4, fig. 78; Ishchenko 1956, pl. 7, fig. 88) indicates more appropriate inclusion within *Reticulatisporites*.

Amplification of diagnosis. Spores radial, trilete; amb circular to subcircular. Laesurae usually distinct, length approximately two-thirds to three-quarters amb radius; bounded by flat, slightly elevated lips (3–6 μ wide) having more or less straight outer margins. Prominent, comprehensive, fairly coarse, reticulate sculpture of smooth, rounded muri enclosing large, polygonal lumina. Muri 2.5–6.5 μ wide, up to 10 μ high, frequently expanded at their junctions, usually clearly evident in optical section as conspicuous projections at equator. Width of lumina 6–40 μ , typically variable on individual specimens. Thickness of exine (excluding muri) 2–6 μ .

Dimensions (100 specimens). Equatorial diameter 70–132 μ (mean 99 μ). This corresponds closely to the size range of 75–130 μ stated by Ishchenko (1956, 1958) for *Dictyotriletes cancellatus* (Waltz).

Holotype. Plate 1, fig. 8 of Luber and Waltz 1938 (designated by Luber 1955).

Locus typicus. Kizel region, Verkhani-Goubakhine mine, Kalinine shaft, bed 7 (after Luber and Waltz 1938; Luber 1955).

Previous records. From the Lower Carboniferous of Russia (Luber and Waltz 1938, 1941, Luber 1955, Ishchenko 1956, 1958, and Kedo 1957, 1958), and of Canada (Hacquebard and Barsz 1957). Ishchenko (1958, stratigraphical range table 3) indicates that the species ranges from Upper Devonian to Viséan.

Reticulatisporites planus Hughes and Playford 1961

Plate 83, figs. 6, 7

Dimensions (40 specimens). Equatorial diameter 63–104 μ (mean 81 μ). Based on an additional twenty-six specimens, this exceeds by 18 μ the upper limit of the size range stated by Hughes and Playford (1961, p. 31).

Reticulatisporites variolatus sp. nov.

Plate 84, figs. 5–8; text-fig. 5a

Diagnosis. Spores radial, trilete; originally spherical; amb circular to subcircular. Laesurae distinct to perceptible, straight, length one-half to three-quarters spore radius; simple or accompanied by narrow lip development. Comprehensively sculptured with smooth, strongly developed muri of more or less uniform width (5–7 μ) enclosing polygonal to irregularly rounded lumina ranging from 6 to 47 μ in longest diameter. Muri

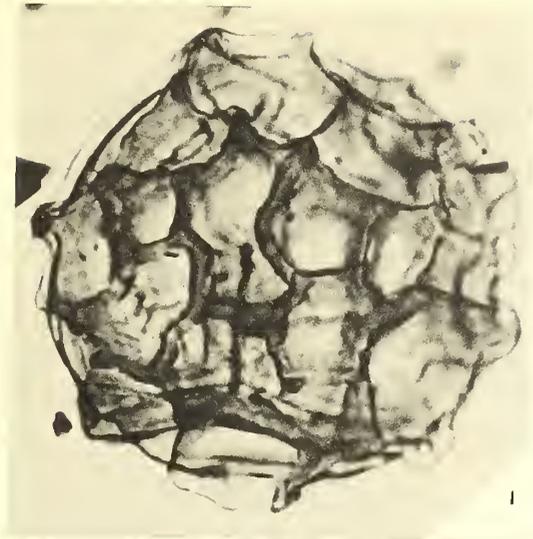
EXPLANATION OF PLATE 83

All figures $\times 500$, and from unretouched negatives.

Figs. 1, 2. *Reticulatisporites cancellatus* (Waltz) comb. nov. 1, Distal surface; preparation P152/3, 44.4 111.8 (L.1041). 2, Proximal surface; preparation P148/3, 29.2 99.0 (L.1040).

Figs. 3–5. *Dictyotriletes caperatus* sp. nov. 3, Holotype; proximal surface. 4, Proximal surface; preparation P163/4, 49.7 93.9 (L.1033). 5, Sub-polar view; preparation P148/20, 34.7 106.1 (L.1034).

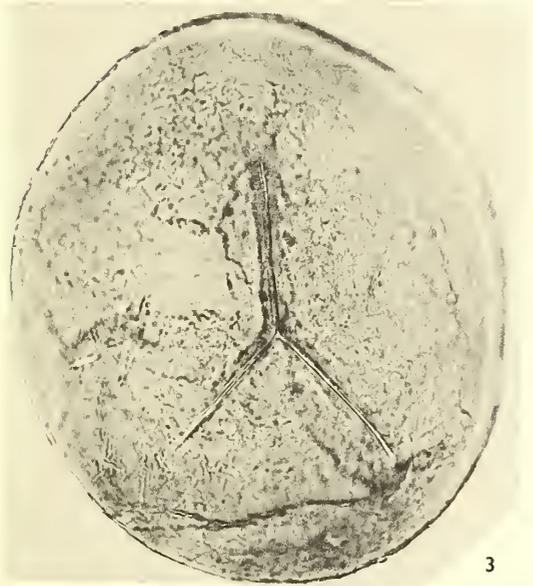
Figs. 6, 7. *Reticulatisporites planus* Hughes and Playford 1961. 6, Proximal surface; preparation P226/3, 39.5 101.0 (L.1043). 7, Distal surface; preparation P148/2, 35.1 94.8 (L.1042).



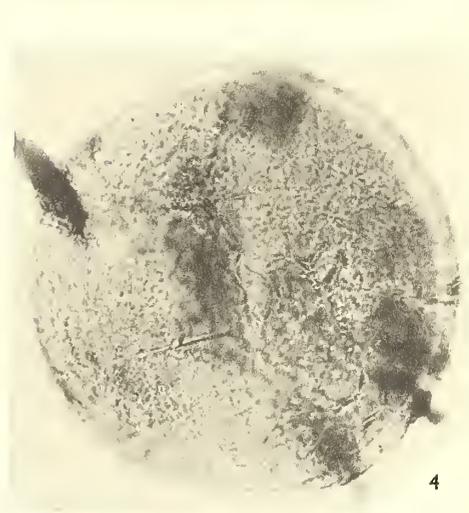
1



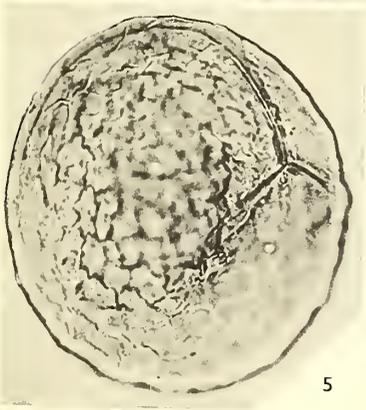
2



3



4



5



6



7

4–8 μ high, with characteristic clavate (mushroom-shaped) profile. Exine very thick (9–12 μ , exclusive of muri); laevigate to finely punctate.

Dimensions (86 specimens). Equatorial diameter 77–124 μ (mean 98 μ).

Holotype. Preparation P165/3, 26.6 109.3. L.1044.

Locus typicus. Blårevbreen (sample Q55), Spitsbergen; Lower Carboniferous.

Description. Holotype subcircular, 108 μ in diameter; simple laesurae 29 μ long; coarsely reticulate with muri 6 μ high and 6.5 μ broad at top, enclosing lumina 10 μ –30 μ in longest diameter; exine 12 μ thick, excluding muri. In some specimens the lumina on the proximal hemisphere are markedly larger than those enclosed distally. The exceptionally thick spore wall may simulate a definite equatorial structure; its true nature is apparent, however, from a study of specimens compressed in orientations other than polar.

Comparison. *Reticulatisporites speciosus* Hacquebard and Barss 1957 (p. 18; pl. 2, fig. 17) is distinguishable on the basis of its exclusively distal, reticulate sculpture. *Euryzonotriletes semirotondus* (Waltz) Ishchenko 1956 (pp. 59–60; pl. 10, fig. 124) appears to represent a different species from that described and illustrated initially (Waltz in Lubert and Waltz 1941, p. 36; pl. 7, fig. 106), and may well be conspecific with *Reticulatisporites variolatus* sp. nov.

Previous records. Possibly recorded by Ishchenko (as above) from Tournaisian/Viséan strata of the western extension of the Donetz Basin.

Reticulatisporites peltatus sp. nov.

Plate 84, figs. 1–4

Diagnosis. Spores radial, trilete; originally spherical; amb circular to subcircular. Laesurae simple, straight, length almost equal to body radius; often obscured by sculpture. Exinal sculpture coarsely reticulate with smooth, rounded muri (2–5.5 μ wide and 2–3 μ high) enclosing irregularly polygonal lumina 6–46 μ in longest diameter (average 14 μ). Numerous, conspicuous, peltate (mushroom-like) processes are developed on, and characteristically at junctions of, the muri; processes 6–15 μ long (average 8 μ), 4–6.5 μ broad at base, (expanded) apices 5–13 μ in diameter; profile clearly evident at equator. Exine (exclusive of sculpture) 3.5–4.5 μ thick.

Dimensions (30 specimens). Equatorial diameter (excluding processes) 50–105 μ (mean 77 μ).

Holotype. Preparation P167B/14, 36.2 102.9. L.1048.

Locus typicus. Birger Johnsonfjellet (sample G1098), Spitsbergen; Lower Carboniferous.

Description. Holotype subcircular, body diameter 90 μ , laesurae distinct and long; muri 5 μ broad, 3 μ high; peltate processes up to 10 μ long and 11 μ wide at top; exine (excluding sculpture) 4 μ thick. Width of muri and length of processes are typically fairly uniform on any one specimen.

Comparison. This species is similar in construction to *Raistrickia boleta* Staplin 1960

(p. 14; pl. 2, figs. 25, 27), but differs in being more definitely and regularly reticulate, and in possessing longer laesurae together with less coarse, more uniform, and generally shorter accessory projections. Closer comparison is difficult, however, owing to the brevity of Staplin's description, and the evident corrosion of his illustrated specimens.

Reticulatisporites? sp.

Plate 85, figs. 1, 2

Description of specimens. Spores radial, trilete. Equatorial outline of body subtriangular with concave sides and rounded apices; interradial concavity often pronounced. Laesurae distinct, simple, straight, length approximately three-quarters body radius. Comprehensively sculptured with very high, narrow, membranous muri which ramify to form an irregular, wide-meshed reticulum. Equatorial muri simulate a broad flange extending outwards as much as $32\ \mu$; proximal and distal muri flattened due to compression. Muri approximately $1\ \mu$ wide; their greater part frequently lost in preservation and/or preparation, but junctions often persist as saetae-like projections. Exine (excluding sculpture) $3.5\text{--}5\ \mu$ around apices, $2\text{--}3\ \mu$ elsewhere.

Dimensions (9 specimens). Equatorial diameter of body $59\text{--}66\ \mu$ (mean $63\ \mu$).

Remarks. This unusual species appears distinct from any previously described representatives of the Murornati. Its inclusion within *Reticulatisporites* is tentative, since it is not entirely conformable with that genus. Although not stated in the formal emendation (Potonié and Kremp 1954, p. 144) of *Reticulatisporites*, most authors (e.g. Schopf, Wilson, and Bentall 1944, p. 44; Hoffmeister, Staplin, and Malloy 1955b, p. 395; Bhardwaj 1957, p. 121) consider circular or subcircular amb as a diagnostic attribute of the genus. Moreover, the exceptionally high, membranous muri together with slight exinal thickening at the apices seem unusual for *Reticulatisporites*. Thus the erection of a new genus may later become justified, dependent upon the discovery of further specimens similar, if not identical, to those described above. The nine specimens here recorded are, however, considered insufficient for the institution of even a formally named species. Similarity exists between this species and spores of the *Selaginella megastachys* group figured by Knox (1950, pl. 12, figs. 90–97).

Genus FOVEOSPORITES Balme 1957

Type species. *F. canalis* Balme 1957.

Discussion. This genus was instituted by Balme (1957, p. 17) for the reception of circular or roundly triangular trilete spores possessing a sculpture of 'pits or short channels

EXPLANATION OF PLATE 84

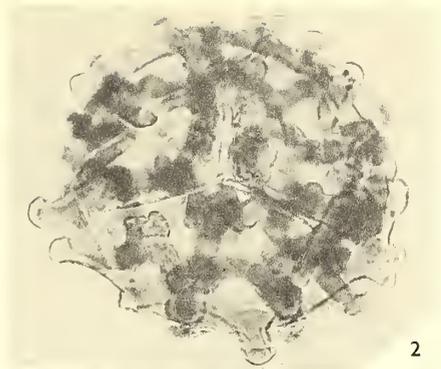
All figures $\times 500$, and from unretouched negatives.

Figs. 1–4. *Reticulatisporites peltatus* sp. nov. 1, 2, Holotype; distal and proximal surfaces respectively. 3, Distal surface; preparation P145B/41, $37.6\ 102.7$ (L.1049). 4, Distal surface; preparation P179/1, $33.2\ 102.8$ (L.1050).

Figs. 5–8. *R. variolatus* sp. nov. 5, 6, Holotype; distal and proximal surfaces respectively. 7, Distal surface; preparation P165/3, $54.4\ 97.9$ (L.1045). 8, Proximal surface; preparation P165/2, $43.7\ 101.6$ (L.1046).



1



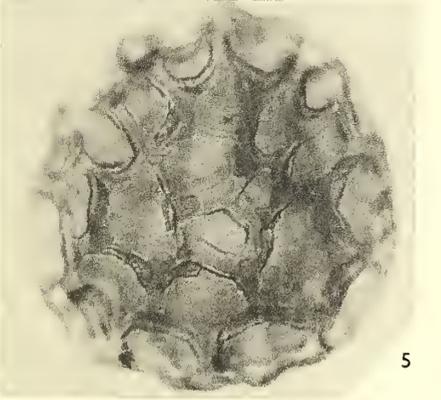
2



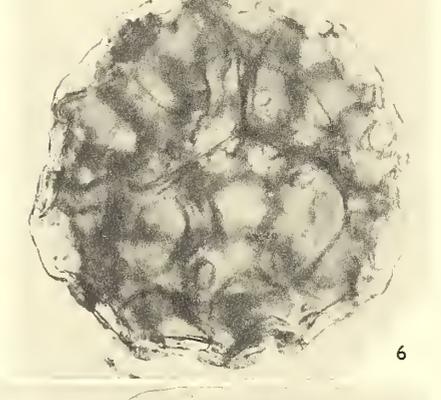
3



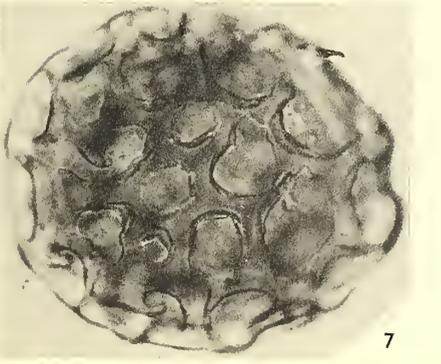
4



5



6



7



8

irregularly distributed'. Although the type species is from the Mesozoic (of Western Australia), there is no justification for erecting a new genus to include Palaeozoic spores, such as the species described below, which conform with the diagnosis of *Foveosporites*.

Affinity. Balme (loc. cit.) has pointed out the resemblance between *F. canalis* and spores of the *Lycopodium verticillatum* group, which were described and illustrated by Knox (1950, pp. 227–8; pl. 9, figs. 44–48).

Foveosporites insculptus sp. nov.

Plate 85, figs. 3–5

Diagnosis. Spores radial, trilete; amb circular to subcircular; originally spherical. Laesurae distinct, simple, straight or slightly curved, length three-fifths to four-fifths spore radius. Exine has prominent, comprehensive sculpture of sharply defined, irregularly distributed punctae, together with very narrow grooves, which often bifurcate but never coalesce to the extent of constituting a negative reticulum; depth of incisement up to $2\ \mu$. Thickness of exine $3\text{--}5.5\ \mu$. Equatorial margin slightly indented.

Dimensions (35 specimens). Equatorial diameter $63\text{--}97\ \mu$ (mean $78\ \mu$).

Holotype. Preparation P149A/7, 35.8 102.3. L.1054.

Locus typicus. Triungen (sample G1470), Spitsbergen; Lower Carboniferous.

Description. Holotype $71\ \mu$, circular; laesurae $28\ \mu$ long; exine $4\ \mu$ thick, with characteristic, discontinuous, punctate/vermiculate sculpture.

Comparison. This species is distinguishable from *Punctatisporites parvivermiculatus* sp. nov. in its relatively coarse sculpture and thicker exine. Another similar species occurring in the Spitsbergen material, *Punctatisporites stabilis* sp. nov., is essentially punctate and has a thinner spore wall than *Foveosporites insculptus* sp. nov. *Punctatisporites vermiculatus* Kosanke 1950 (p. 19; pl. 2, fig. 4) has a thicker exine, rather indistinct laesurae, together with wider, more deeply incised grooves which appear to form a fairly well-developed network.

Subturma PERINOTRILITES Erdtman 1947
Genus PEROTRILITES (Erdtman) ex Couper 1953

Type species. *P. granulatus* Couper 1953.

Discussion. Balme and Hassell (1962, p. 20) assigned to their new genus *Diaphanospora* some Australian Upper Devonian spores which they stated 'could be placed, on purely morphographic grounds, in the genus *Perotriletes* [*sic*] (Erdtman) ex Couper'. The apparent absence of such perinate forms in the Permian and Triassic of Australia is not considered sufficient justification for their assignment to a form genus other than *Perotrilites*. *Perotrilites* of Devonian age was reported earlier by McGregor (1960, p. 35).

Affinity. Spores of the Recent *Selaginella sibirica* group figured by Knox (1950, pl. 11, figs. 76–82) appear conformable with *Perotrilites*.

Perotrilites perinatus Hughes and Playford 1961

Plate 85, figs. 6, 7

Dimensions (80 specimens). Diameter of spore body 44–90 μ (mean 70 μ).

Comparison. The spores figured and described briefly by Balme (1960, p. 29; pl. 4, figs. 18, 19) as *Auroraspora* sp., from the Laurel Beds (Lower Carboniferous) of the Fitzroy Basin, Western Australia, are perhaps conspecific with *P. perinatus*. *Diaphanospora riciniata* Balme and Hassell 1962 (p. 22; pl. 4, figs. 1–4; text-fig. 5) has pronounced lip development and its central body wall is equatorially thickened.

Perotrilites magnus Hughes and Playford 1961

Plate 85, fig. 8

Dimensions (55 specimens). Diameter of spore body 97–160 μ (mean 125 μ).

Turma ZONALES (Bennie and Kidston) R. Potonié 1956
 Subturma AURITOTRILETES Potonié and Kremp 1954
 Infraturma AURICULATI (Schopf) Potonié and Kremp 1954
 Genus TRIQUITRITES (Wilson and Coe) Potonié and Kremp 1954

Type species. *T. arcuatus* Wilson and Coe 1940.

Affinity. Definite evidence of the botanical affinity of this distinctive group of spores appears to be lacking. Schopf, Wilson, and Bentall (1944, p. 46) have suggested a possible filicean relationship.

Triquitrites trivalvis (Waltz) Potonié and Kremp 1956

Plate 85, figs. 13, 14

1938 *Zonotrilites trivalvis* Waltz in Luber and Waltz, pp. 18–19; pl. 4, fig. 41.
 1956 *Triquitrites trivalvis* (Waltz) Potonié and Kremp, p. 88.

EXPLANATION OF PLATE 85

All figures $\times 500$, and from unretouched negatives.

Figs. 1, 2. *Reticulatisporites?* sp. 1, Distal surface; preparation P145B/43, 39.6 99.0 (L.1052). 2, Proximal surface; preparation P145C/4, 33.2 108.7 (L.1053).

Figs. 3–5. *Foveosporites insculptus* sp. nov. 3, Proximal surface; preparation P164/6, 20.0 105.0 (L.1055). 4, 5, Holotype; distal and proximal surfaces respectively.

Figs. 6, 7. *Perotrilites perinatus* Hughes and Playford 1961. 6, Distal surface; preparation P172/3, 44.3 103.8 (L.1057). 7, Distal surface; preparation P163/7, 54.3 101.1 (L.1058).

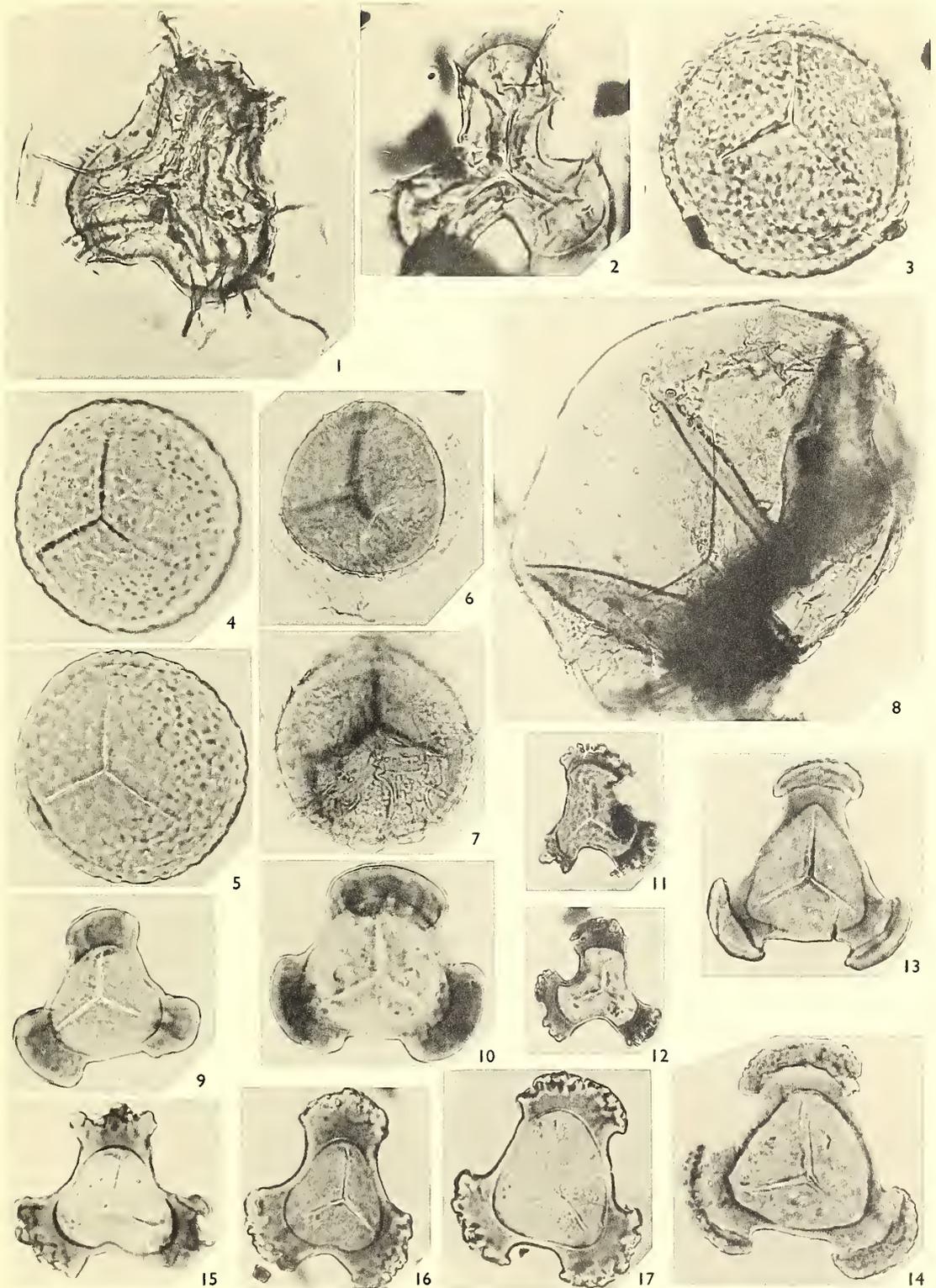
Fig. 8. *P. magnus* Hughes and Playford 1961. Proximal surface; preparation M811/2, 56.4 102.4 (L.1258).

Figs. 9, 10. *Triquitrites batillatus* Hughes and Playford 1961. 9, Proximal surface; preparation P158/7, 25.5 106.2 (L.1062). 10, Proximal surface; preparation P158/7, 27.7 113.0 (L.1061).

Figs. 11, 12. *Tripartites complanatus* Staplin 1960. 11, Proximal surface; preparation P034/1, 42.7 95.2 (L.1066). 12, Proximal surface; preparation P034/2, 31.3 94.5 (L.1067).

Figs. 13, 14. *Triquitrites trivalvis* (Waltz) Potonié and Kremp 1956. 13, Proximal surface; preparation P180B/4, 21.0 95.5 (L.1059). 14, Proximal surface; preparation P166/4, 20.6 95.8 (L.1060).

Figs. 15–17. *Tripartites incisotrilobus* (Naumova) Potonié and Kremp 1956. 15, Proximal surface; preparation P163/10, 34.2 102.1 (L.1064). 16, Proximal surface; preparation P145C/3, 20.9 104.3 (L.1063). 17, Distal surface; preparation P155/3, 37.6 94.0 (L.1065).



PLAYFORD, Lower Carboniferous microspores

1956 *Trilobozonotriletes trivalvis* (Waltz) Ishchenko, p. 97; pl. 19, figs. 231–3.

1958 *Tripartites incisotrilobus* (Naumova) Potonić and Kremp; Butterworth and Williams, pp. 373–4; pl. 3, fig. 2 (? 3, 4).

Description of specimens. Spores radial, trilete; amb subtriangular. Laesurae distinct, straight, simple; length two-thirds of, to almost equal to, spore body radius. Spore body essentially laevigate; equatorial outline subtriangular with rounded apices and convex to slightly concave sides (often straight). Cingulum narrow interradially (about $2\text{--}4\ \mu$), greatly expanded around radial areas to form prominent auriculae. Outer margins of auriculae thickened, laterally expanded, smooth to crenulate; thus constituting well-defined, massive, cushion-like cappings averaging $30\ \mu \times 7\ \mu$ in polar view.

Dimensions (30 specimens). Overall equatorial diameter $38\text{--}66\ \mu$ (mean $51\ \mu$); diameter of spore body $24\text{--}44\ \mu$ (mean $34\ \mu$).

Remarks. As noted by Potonić (1956, p. 55), *Trilobozonotriletes* Naumova apparently lacks type-species designation, and many forms assigned to this 'sub-group' by Russian authors, e.g. *Trilobozonotriletes trivalvis* (Waltz) Ishchenko 1956, are more correctly included within *Triquitrites* (Wilson and Coe).

Butterworth and Williams (1958, p. 373) list *Zonotriletes trivalvis* Waltz as synonymous with *Tripartites incisotrilobus* (Naumova) and subdivided the latter into two varieties (*incisotrilobus* and *trivalvis*). As will be discussed below, none of the spores illustrated by Butterworth and Williams (1958, pl. 3, figs. 2–4) appears truly conformable with *T. incisotrilobus*. However, at least one of their figures (pl. 3, fig. 2), exhibiting well-defined, thickened, crenulate cappings to the auriculae together with narrow, interradiial, cingulate development, is representative of *T. trivalvis*.

Sullivan (1958, p. 132) relegated *T. trivalvis* to varietal status within his interpretation of *Simozonotriletes intortus* (Waltz). The single spore illustrated of this variety (Sullivan 1958, pl. 28, fig. 3, and text-fig. 9b) differs from *T. trivalvis*, by direct comparison with text-fig. 9a of Sullivan (reproduction of Luber and Waltz's pl. 4, fig. 41) in the following respects. The cingulum is much more pronounced, particularly in the interradiial areas; marginal auriculate thickenings are larger and of a different shape, lacking the distinctive 'sausage-like' aspect characteristic of *T. trivalvis* (Waltz); and the spore body has more strongly concave sides.

It should be added that the numerous Spitsbergen representatives recorded herein conform more or less faithfully with the original description and illustration of *T. trivalvis*; morphographical deviations approaching *Simozonotriletes intortus* Waltz var. *trivalvis* Sullivan have not been observed.

The species is appropriately assigned to *Triquitrites* rather than to *Murospora* (or *Simozonotriletes*) on the basis of its prominent, more or less smooth, undivided auriculae and strictly subordinate interradiial cingulate development.

Previous records. Luber and Waltz (1938, 1941) recorded this species from the Lower Carboniferous of the Moscow Basin, and Kizel, Selizharovo, Borovichi, and Voronezh regions, U.S.S.R. Subsequently, Ishchenko (1956, 1958) has reported its restriction to strata of Viséan age, in the Donetz Basin (western extension) and the Dnieper–Donetz Basin, respectively. *T. trivalvis* is present also in the Scottish Namurian A assemblages described by Butterworth and Williams (1958).

Triquitrites batillatus Hughes and Playford 1961

Plate 85, figs. 9, 10

Dimensions (60 specimens). Overall equatorial diameter 45–73 μ (mean 58 μ); diameter of spore body 32–56 μ (mean 43 μ).

Genus TRIPARTITES Schemel 1950

Type species. *T. vetustus* Schemel 1950.

Affinity. Unknown.

Tripartites incisotrilobus (Naumova) Potonié and Kremp 1956

Plate 85, figs. 15–17

1884 Type 363 of Reinsch, p. 36; pl. 3, fig. 39.

1938 *Zonotriletes incisotrilobus* (Naumova) Waltz in Lubert and Waltz, p. 19; pl. 4, fig. 42, and pl. A, fig. 10.

1956 *Tripartites incisotrilobus* (Naumova) Potonié and Kremp, p. 92.

1956 *Trilobozonotriletes incisotrilobus* Naumova; Ishchenko, p. 94, pl. 18, fig. 220.

1960 *Tripartites incisotrilobus* (Waltz) Potonié and Kremp; Staplin, pp. 26–27; pl. 5, fig. 17.

1960 *Tripartites golatensis* Staplin, p. 27; pl. 5, figs. 15, 16.

Description of specimens. Spores radial, trilete; amb subtriangular. Laesurae distinct, simple, more or less straight, length at least four-fifths spore body radius. Spore body subtriangular with slightly concave to slightly convex sides and rounded apices; laevigate to finely granulate. Prominent, expanded auriculae developed about apices of spore body, and connected interradially by narrow, smooth equatorial flange. Radial extremities of auriculae conspicuously fluted or lobed; sometimes markedly expanded in a tangential direction resulting in a recurved or reflexed outline. Equatorial girdle (auriculae and flange) much darker than spore body.

Dimensions (50 specimens). Overall equatorial diameter 38–73 μ (mean 53 μ); diameter of spore body 27–54 μ (mean 39 μ).

Remarks. The morphographical variation within *Tripartites incisotrilobus* (Naumova) was adequately illustrated by Lubert and Waltz (1938, 1941), and is confirmed by the Spitsbergen specimens described above. *T. golatensis* Staplin 1960 (p. 27; pl. 5, figs. 15, 16) was distinguished from *T. incisotrilobus* in exhibiting 'less pronounced expansion and reflexion of the girdle' (Staplin, loc. cit.). However, the second specimen of *T. incisotrilobus* figured by Lubert and Waltz (1938, pl. A, fig. 10), showing comparatively minor tangential expansion of the auriculae, seems to be very closely paralleled by *T. golatensis* Staplin, whose recognition as a distinct species is therefore considered unjustified.

Butterworth and Williams (1958, pp. 373–4) included *Zonotriletes trivalvis* Waltz within *Tripartites incisotrilobus* (Naumova), and instituted two varieties within the latter species. However, the spores illustrated by these authors (pl. 3, figs. 2–4) possess fine auriculate crenulation and as such appear distinct from *T. incisotrilobus*.

Previous records. Apparently widespread in Lower Carboniferous deposits of the Northern Hemisphere, this species has been reported previously from Russia (Lubert and Waltz 1938, 1941, Ishchenko 1956,

1958, Bludorov and Tuzova 1956, Byvsheva 1957, 1960, Kedo 1957, 1958, 1959, Loginova 1959), Canada (Staplin 1960), and Spitsbergen (Hughes and Playford 1961).

Tripartites complauatus Staplin 1960

Plate 85, figs. 11, 12

Description of specimens. Spores radial, trilete; amb concavely subtriangular. Laesurae distinct, simple, straight, length approximately one-half to two-thirds spore body radius. Spore body finely granulate; equatorial outline subtriangular with concave sides and very broadly rounded apices which bear well-defined, dark auriculae. Radial extremities of auriculae differentiated into three to six bluntly rounded processes (average $2\ \mu$ long); auriculae otherwise smooth, not connected interradially.

Dimensions (25 specimens). Overall equatorial diameter $23\text{--}34\ \mu$ (mean $28\ \mu$); diameter of spore body $18\text{--}25\ \mu$ (mean $22\ \mu$).

Comparison. This species is distinct from *Tripartites vetustus* Schemel 1950 (p. 243; pl. 40, fig. 11) which has longer laesurae, together with more extensive, plicated auriculae. *Trilobozonotriletes terjugus* Ishchenko 1956 (pp. 96–97; pl. 18, fig. 228) is larger and less distinctly auriculate than *T. complauatus*.

Previous records. From the Golata formation (Upper Mississippian) of Alberta, Canada (Staplin 1960).

Subturma ZONOTRILETES Waltz 1935

Infraturma CINGULATI Potonié and Klaus 1954

Genus STENOZONOTRILETES (Naumova) Potonié 1958

Type species. *S. conformis* Naumova 1953.

Discussion. Obvious difficulties arise in attempting to distinguish true representatives of *Stenozonotriletes* from specimens of *Punctatisporites* (or *Leiotriletes*) having a relatively thick wall, which in polar view may simulate a narrow cingulum. It is necessary therefore to examine all such specimens closely and critically before generic assignment. In the case of *Stenozonotriletes* (polar view) an optical section of the spore body wall should be visible along the inner margin of the cingulum. An examination of individual specimens (unmounted in glycerine) in various orientations (particularly equatorial aspect) is invaluable in determining the true morphological features.

Affinity. Unknown.

Stenozonotriletes facilis Ishchenko var. *praecrassus* Ishchenko 1956

Plate 86, fig. 1

Description of specimens. Spores radial, trilete; amb circular to subcircular, smooth. Distinct spore body and relatively narrow cingulum; entirely laevigate. Distinct, straight, simple laesurae equal two-thirds to three-quarters spore body radius. Cingulum slightly darker in colour than spore body; width $8.5\text{--}12\ \mu$ (average $10\ \mu$), more or less uniform on any one specimen.

Dimensions (30 specimens). Overall equatorial diameter $68\text{--}108\ \mu$ (mean $85\ \mu$); spore body diameter $51\text{--}87\ \mu$ (mean $66\ \mu$).

Remarks. Apart from a somewhat broader size range, the specimens conform closely to the diagnosis given by Ishchenko (1956, p. 72; pl. 14, fig. 161).

Previous records. Ishchenko (1956, stratigraphical range table 3) indicates Tournaisian, Viséan, and Namurian occurrences for this variety.

Stenozonotriletes stenozonalis (Waltz) Ishchenko 1958

Plate 86, figs. 2, 3

1938 *Zonotriletes stenozonalis* Waltz *in* Luber and Waltz, p. 16; pl. 3, fig. 34 and pl. A, fig. 14.

1958 *Stenozonotriletes stenozonalis* (Waltz) Ishchenko, p. 86; pl. 10, fig. 135.

Description of specimens. Spores radial, trilete; equatorial outline convexly subtriangular to subcircular, smooth to slightly discontinuously dentate. Laesurae distinct, simple, straight or slightly sinuous, extending almost to spore body margin. Spore body finely granulate; sculpture usually more pronounced on distal surface. Cingulum uniform, laevigate; width averages one-sixth of spore body diameter.

Dimensions (15 specimens). Overall equatorial diameter 58–67 μ (mean 62 μ); cingulum width 6–11 μ (mean 8 μ).

Discussion. The description of this species given by Ishchenko (1958) is somewhat broader than the original diagnosis (Waltz *in* Luber and Waltz 1938) with respect to dimensions and equatorial outline, but that it probably does not exceed reasonable specific limits is suggested by the Spitsbergen specimens observed and described above.

Hacquebard (1957, p. 314) provisionally assigned to *Stenozonotriletes* four specimens questionably referred to *Zonotriletes stenozonalis* Waltz. Earlier, Hacquebard and Barss (1957, p. 24) recorded two specimens as *Cincturasporites* cf. *Z. stenozonalis* (Waltz, 1938) which from the description and illustration appear to be very doubtful representatives of *S. stenozonalis*.

Previous records. Previous definite records from Tournaisian/Viséan of the Moscow Basin (Luber and Waltz 1938, 1941), and from Upper Devonian/Lower Carboniferous of the Dnieper–Donetz Basin (Ishchenko 1958).

Stenozonotriletes simplex Naumova 1953

Plate 86, fig. 10

Description of specimens. Spores radial, trilete; amb convexly subtriangular. Spore body encompassed by conformable, narrow (2–4 μ) cingulum. Entirely laevigate. Laesurae simple, straight, extending to margin of spore body.

Dimensions (30 specimens). Overall equatorial diameter 40–63 μ (mean 53 μ).

Previous records. Naumova (1953) and Ishchenko (1956) report this species from the U.S.S.R. and both note its stratigraphical distribution as Palaeozoic/Mesozoic.

Stenozonotriletes inductus Ishchenko 1956

Plate 86, figs. 6, 7

Description of specimens. Spores radial, trilete; amb subcircular to roundly subtriangular. Spore body surface of slightly roughened appearance. Very narrow cingulum (2–4.5 μ)

somewhat darker in colour than spore body; equatorial margin dentate. Laesurae distinct, simple, straight to slightly sinuous, length at least two-thirds spore body radius.

Dimensions (30 specimens). Overall equatorial diameter 36–54 μ (mean 44 μ).

Previous records. According to Ishchenko (1956) this species is restricted, in the western extension of the Donetz Basin, to sediments of Tournaisian age.

Stenozonotriletes clarus Ishchenko 1958

Plate 86, figs. 4, 5

Dimensions (50 specimens). Overall equatorial diameter 47–80 μ (mean 62 μ); width of cingulum 4–7 μ (mean 5 μ).

Previous records. *S. clarus* was described initially from Upper Devonian, Tournaisian, and Viséan strata of the Dnieper–Donetz Basin (Ishchenko 1958). Hughes and Playford (1961) reported some representatives of the species in one sample (B685) of the Spitsbergen Lower Carboniferous.

Stenozonotriletes perforatus sp. nov.

Plate 86, figs. 8, 9; text-fig. 5e

Diagnosis. Spores radial, trilete; amb convexly subtriangular, smooth. Laesurae distinct, simple, straight or slightly sinuous; length three-quarters of, to slightly less than, the spore body radius. Spore body finely punctate, margin conformable with equator. Cingulum narrow, uniform, laevigate.

Dimensions (35 specimens). Overall equatorial diameter 58–73 μ (mean 65 μ); width of cingulum 3–6.5 μ (mean 4.5 μ).

Holotype. Preparation P173/3, 51.4 95.2. L.1076.

Locus typicus. Citadellet (sample G1446), Spitsbergen; Lower Carboniferous.

Description. Holotype subtriangular with convex sides and rounded apices, 64 μ overall; spore body distinctly and finely punctate, diameter 52 μ ; cingulum laevigate, 6 μ in width; laesurae prominent, slightly sinuous, length almost equal to spore body radius.

Comparison. *Stenozonotriletes stenozonalis* (Waltz in Luber and Waltz 1938, p. 14; pl. 3, fig. 34 and pl. A, fig. 14) Ishchenko 1958 has granulate sculpture, but is otherwise similar.

Stenozonotriletes cf. *spetcandus* Naumova 1953

Plate 86, fig. 11

Description of specimens. Spores radial, trilete; amb roundly subtriangular, more or less conformable with body outline. Spore body and cingulum laevigate (corroded specimens irregularly punctate). Laesurae distinct, straight, equal to, or slightly less than, spore body radius; bordered by smooth, elevated lips, individually 6–9 μ broad.

Dimensions (12 specimens). Overall equatorial diameter 56–88 μ (mean 70 μ); width of cingulum 6–9 μ (mean 7 μ).

Comparison. The above specimens are insufficient to warrant definite assignment to *Stenozonotriletes spetcandus* which Naumova (1953) described from Upper Frasnian

deposits of the Voronezh region, U.S.S.R. In her brief description Naumova stated a size range of 55–65 μ , which is exceeded considerably by these Spitsbergen specimens.

Genus MUROSPORA Somers 1952

1952 *Murospora* Somers, p. 20.

1954 *Simozonotriletes* (Naumova 1939) ex Potonié and Kremp, p. 159; pl. 12, fig. 53.

1958 *Simozonotriletes* Potonié and Kremp; Sullivan, pp. 126–7.

1958 *Westphalensisporites* Alpern, p. 78.

Type species. *M. kosankei* Somers 1952.

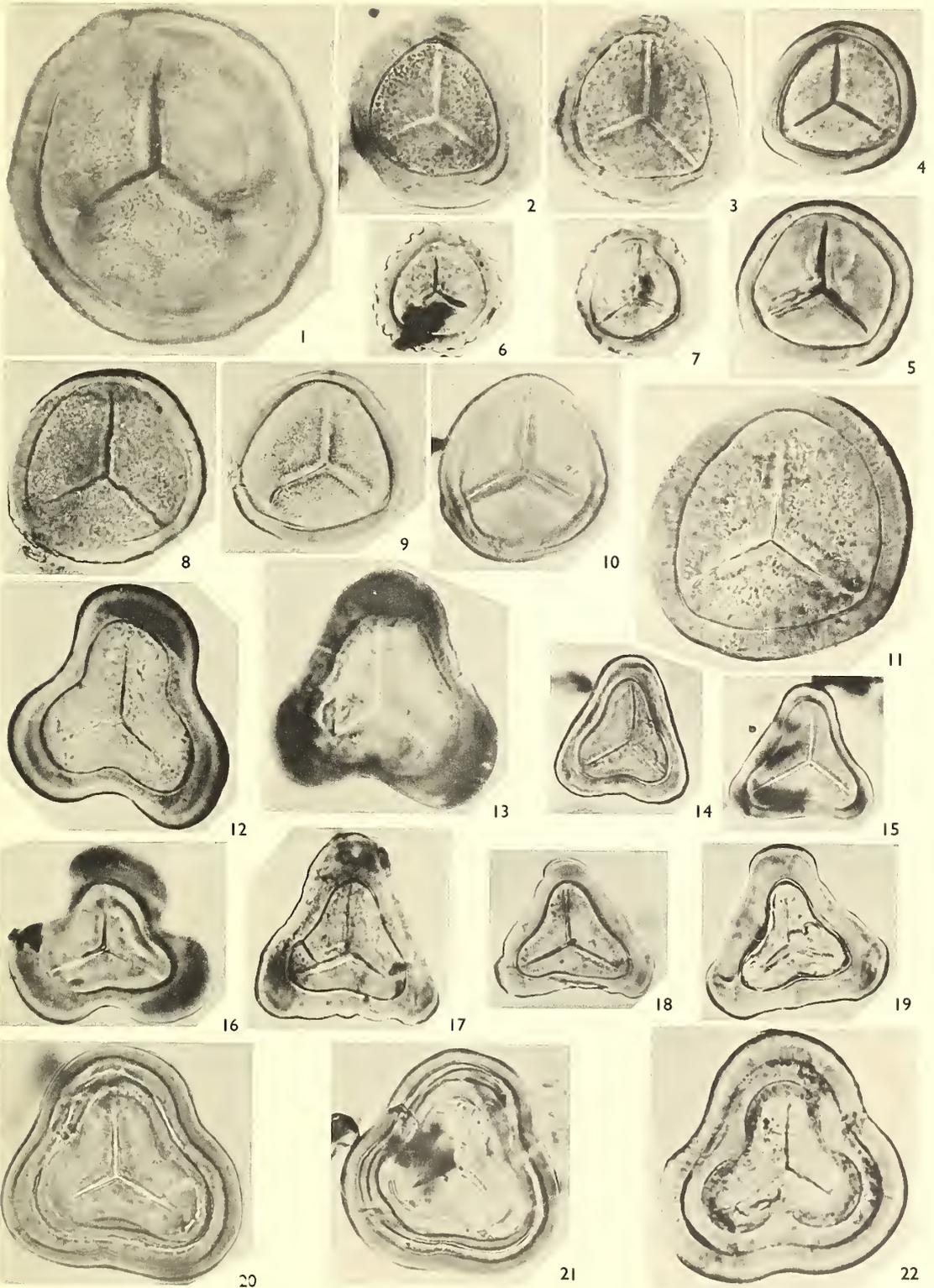
Discussion. As noted recently by Staplin (1960, pp. 28–29) there appears to be little doubt concerning the synonymy of the genera *Murospora* Somers, *Simozonotriletes* (Naumova), and *Westphalensisporites* Alpern. Their diagnoses embrace morphographically similar, cingulate microspores which are distinctly triangular in equatorial outline; the cingulum is often somewhat irregular, showing noticeable variations in width and/or thickness. Certainly, the spores described as *Westphalensisporites irregularis* Alpern 1958 (p. 78; pl. 1, figs. 15–17), with generally broad, flat cingula and apparent stratigraphical restriction to the Westphalian D, can scarcely be considered sufficient basis for the erection of a genus morphographically distinct from *Murospora* (or *Simozonotriletes*). Of the latter two genera, *Murospora* has the priority, since its formal institution preceded the validation (by Potonié and Kremp 1954) of Naumova's 1939 'sub-group' *Simozonotriletes*.

Affinity. Unknown.

EXPLANATION OF PLATE 86

All figures $\times 500$, and from unretouched negatives.

- Fig. 1. *Stenozonotriletes facilis* Ishchenko var. *praecrassus* Ishchenko 1956. Proximal surface; preparation P148/43, 38·8 107·0 (L.1068).
- Figs. 2, 3. *S. stenozonalis* (Waltz) Ishchenko 1958. 2, Proximal surface; preparation P173/1, 53·6 94·0 (L.1069). 3, Proximal surface; preparation P173/2, 38·3 94·9 (L.1070).
- Figs. 4, 5. *S. clarus* Ishchenko 1958. 4, Proximal surface; preparation P226/2, 48·1 103·7 (L.1074). 5, Proximal surface; preparation P226/1, 29·4 99·1 (L.1075).
- Figs. 6, 7. *S. inductus* Ishchenko 1956. 6, Proximal surface; preparation P169/3, 45·2 98·7 (L.1072). 7, Proximal surface; preparation P169/1, 46·7 100·3 (L.1073).
- Figs. 8, 9. *S. perforatus* sp. nov. 8, Holotype; distal surface. 9, Proximal surface; preparation P226/3, 32·8 107·9 (L.1077).
- Fig. 10. *S. simplex* Naumova 1953. Proximal surface; preparation P171A/2, 39·5 104·6 (L.1071).
- Fig. 11. *S. cf. spetcandus* Naumova 1953. Proximal surface; preparation P148/65, 37·4 106·5 (L.1079).
- Figs. 12, 13. *Murospora intorta* (Waltz) comb. nov. 12, Proximal surface; preparation P145B/40, 35·6 101·3 (L.1080). 13, Proximal surface; preparation P034/1, 31·8 94·6 (L.1081).
- Figs. 14, 15. *M. conduplicata* (Andrejeva) comb. nov. 14, Proximal surface; preparation P145B/3, 34·8 103·8 (L.1108). 15, Proximal surface; preparation P145C/4, 23·8 106·9 (L.1107).
- Fig. 16. *M. tripulvinata* Staplin 1960. Proximal surface; preparation P188/2, 19·3 110·9 (L.1116).
- Figs. 17–19. *M. sublobata* (Waltz) comb. nov. 17, Distal surface; preparation P163/1, 36·5 108·3 (L.1109). 18, Proximal surface; preparation P145A/2, 32·1 93·7 (L.1111). 19, Distal surface; preparation P148/4, 29·2 105·8 (L.1110).
- Figs. 20, 21. *M. strigata* (Waltz) comb. nov. 20, Proximal surface; preparation P145B/1, 19·1 113·6 (L.1114). 21, Proximal surface; preparation P145A/2, 44·1 96·8 (L.1115).
- Fig. 22. *M. dupla* (Ishchenko) comb. nov. Proximal surface; preparation P201/1, 22·6 104·4 (L.1112).



PLAYFORD, Lower Carboniferous microspores

Murospora intorta (Waltz) comb. nov.

Plate 86, figs. 12, 13

1938 *Zonotriletes intortus* Waltz in Luber and Waltz, p. 22 (no description); pl. 2, fig. 24.1954 *Simozonotriletes intortus* (Waltz) Potonié and Kremp, p. 159.1956 *Simozonotriletes intortus* (Waltz) Ishchenko, pp. 88–89; pl. 17, fig. 204.

Description of specimens. Spores radial, trilete; amb subtriangular with concave sides and rounded apices, smooth, conformable with spore body outline. Laesurae distinct, simple, straight, length at least two-thirds spore body radius. Spore body laevigate to infragranulate. Cingulum well defined, laevigate; uniform or may be perceptibly thicker and/or broader about apices; inner margin often corroded.

Dimensions (50 specimens). Overall equatorial diameter 50–82 μ (mean 65 μ); diameter of spore body 33–57 μ (mean 44 μ).

Remarks. In 1954 Potonié and Kremp designated *Simozonotriletes intortus* (Waltz) as the type species of *Simozonotriletes* (Naumova). The assignment of the species to *Murospora* is necessitated through generic priority (discussed above).

Sullivan (1958) has described *S. intortus* (Waltz) Potonié and Kremp from the three discrete horizons (Middle Westphalian A, Upper Westphalian A, and Middle Westphalian B) in the British Upper Carboniferous. This author recorded interesting morphographical diversity within the species, and upon this basis proposed nine varieties. Some of these variations are exhibited by the Spitsbergen specimens. However, the continuous intergradation of the variants (principally width and thickening of cingulum) does not, in the present writer's view, lend itself to morphographical subdivision, even at varietal level. Furthermore, from the evident corrosion of Sullivan's illustrated specimens, and the absence of statistical information, it would seem that his proposed varieties and their postulated interrelationships within the species are of questionable significance and validity. As discussed previously, Sullivan has incorrectly equated his *S. intortus* var. *trivalvis* with *Triquitrites trivalvis* (Waltz) Potonié and Kremp.

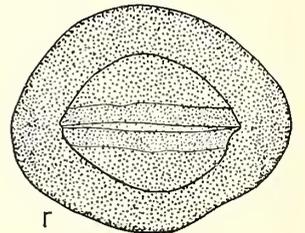
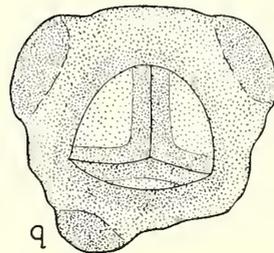
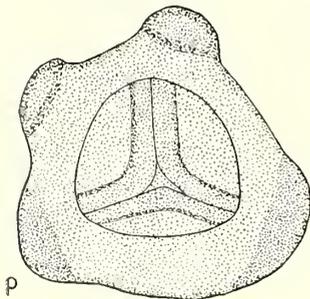
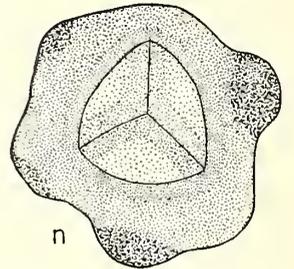
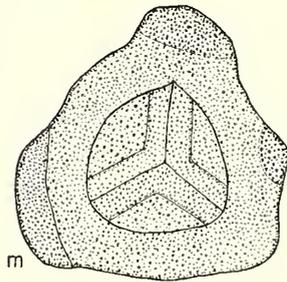
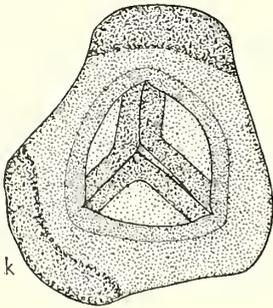
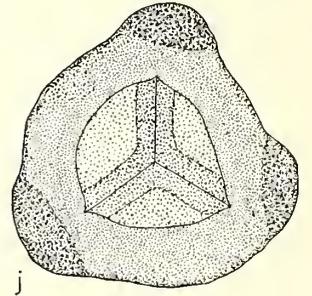
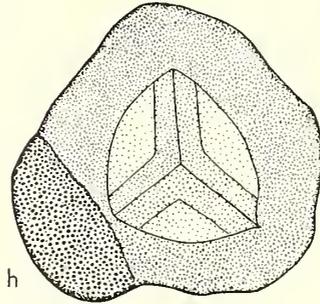
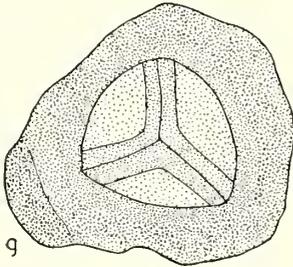
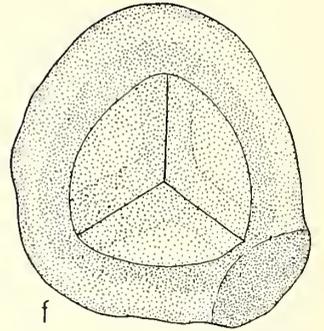
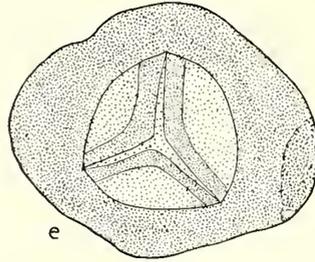
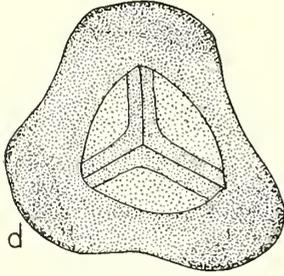
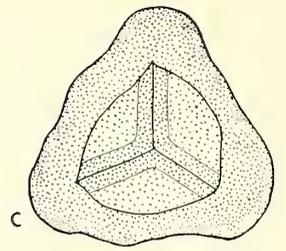
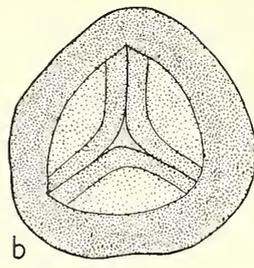
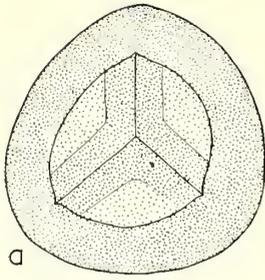
Previous records. Reinsch (1884) illustrated many spores conformable with *Murospora intorta* (Waltz) comb. nov. Since then the species has been reported from the Carboniferous by numerous workers, and particularly from the Lower Carboniferous. The highest known stratigraphical occurrence is from the Middle Westphalian B of Nottinghamshire, England (Sullivan 1958).

Murospora aurita (Waltz) comb. nov., emend.

Plate 87, figs. 1–6; text-figs. 6a–q, 7

1938 *Zonotriletes auritus* Waltz in Luber and Waltz, p. 17; pl. 2, fig. 23.1956 *Simozonotriletes auritus* (Waltz) Potonié and Kremp, p. 109.1957 *Cincturasporites auritus* (Waltz) Hacquebard and Barss, p. 23; pl. 3, fig. 1.1957 *Cincturasporites irregularis* Hacquebard and Barss, pp. 25–26; pl. 3, fig. 9.1960 *Murospora varia* Staplin, p. 30; pl. 6, figs. 16–18.1960 *Murospora* sp. cf. *M. varia* Staplin, p. 30; pl. 6, fig. 19.

Emended diagnosis. Spores radial, trilete; amb subtriangular to irregular; margin smooth to undulating. Laesurae distinct, straight, reaching spore body margin or almost so; bordered by more or less distinct, smooth, broad, slightly elevated lips, individually



3.5–6.5 μ wide. Spore body well defined, subtriangular, with convex sides and pointed or rounded apices; laevigate. Cingulum laevigate; uniform, or showing marked variation in width and/or thickness. Cingulate thickenings peripheral, commonly situated at one or more of amb apices, but placement often highly irregular; up to five in number on any one specimen.

Dimensions (140 specimens). Overall equatorial diameter 45–94 μ (mean 68 μ); diameter of spore body 28–51 μ (mean 39 μ).

Holotype (here designated). Plate 2, fig. 23 of Luber and Waltz (1938).

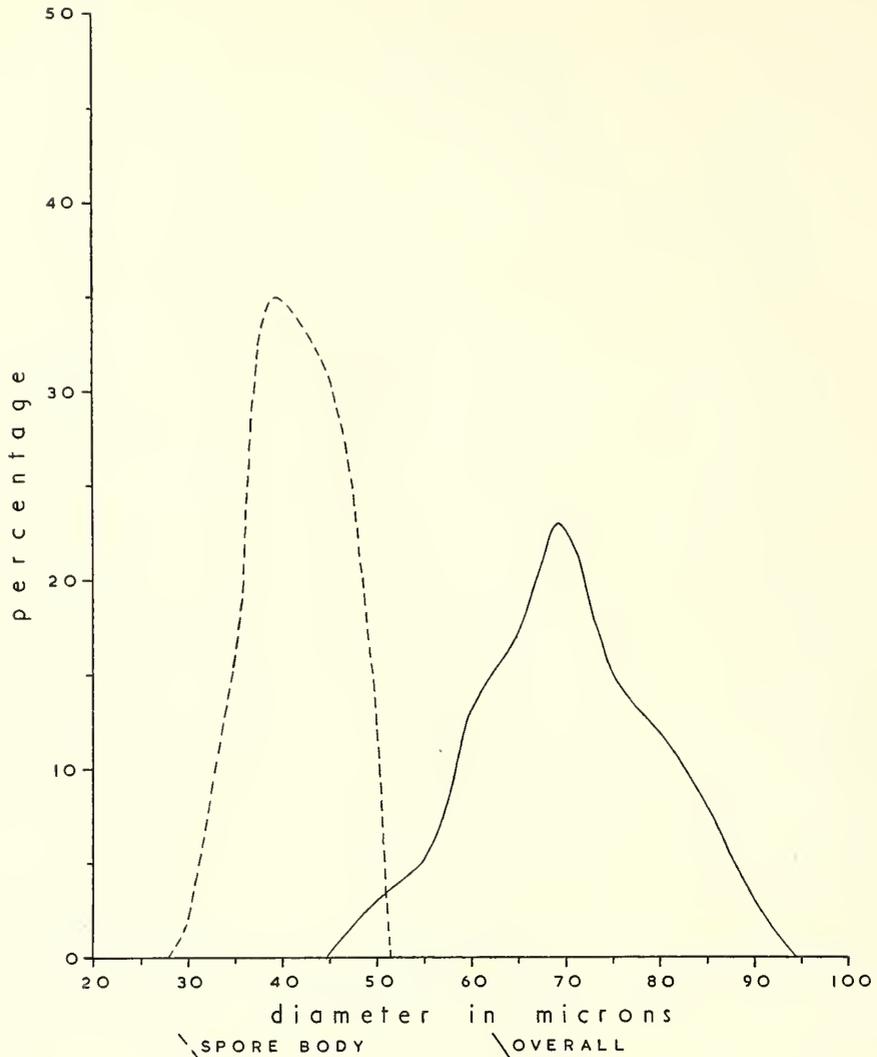
Locus typicus. U.S.S.R.—Kizel region, New Kizel mines, oblique shaft 24, bed 4 (after Luber and Waltz 1938, p. 17).

Remarks. The spores described above occur abundantly, often predominantly, in many of the samples examined from the Lower Carboniferous of Spitsbergen. Detailed study of the considerable diversity exhibited by the cingula of these specimens (occurring associated in any given sample) indicates that the variants (cingulum width and thickness) constitute a continuous morphographical series, the specific (or subspecific) subdivision of which appears neither warranted nor desirable. For this reason *Zonotriletes auritus* Waltz is here emended and thus given a somewhat broader diagnosis, enabling its valid reception of spores closely allied, indeed continuously linked, with that originally figured by Waltz (i.e. the holotype, designated herein). As such, the species now incorporates several previously described species (see synonymy above). Staplin (1960) described and illustrated a similar range of variation in his species *Murospora varia*, which is conspecific with *M. aurita* (Waltz) as emended above. The same applies to *Cincturasporites auritus* (Waltz) Hacquebard and Barss 1957 and *C. irregularis* Hacquebard and Barss 1957.

The species is entirely conformable with *Murospora* Somers 1952. An assignment to *Cincturasporites* Hacquebard and Barss 1957 is rejected on the grounds that the so-called 'overlap' of the cingulum (Hacquebard and Barss 1957, p. 21, fig. 2), which is a diagnostic feature of the latter genus, does not appear to be a constant attribute of *M. aurita* (Waltz). Potonié (1960, p. 57) has already noted the close similarity between *Cincturasporites* and *Murospora* (al. *Simozonotriletes*). Indeed, *Cincturasporites* appears to embrace the connotations of several other well-established genera, viz. *Knoxisporites*, *Stenozonotriletes*, and *Lophozonotriletes*, and its recognition as a distinct form-genus does not, at this stage, seem justified.

Comparison. *Murospora intorta* (Waltz) shows similar cingulate variation to *M. aurita*

TEXT-FIG. 6. Camera-lucida drawings; all magnifications $\times 500$. a–q, *Murospora aurita* (Waltz) comb. nov., emend. Illustrating characteristic morphographical variation of this species as represented in a single sample (G1092). a, Preparation P158/7, 41.9 100.7 (L.1088). b, Preparation P158/7, 27.8 94.5 (L.1089). c, Preparation P158/7, 40.9 100.1 (L.1091). d, Preparation P158/4, 28.3 94.3 (L.1092). e, Preparation P158/6, 32.3 106.3 (L.1093). f, Preparation P158/7, 31.5 111.1 (L.1094). g, Preparation P158/6, 32.4 110.6 (L.1095). h, Preparation P158/5, 54.2 94.0 (L.1096). j, Preparation P158/4, 30.4 107.8 (L.1097). k, Preparation P158/4, 43.0 94.1 (L.1098). m, Preparation P158/4, 44.4 112.1 (L.1101). n, Preparation P158/4, 25.2 103.3 (L.1100). p, Preparation P158/5, 54.2 102.5 (L.1099). q, Preparation P158/7, 32.8 114.3 (L.1102). r, Probable aberrant form of *Murospora aurita*, one of several observed in preparations of sample Q55, in which the typical representatives (as in a–q above) are the predominant microfloral constituents; preparation P165/1, 42.8 95.7 (L.1106).



TEXT-FIG. 7. Graphs showing variation in overall and spore body diameters of *Murospora aurita* (Waltz) comb. nov., emend. (based upon measurement of 140 specimens in full polar view).

(Waltz) comb. nov., emend., but is distinguishable in having simple laesurae, together with a spore body which in equatorial outline is decidedly less roundly triangular. The cingulum of *Zonotriletes sulcatus* Waltz (*in* Lubert and Waltz 1938, p. 18; pl. 2, fig. 20) shows distinct, concentric furrowing. *Zonotriletes turgidus* Waltz (*in* Lubert and Waltz 1941, p. 22; pl. 4, fig. 53) is subcircular and has a narrow, uniform cingulum.

Previous records. Reinsch (1884) figured many specimens conformable with *Murospora aurita* (Waltz), which were recovered from Russian Carboniferous sediments. Subsequently the species has been reported from the Lower Carboniferous of the Moscow Basin and Kizel, Selizharovo, Borovichi, and Voronezh regions, U.S.S.R. (Lubert and Waltz 1938, 1941); from the Upper Mississippian of Canada

(Hacquebard and Barss 1957, Staplin 1960); and from the Lower Carboniferous of Spitsbergen (Hughes and Playford 1961).

Probable aberrant forms. A number of spores have been observed spasmodically which are strongly reminiscent of *Murospora aurita* (Waltz) with respect to overall size, characteristic cingulum variation, and development of lips, but differ in being distinctly monolete and in possessing an oval to elliptical spore body (see Plate 87, figs. 8, 9; text-fig. 6r). One form (Plate 87, fig. 7) intermediate between the trilete and monolete conditions provides good evidence that these spores in fact represent abnormal deviations from the albeit variable category of *M. aurita*. It is noteworthy that such forms invariably occur in assemblages marked by abundance (at least 5 per cent.) of *M. aurita*. The forms rarely attain 1 per cent. of the total *M. aurita* content.

Based upon twenty-five measured specimens, the following is the observed size range: overall length 60–90 μ (mean 73 μ), width 42–67 μ (mean 56 μ); spore body length 38–62 μ (mean 49 μ), width 29–46 μ (mean 36 μ). The 'aberrant' forms have been noted in the following samples: G1098, G1102 (Birger Johnsonfjellet); G1466 (Triungen); W217 (Adolfbukta, north shore); F20, G1278, G1276 (Anservika); M365, Q55 (Blårevbreen); G1339 (Margaretbreen); G636 (De Geerfjellet); R38 (Ragnarbreen).

One of the figures given by Alpern (1958, pl. 1, fig. 18) of his species *Densosporites major* shows a large, elongate, cingulate spore which may possibly be monolete, whereas the other figure of the species (pl. 1, fig. 19) is of a roundly triangular, distinctly trilete spore. However, Alpern's brief description contains no reference to the presence of monolete variants within the species. Divergence in the character of the tetrad mark is known within the spores of certain modern plants, such as *Asplenopsis* and *Marattia* (see Erdtman 1957, p. 48, fig. 81; Harris 1955, p. 60).

Murospora conduplicata (Andrejeva) comb. nov.

Plate 86, figs. 14, 15

1941 *Zonotriletes conduplicatus* Andrejeva in Luber and Waltz, p. 38; pl. 7, fig. 113.

1956 *Simozonotriletes conduplicatus* (Andrejeva) Ishchenko, p. 89; pl. 17, figs. 206, 207.

Description of specimens. Spores radial, trilete; entirely laevigate. Amb subtriangular with rounded apices and concave to almost straight sides. Laesurae distinct, simple, straight, length equal to, or slightly less than, spore body radius. Cingulum undifferentiated and uniform in width; often slightly darker in colour than spore body.

Dimensions (60 specimens). Overall equatorial diameter 36–55 μ (mean 45 μ); diameter of spore body 25–39 μ (mean 32 μ).

Previous records. This species was first described from the Lower Carboniferous of the Moscow Basin and Selizharovo district, U.S.S.R. (Andrejeva in Luber and Waltz 1941). It has recently been reported from Tournaisian/Viséan sediments of the Donetz Basin (western extension) and Dnieper-Donetz Basin (Ishchenko 1956, 1958) and of the Volga-Ural region (Byvsheva 1960).

Murospora sublobata (Waltz) comb. nov.

Plate 86, figs. 17–19

1938 *Zonotriletes sublobatus* Waltz in Luber and Waltz, p. 17; pl. 2, fig. 22.

1956 *Simozonotriletes sublobatus* (Waltz) Potonié and Kremp, p. 110.

1957 *Triquitrites tendoris* Hacquebard and Barss, p. 18; pl. 2, figs. 18, 19.

1960 *Murospora laevigata* Staplin, pp. 29–30; pl. 6, fig. 21.

Description of specimens. Spores radial, trilete; amb subtriangular with concave to straight sides and rounded apices. Laesurae distinct, length four-fifths of, to almost equal to, spore body radius; simple or occasionally with incipient lips. Spore body concavely subtriangular with rounded apices; laevigate to infrapunctate (corroded specimens irregularly punctate). Cingulum laevigate; perceptibly to markedly widened and thickened around spore body apices, but rarely to the extent of constituting well-defined valvae. A study of representatives of this species present in poorly preserved assemblages suggests that such differences in cingulum thickness, which might not otherwise be apparent, coupled with fine punctation of the spore body are, in fact, emphasized by corrosion.

Dimensions (60 specimens). Overall equatorial diameter 34–58 μ (mean 47 μ); diameter of spore body 22–38 μ (mean 30 μ).

Remarks. From an exhaustive study of approximately 150 specimens occurring in a variety of the Spitsbergen samples, it became clear that any apparently significant differences which may exist between specimens identical to *Zonotriletes sublobatus* Waltz, *Triquitrites tendoris* Hacquebard and Barss, and *Murospora laevigata* Staplin are negated by the presence of numerous intermediate forms. Accordingly the two latter species are here considered synonymous with *Z. sublobatus* Waltz, the original description of which is sufficiently broad to accommodate both. The presence of a well-defined, continuous equatorial girdle indicates the correct assignment of the species to *Murospora*, rather than to *Triquitrites*.

Comparison. *Murospora conduplicata* (Andrejeva) differs from *M. sublobata* (Waltz) comb. nov. in possessing an undifferentiated cingulum of essentially uniform width. *M. intorta* (Waltz) is generally considerably larger, and the sides of its spore body are more sharply concave.

The spores described by Sullivan (1958, pp. 130–1; pl. 26, figs. 10–12; text-figs. 5a, b) as *Simozonotriletes intortus* var. *sublobatus* (Waltz) are larger (66.5–80 μ) and possess well-defined valvae; direct comparison is necessary to establish conspecificity with *M. sublobata* (Waltz).

Previous records. *Murospora sublobata* (Waltz) has been recorded from Lower Carboniferous strata of the Moscow Basin, and Kizel, Selizharovo, Borovichi, and Voronezh regions, U.S.S.R. (Luber and Waltz 1938, 1941); and from the Upper Mississippian of Canada (Hacquebard and Barss 1957, Staplin 1960).

Murospora dupla (Ishchenko) comb. nov.

Plate 86, fig. 22; text-fig. 8a

1956 *Simozonotriletes duplus* Ishchenko, p. 93; pl. 17, fig. 216.

Description of specimens. Spores radial, trilete; amb subtriangular with concave sides and broadly rounded apices. Laesurae distinct, simple, straight, length at least four-fifths spore body radius. Body laevigate; outline more or less conformable with equator, but sides may be more sharply concave. Cingulum laevigate; divided equally by clearly defined, continuous, narrow, shallow groove proximally incised parallel to equator.

Dimensions (4 specimens). Overall equatorial diameter $72\text{--}82\mu$ (mean 75μ); diameter of spore body $40\text{--}45\mu$ (mean 43μ).

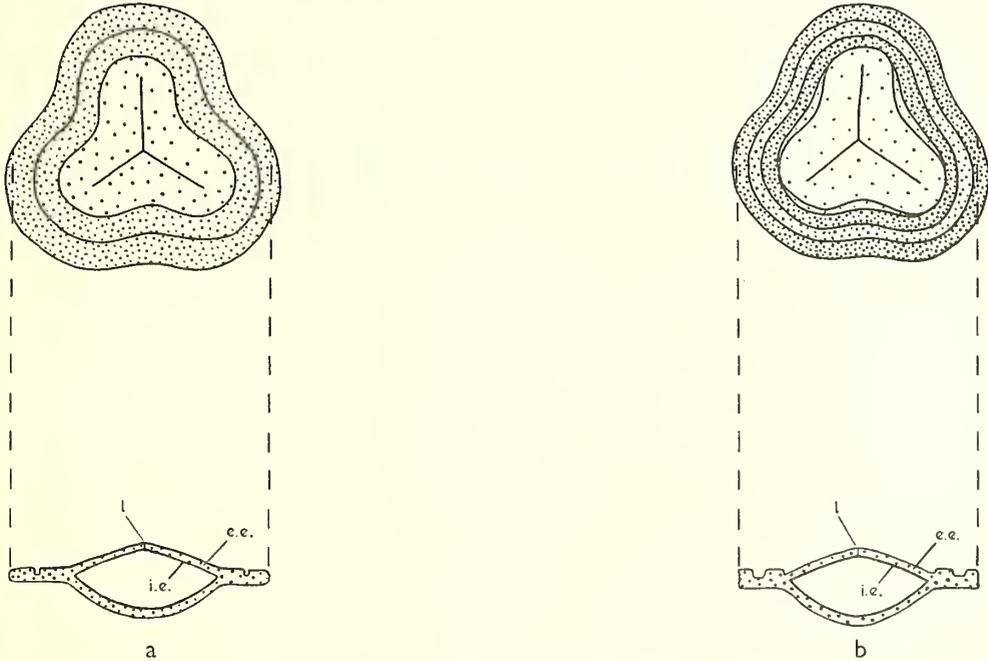
Previous records. According to Ishchenko (1956) this species is restricted to Middle Viséan strata of the Donetz Basin (western extension).

Murospora strigata (Waltz) comb. nov.

Plate 86, figs. 20, 21; text-fig. 8b

1941 *Zonotriletes strigatus* Waltz in Luber and Waltz, p. 19; pl. 3, fig. 41.

1958 *Simozonotriletes strigatus* (Waltz) Ishchenko, p. 88; pl. 11, fig. 141.



TEXT-FIG. 8. Camera-lucida drawings and generalized, hypothetical, polar sections. *a*, *Murospora dupla* (Ishchenko) comb. nov.; preparation P201/2, $40.1\text{--}103.1$ (L.1113). *b*, *Murospora strigata* (Waltz) comb. nov.; preparation P145A/2, $44.1\text{--}96.8$ (L.1115). e.e.=exoexine; i.e.=intexine; l=laesura. Magnifications $\times 500$.

Description of specimens. Spores radial, trilete; amb subtriangular with broadly rounded apices and concave sides. Laesurae distinct, simple, straight, length two-thirds of, to almost equal to, spore body radius. Spore body laevigate to very finely punctate; concavely subtriangular. Proximal surface of cingulum differentiated into three, subequal, concentric bands consisting of a smooth, flat-topped, outer (equatorial) ridge separated from a similar inner ridge by a continuous channel of approximately the same width as the ridges; the inner ridge is situated at, or just equatorially beyond, the spore body margin. Distal surface of cingulum smooth.

Dimensions (15 specimens). Overall equatorial diameter $60\text{--}82\mu$ (mean 70μ); diameter of spore body $36\text{--}46\mu$ (mean 40μ).

Remarks. The specimens conform closely with the original description of *Zonotriletes strigatus* given by Waltz (*in* Luber and Waltz 1941), who described the cingulum as 'complex, consisting of two thick but flat rims between which is disposed a thinner, more transparent area'; Waltz noted the conformity of the cingulate elements with the spore body outline.

Spores assigned to this species could conceivably have resulted from a widening (due to corrosion) of the narrow proximal groove characteristic of the cingulum in *Murospora dupla* (Ishchenko). However, the generally well-preserved nature of the specimens observed, and the absence of intermediate forms, support the recognition of the two species as morphographically discrete.

Comparison. *Simozonotriletes trigonalis* Ishchenko 1956 (p. 93; pl. 17, fig. 217) appears to possess lipped laesurae, but otherwise resembles *Murospora strigata* (Waltz) comb. nov.

Previous records. This species was first described from Lower Carboniferous deposits of the Selizharovo region, U.S.S.R. (Luber and Waltz 1941). Recently, Ishchenko (1958) has reported its restriction, in the Dnieper-Donetz Basin, to sediments of Viséan age.

Murospora tripulvinata Staplin 1960

Plate 86, fig. 16

Description of specimens. Spores radial, trilete; amb concavely subtriangular. Laesurae distinct, simple, straight, length approximately four-fifths body radius. Spore body subtriangular with rounded apices and slightly concave to slightly convex sides. Cingulum narrow interradially; conspicuously expanded at radial corners to form prominent, rounded, subequal valvae. Spore body and cingulum laevigate.

Dimensions (25 specimens). Overall equatorial diameter 49–62 μ (mean 55 μ); diameter of spore body 32–48 μ (mean 39 μ).

Comparison. *Triquitrites trivalvis* (Waltz) Potonié and Kremp 1956 possesses well-

EXPLANATION OF PLATE 87

All figures $\times 500$, and from unretouched negatives.

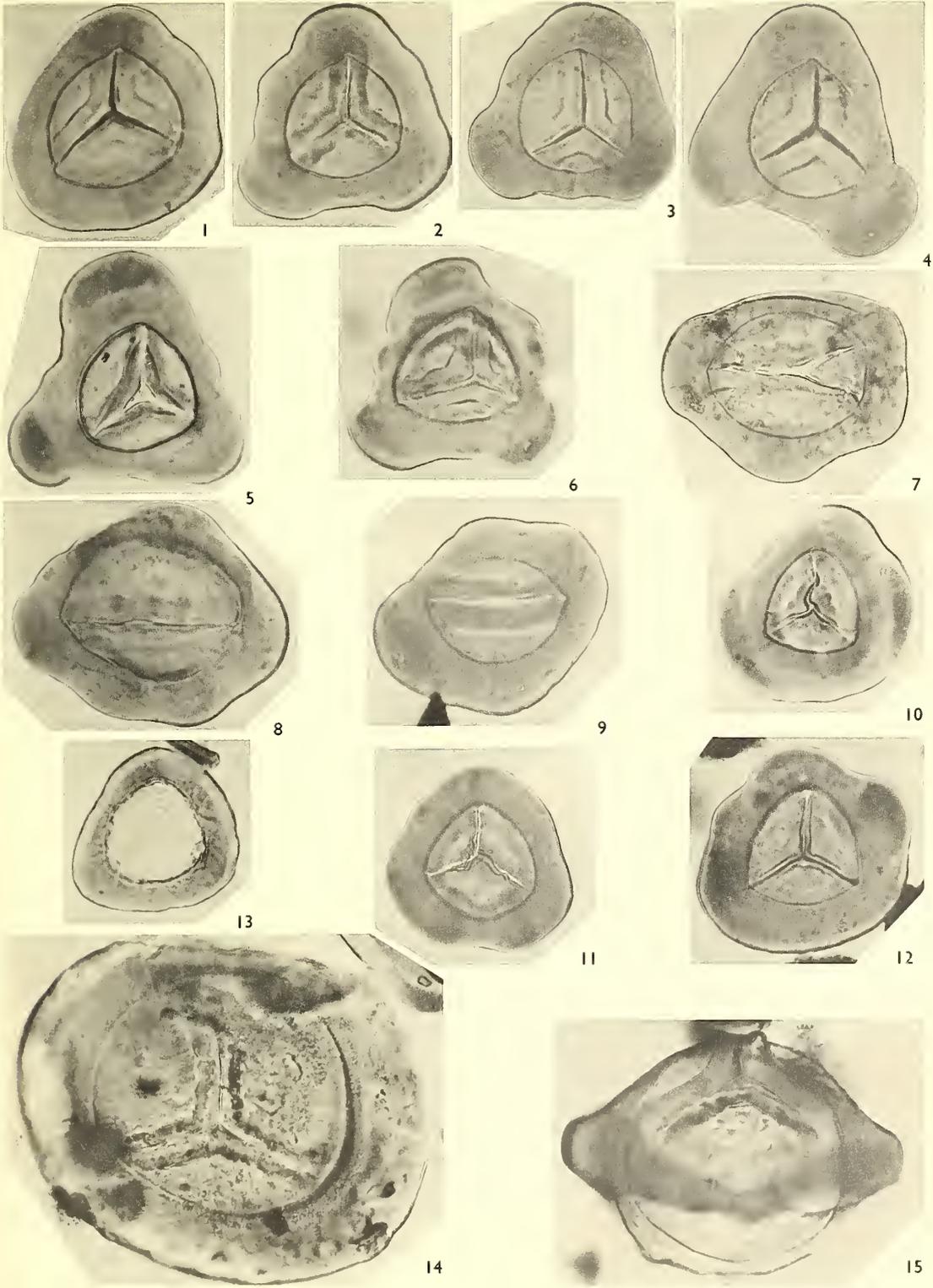
Figs. 1–6. *Murospora aurita* (Waltz) comb. nov., emend. 1, Proximal surface; preparation P167B/5, 37.7 103.9 (L.1082). 2, Proximal surface; preparation P167B/6, 38.5 105.5 (L.1083). 3, Proximal surface; preparation P167B/1, 40.4 99.9 (L.1084). 4, Proximal surface; preparation P167B/15, 40.4 102.8 (L.1085). 5, Proximal surface; preparation P145B/8, 35.6 103.6 (L.1086). 6, Proximal surface; preparation P188/1, 21.7 104.2 (L.1087).

Figs. 7–9. Probable aberrant forms of *M. aurita* (Waltz) comb. nov., emend., showing variation in laesurate character. 7, Preparation P165/3, 25.8 93.9 (L.1103). 8, Preparation P167B/12, 35.5 103.9 (L.1105). 9, Preparation P167B/1, 25.2 100.8 (L.1104).

Figs. 10–12. *M. friendii* sp. nov. 10, Holotype; proximal surface. 11, Proximal surface; preparation P145B/35, 37.8 103.7 (L.1118). 12, Proximal surface; preparation P167B/2, 42.0 106.7 (L.1119).

Fig. 13. *Anulatisporites anulatus* (Loose) Potonié and Kremp 1954. Distal surface; preparation P175/4, 20.1 95.9 (L.1121).

Figs. 14, 15. *A. labiatus* Hughes and Playford 1961. 14, Proximal surface; preparation P172/2, 23.2 92.8 (L.1122). 15, Lateral view; preparation P181/3, 22.9 101.4 (L.1123).



PLAYFORD, Lower Carboniferous microspores

defined thickenings around outer margins of auriculae, contrasting with the uniform lobate expansions of the cingulum in *Murospora tripulvinata*.

Previous records. From the Golata formation (Upper Mississippian) of Alberta, Canada (Staplin 1960).

Murospora friendii sp. nov.

Plate 87, figs. 10–12

Diagnosis. Spores radial, trilete; amb subtriangular, generally conformable with spore body margin. Laesurae distinct, straight, reaching to inner margin of cingulum; accompanied by very narrow (individually 1–1.5 μ broad), elevated (up to 2.5 μ high) lips which often appear highly contorted due to compression. Spore body subtriangular with convex sides and pointed to rounded apices; laevigate to infrapunctate. Cingulum laevigate; width uniform or irregular on any one specimen; colour usually slightly darker than spore body. Equatorial margin smooth to undulating.

Dimensions (40 specimens). Overall equatorial diameter 46–70 μ (mean 57 μ); diameter of spore body 27–40 μ (mean 33 μ).

Holotype. Preparation P188/3, 36.3 95.2. L.1117.

Locus typicus. Birger Johnsonfjellet (sample G1102), Spitsbergen; Lower Carboniferous.

Description. Holotype 63 μ overall, entirely laevigate; spore body diameter 32 μ ; cingulum variable in width (range 10–19 μ); laesurate lips very narrow, sinuous.

Comparison. *Euryzonotriletes translaticius* Ishchenko 1956 (p. 48; pl. 8, fig. 99) resembles *Murospora friendii* sp. nov., but differs in possessing simple, sinuous laesurae which do not reach the spore body margin, and in being constantly smaller (35–45 μ). According to Ishchenko (1956) the spore body exine of *E. translaticius* is frequently destroyed whilst the cingulum is comparatively thick, hence robust.

The species is named for Mr. P. F. Friend, of the Sedgwick Museum, Cambridge.

Genus ANULATISPORITES (Loose) Potonié and Kremp 1954

Type species. *A. anulatus* (Loose) Potonié and Kremp 1954.

Affinity. Unknown.

Anulatisporites anulatus (Loose) Potonié and Kremp 1954

Plate 87, fig. 13

1932 *Sporonites anulatus* Loose in Potonié, Ibrahim, and Loose, p. 451; pl. 18, fig. 44.

1934 *Zonales-sporites (Anulati-sporites) annulatus* (Loose) Loose, p. 151.

1944 *Densosporites annulatus* (Loose) Schopf, Wilson, and Bentall, p. 40.

1954 *Anulatisporites anulatus* (Loose) Potonié and Kremp, p. 159; pl. 20, fig. 7.

Description of specimens. Spores radial, trilete; amb subcircular to roundly subtriangular. Laesurae obscure to perceptible, simple, reaching to inner margin of cingulum. Massive, uniform, laevigate cingulum much darker in colour than fragile, infragranulate spore body.

Dimensions (50 specimens). Overall equatorial diameter 36–63 μ (mean 48 μ); diameter of spore body 21–38 μ (mean 29 μ).

Comparison. The Scottish Lower Carboniferous species *Densosporites pseudoannulatus* Butterworth and Williams 1958 (pp. 379–80; pl. 3, figs. 42, 43), recorded also by Love (1960, p. 109), seems close to *A. anulatus*.

Previous records. This species, described initially from the Westphalian of the Ruhr district (see Potonié and Kremp 1956a, p. 112; pl. 17, figs. 365–72) appears to have fairly extensive distribution within the Carboniferous. Dybová and Jachowicz (1957) record it from Upper Silesian coals ranging in age from Namurian A to Westphalian C; these authors list in the synonymy two Upper Carboniferous species of Kosanke (1950): *Densosporites reynoldsburgensis* and *D. sphaerotriangularis*. Smith (1960) notes the occurrence of *A. anulatus* in the Lower Coal Measures (Westphalian A) of Durham, England. Hacquebard and Barss (1957) describe it from Upper Mississippian coal of the South Nahanni River area, Northwest Territories, Canada.

Anulatisporites labiatus Hughes and Playford 1961

Plate 87, figs. 14, 15

Dimensions (75 specimens). Overall equatorial diameter 71–136 μ (mean 102 μ); diameter of spore body 42–88 μ (mean 62 μ); width of cingulum 12–30 μ (mean 20 μ).

Comparison. This species resembles closely *Murospora paenulata* Staplin 1960 (p. 30; pl. 7, figs. 1–4) although the specimens figured by Staplin appear to be corroded. The principal difference, however, lies in the fact that *A. labiatus* possesses a definite cingulum in the usually accepted sense (Potonié and Kremp 1955, p. 15) whereas *M. paenulata* is said to have a ‘capsula’ (the precise definition of which is uncertain) as distinct from what Staplin terms a ‘true cingulum’.

From Plate 87, fig. 15, illustrating a specimen of *A. labiatus* in equatorial aspect, it is evident that the exoexine shows a marked and abrupt centrifugal increase in thickness in the equatorial region, constituting a broad, massive, cingulate border to the spore body. In this respect it is similar to *Cincturasporites* Hacquebard and Barss (1957, fig. 2b), although the ‘overlap’ said to be characteristic of that genus is not represented.

Staplin’s (1960) usage of the genus *Murospora*, without formal emendation, diverges considerably from the original diagnosis (Somers 1952) which is here accepted.

Previous records. Described initially by Hughes and Playford (1961) from one sample (B685) of the Lower Carboniferous of Spitsbergen, this species was probably recorded as *Zonotriletes macrodiscus* Waltz (*in* Luber and Waltz 1938, 1941: no description) from the Lower Carboniferous of the Moscow Basin, and Selizharovo and Borovich regions, U.S.S.R.

[To be concluded in *Palaeontology*, Vol. 5, Part 4]

THE PALAEOONTOLOGICAL ASSOCIATION

COUNCIL 1962

President

Professor T. NEVILLE GEORGE, The University, Glasgow, W. 2

Vice-Presidents

Professor O. M. B. BULMAN, Sedgwick Museum, Cambridge

Professor W. F. WHITTARD, The University, Bristol

Dr. W. H. C. RAMSBOTTOM, Geological Survey Office, Leeds

Treasurer

Professor P. C. SYLVESTER-BRADLEY, The University, Leicester

Assistant Treasurer

Dr. T. D. FORD, The University, Leicester

Secretary

Dr. C. H. HOLLAND, Department of Geology, Bedford College, London, N.W. 1

Editors

Mr. N. F. HUGHES, Sedgwick Museum, Cambridge

Dr. W. S. MCKERROW, University Museum, Oxford

Dr. GWYN THOMAS, Department of Geology, Imperial College of Science, London, S.W. 7

Other members of Council

Dr. F. T. BANNER, British Petroleum Company, Sunbury on Thames

Dr. F. M. BROADHURST, The University, Manchester

Dr. A. J. CHARIG, British Museum (Natural History), London

Dr. L. R. COX, British Museum (Natural History), London

Dr. W. T. DEAN, British Museum (Natural History), London

Dr. C. DOWNIE, The University, Sheffield

Dr. R. GOLDRING, The University, Reading

Dr. J. C. HARPER, The University, Liverpool

Dr. M. R. HOUSE, The University, Durham

Dr. J. W. NEALE, The University, Hull

Dr. R. J. G. SAVAGE, The University, Bristol

Mr. J. J. D. SMITH, Geological Survey and Museum, London

Dr. C. D. WATERSTON, Royal Scottish Museum, Edinburgh

Mr. C. W. WRIGHT, London

Overseas Representatives

Australia: Professor DOROTHY HILL, Department of Geology, University of Queensland, Brisbane

Canada: Dr. D. J. McLAREN, Geological Survey of Canada, Department of Mines and Technical Surveys, Ottawa

India: Professor M. R. SAHNI, Department of Geology, Panjab University, Chandigarh

New Zealand: Dr. C. A. FLEMING, New Zealand Geological Survey, P.O. Box 368, Lower Hutt

West Indies and Central America: Dr. L. J. CHUBB, Geological Survey Department, Kingston, Jamaica

Eastern U.S.A.: Professor H. B. WHITTINGTON, Museum of Comparative Zoology, Harvard University, Cambridge 38, Mass.

Western U.S.A.: Dr. J. WYATT DURHAM, Department of Paleontology, University of California, Berkeley 4, Calif.

PALAEONTOLOGY

VOLUME 5 • PART 3

CONTENTS

The Palaeontology of the Namurian rocks of Slieve Anierin, Co. Leitrim, Eire. <i>By the late</i> PATRICIA J. YATES	355
Further studies on micro-organisms and the presence of syngenetic pyrite. <i>By</i> LEONARD G. LOVE	444
The Silurian trilobite <i>Encrinurus punctatus</i> (Wahlenberg) and allied species. <i>By</i> R. P. TRIPP	460
Microplankton from the Ampthill Clay of Melton, South Yorkshire. <i>By</i> W. A. S. SARJEANT	478
Some Diplograptids from the British Lower Silurian. <i>By</i> G. H. PACKHAM	498
New ammonites from the Barremian of North Bulgaria. <i>By</i> J. R. MANOLOV	527
Some Wenlockian fenestrate Bryozoa. <i>By</i> T. G. MILLER	540
Lower Carboniferous microfloras of Spitsbergen—Part I. <i>By</i> G. PLAYFORD	550

VOLUME 5 · PART 4

Palaeontology

FEBRUARY 1963

PUBLISHED BY THE
PALAEOLOGICAL ASSOCIATION
LONDON

Price £3

THE PALAEOONTOLOGICAL ASSOCIATION

The Association was founded in 1957 to further the study of palaeontology. It holds meetings and demonstrations, and publishes the quarterly journal *Palaeontology*. Membership is open to individuals, institutions, libraries, &c., on payment of the appropriate annual subscription:

Institutional membership	£5. 5s. (\$15.50)
Ordinary membership	£3. 3s. (\$ 9.50)
Student membership	£2. 2s. (\$ 6.50)

There is no admission fee. Student members will be regarded as persons receiving full-time instruction at educational institutions recognized by the Council. Subscriptions are due each January, and should be sent to the Treasurer, Professor P. C. Sylvester-Bradley, Department of Geology, The University, Leicester, England.

Palaeontology is devoted to the publication of papers (preferably illustrated) on all aspects of palaeontology and stratigraphical palaeontology. Four parts are published each year and are sent free to all members of the Association. Members who join for 1963 will receive Volume 6, Parts 1 to 4.

All back numbers are still in print and may be ordered from B. H. Blackwell, Broad Street, Oxford, England, at the prices shown below (post free):

Vol. 1 (for 1957-8) in 4 parts at £2 or \$6.00 per part.

Vol. 2 (for 1959) in 2 parts at £2 or \$6.00 per part.

Vol. 3 (for 1960) in 4 parts at £2 or \$6.00 per part.

Vol. 4 (for 1961) in 4 parts at £2 or \$6.00 per part.

Vol. 5 (for 1962) in 4 parts at £3 or \$9.00 per part.

A complete set, Volumes 1-5, consists of 18 parts and costs £40 or \$120.

Manuscripts on all aspects of palaeontology and stratigraphical palaeontology are invited. They should conform in style to those already published in this journal, and should be sent to Mr. N. F. Hughes, Sedgwick Museum, Cambridge, England. A sheet of detailed instructions for authors will be supplied on request.

LOWER CARBONIFEROUS MICROFLORAS OF SPITSBERGEN

by G. PLAYFORD

PART TWO

Part I of this paper will be found in Volume 5, Part 3, pages 550–618, with an abstract on page 550; it includes the list of references. Part II continues and concludes the paper; a contents list is placed at the end of this part.

Anulatisporites orbiculatus (Waltz) comb. nov.

Plate 88, fig. 1

1941 *Zonotriletes orbiculatus* Waltz in Lubert and Waltz, p. 24; pl. 4, fig. 60.

1957 *Euryzonotriletes orbiculatus* (Waltz) Naumova; Kedo, p. 1168.

Diagnosis. The following is the present writer's translation of the diagnosis given by Waltz (in Lubert and Waltz 1941, p. 24): 'Diameter—92·5–137·5 μ . Colour brownish yellow. Spore body outline circular; surface of body smooth. Border wide, rather thick, with even or slightly fluted outer edge. On surface of border small wrinkles or folds having concentric orientation are sometimes observed. Thickness of exine on spore body and on border approximately equal. Trilete fissures very prominent, smooth, equal, slightly elevated or thickened. Length of rays equal to, or slightly less than, spore body radius. *Z. orbiculatus* Waltz is characterized by a considerable variation in the ratio between diameter of spore body and width of border. Diameter of spore body 50–70 μ . Width of border 15–75 μ .'

Description of specimens. The Spitsbergen specimens conform closely to the above diagnosis. Exine thickness is 2·5–4 μ on spore body. Cingulum of any particular specimen is of uniform width. Surface of cingulum laevigate to infrapunctate (oil immersion); punctate in corroded specimens, particularly around spore-body margin.

Dimensions (12 specimens). Overall equatorial diameter 92–120 μ (mean 105 μ); diameter of spore body 49–71 μ (mean 61 μ); width of cingulum 16–30 μ (mean 22 μ).

Remarks. The species is included in the genus *Anulatisporites* on the basis of its broad, sculptureless cingulum.

Previous records. *Anulatisporites orbiculatus* (Waltz) comb. nov. has been recorded from Tournaisian–Viséan strata of the Kizel district, U.S.S.R. (Lubert and Waltz 1941), and from the Viséan of White Russia (Kedo 1957, 1958, 1959).

Anulatisporites canaliculatus sp. nov.

Plate 88, figs. 2, 3

Diagnosis. Spores radial, trilete; amb smooth, subtriangular with well-rounded apices and convex sides. Laesurae distinct, straight, length approximately 1·5–4 μ less than [Palaeontology, Vol. 5, Part 4, 1962, pp. 619–678, pls. 88–95.]

spore-body radius; accompanied by conspicuous, flat, smooth, slightly elevated lips, which extend 4–7 μ on either side of laesurae and often have lobed outer margins. Spore body laevigate. Cingulum distinctively incised on proximal surface by a single, continuous, very narrow furrow situated approximately 2.5–5.5 μ from, and more or less conformable with, smooth spore-body margin. Cingulum otherwise undifferentiated, laevigate (irregularly punctate in corroded specimens), uniformly broad, much darker in colour than spore body.

Dimensions (35 specimens). Overall equatorial diameter 54–86 μ (mean 70 μ); diameter of spore body 33–50 μ (mean 41 μ); width of cingulum 11–21 μ (mean 15 μ).

Holotype. Preparation P173/2, 53.1 100.1. L.1125.

Locus typicus. Citadellet (sample G1446), Spitsbergen; Lower Carboniferous.

Description. Holotype 79 μ overall, spore-body diameter 45 μ , width of cingulum 17 μ ; laesurae extending to within 2.5 μ of spore-body margin, lips individually about 4.5 μ wide; furrow incised in cingulum uniformly about 4 μ from spore-body margin, depth about 2 μ . In some specimens the margin between the spore body and the cingulum on the distal hemisphere may be rather undulating showing only general conformity to equatorial outline.

Comparison. The generally larger *Zonotriletes sulcatus* Waltz (*in* Luber and Waltz 1938, p. 18; pl. 2, fig. 20) has numerous, rather discontinuous, concentric furrows in the cingulum, which is definitely thickened at its inner margin.

GENUS DENSOSPORITES (Berry) Potonié and Kremp 1954

Type species. *D. covensis* Berry 1937.

Discussion. This genus and the morphographically associated *Anulatisporites* Loose *ex* Potonié and Kremp 1954 are presently receiving consideration from a subcommittee of the International Commission for the Microflora of the Palaeozoic; as a result, their redefinition, together with the erection of several other related genera, seems likely. This reappraisal of the densospore group will be based principally upon the sculpture of the cingulum, and it is to be hoped that due regard will be given to the effects of corrosion, both natural and in preparation, which in many cases seems to cause profound cingulate alteration (*cf.* Bharadwaj 1959, p. 70). Pending publication of the Commission's proposals, the Spitsbergen spores concerned are here assigned to either *Densosporites* or to *Anulatisporites* as formally emended by Potonié and Kremp (1954).

Affinity. In view of the abundance of representatives of this genus in sediments (particularly coals) of Carboniferous age, it is surprising that only recently has evidence come forward as to its botanical affinity. Chaloner (1958*a*) reported microspores similar to *Densosporites lorincatus* (Loose) Schopf, Wilson, and Bentall 1944 from a small Upper Carboniferous lycopod cone compression, which he termed *Selaginellites canonbiensis* sp. nov. Subsequently, Bharadwaj (1959) obtained microspores conformable with *Densosporites* from the heterosporous lycopod strobilus *Porostrobus zeilleri* Nathorst 1914 which had been collected from Lower Carboniferous strata at Pyramiden, Spitsbergen. It will be seen that the abundantly occurring *sporae dispersae*, described below as *Densosporites spitsbergensis* sp. nov., resemble closely the microspores obtained by

Bharadwaj (from *P. zeilleri*). In a postscript to his paper, Bharadwaj recommended the inclusion of *Selaginellites canonbiensis* Chaloner within *Bothrostrobus* (Nathorst) Seward.

Densosporites bialatus (Waltz) Potonié and Kremp 1956

Plate 88, figs. 4–7

- 1938 *Zonotriletes bialatus* Waltz in Lubert and Waltz, p. 22; pl. 4, fig. 51.
 1941 *Zonotriletes bialatus* Waltz var. *undulatus* Waltz in Lubert and Waltz, pp. 28–29; pl. 5, fig. 71a, b.
 1941 *Zonotriletes bialatus* Waltz var. *costatus* Waltz in Lubert and Waltz, p. 29; pl. 5, fig. 72.
 1952 *Hymenozonotriletes* aff. *bialatus* (Waltz) Ishchenko, p. 51; pl. 13, fig. 124.
 1956 *Densosporites bialatus* (Waltz) Potonié and Kremp, p. 114.
 1956 *Hymenozonotriletes bialatus* (Waltz) var. *undulatus* (Waltz) Ishchenko, pp. 63–64; pl. 12, figs. 135–7.
 1957 *Cingulizonates tuberosus* Dybová and Jachowicz, p. 171; pl. 53, figs. 1–4.
 1957 *Trematozonotriletes bialatus* (Waltz) Naumova; Byvsheva, p. 1010.

Description of specimens. Spores radial, trilete; amb roundly subtriangular to oval, more or less conformable with convexly subtriangular body outline. Laesurae perceptible or not visible (corroded specimens); simple, straight to sinuous, length approximately equal to body radius. Where preserved, body exine is finely granulate or punctate. Differentiated cingulum, consisting of: an inner, thickened, opaque portion characteristically sculptured with fine, radially elongated pits; surrounded by a thinner, translucent zone which is approximately one-third to half of the total cingulum width. Conspicuous junction between the two parts of the cingulum may be regular, conforming closely with the spore-body outline; in many cases, however, it is irregularly lobed or dentate due to radial, equatorially tapering extensions of the thickened part projecting into, but rarely attaining margin of, the outer thinner portion.

Dimensions (60 specimens). Overall equatorial diameter 46–77 μ (mean 60 μ); diameter of spore body 21–34 μ (mean 27 μ).

Remarks. In her diagnosis of *Zonotriletes bialatus*, Waltz (in Lubert and Waltz 1938, p. 22) drew attention to the variable structure of the inner thickened portion of the cingulum, suggesting its dependence upon the state of preservation. Subsequently, Waltz (in Lubert and Waltz 1941, pp. 28–29) delineated two varieties (*undulatus* and *costatus*) within the species, on the basis of this variation. Both varieties are represented in the Spitsbergen assemblages, but their continuous intergradation does not support their recognition as separate morphographical units. The illustrations of *Cingulizonates tuberosus* Dybová and Jachowicz 1957 (pl. 53, figs. 1–4) strongly suggest conspecificity with *Densosporites bialatus* (Waltz), and indeed Jachowicz (1958, table 8) subsequently equated the two species.

There seems little doubt of the presence of *D. bialatus* within the Upper Mississippian spore assemblage described by Hacquebard and Barss (1957). These authors remarked (p. 32) that their species *Densosporites irregularis* 'may be conspecific with *Zonotriletes bialatus* Waltz, 1938', and certainly the spores represented by their plate 4, figs. 12, 13 (*D. irregularis*) and by plate 4, fig. 10 (*D. cuneiformis*) show close resemblance to *D. bialatus*.

Previous records. *Densosporites bialatus* (Waltz) has been recorded by numerous Russian

palynologists from the Lower Carboniferous of the U.S.S.R. (Luber and Waltz 1938, 1941; Ishchenko 1952, 1956, 1958; Byvsheva 1957, 1960; Loginova 1959). It has been recorded also from the Namurian A to Westphalian B interval of the Upper Silesian Coal Measures (Dybová and Jachowicz 1957; Jachowicz 1958), and is probably present in the Upper Mississippian of the South Nahanni River area, Northwest Territories, Canada (Hacquebard and Barss 1957).

Ishchenko (1956) documented occurrences of the species, in the western Donetz Basin, from Viséan to Namurian, and subsequently (1958), in the Dnieper-Donetz Basin, from Tournaisian to Bashkirian.

Densosporites dentatus (Waltz) Potonié and Kremp 1956

Plate 88, figs. 14, 15

1884 Type 274 of Reinsch, p. 27; pl. 20, fig. 128A.

1938 *Zonotriletes dentatus* Waltz in Luber and Waltz, p. 20; pl. 14, fig. 47.

1956 *Densosporites dentatus* (Waltz) Potonié and Kremp, p. 115.

1958 *Hymenozonotriletes dentatus* (Waltz) Ishchenko, pp. 70-71; pl. 7, fig. 96.

Description of specimens. Spores radial, trilete; amb oval to roundly subtriangular. Laesurae simple, straight to sinuous, extending to spore-body margin. Exine of spore body laevigate to granulate; very thin, hence often poorly preserved or absent. Cingulum uniform, relatively dark in colour, width 9-20 μ , equatorial margin regularly dentate.

Dimensions (50 specimens). Overall equatorial diameter 36-65 μ (mean 49 μ); diameter of spore body 20-31 μ (mean 25 μ).

EXPLANATION OF PLATE 88

All figures $\times 500$, and from unretouched negatives.

Fig. 1. *Anulatisporites orbiculatus* (Waltz) comb. nov. Proximal surface; preparation P148/4, 48.2 95.0 (L.1124).

Figs. 2, 3. *Anulatisporites canaliculatus* sp. nov. 2, Proximal surface; preparation P163/6, 44.2 112.7 (L.1126). 3, Holotype; proximal surface.

Figs. 4-7. *Densosporites bialatus* (Waltz) Potonié and Kremp 1956. 4, Distal surface; preparation P164/5, 38.2 93.1 (L.1129). 5, Distal surface; preparation P164/9, 35.3 101.4 (L.1128). 6, Proximal surface; preparation P167B/3, 50.6 95.1 (L.1130). 7, Distal surface; preparation P167B/1, 28.6 94.3 (L.1131).

Figs. 8, 9. *Densosporites subcrenatus* (Waltz) Potonié and Kremp 1956. 8, Proximal surface; preparation P145B/32, 41.5 103.3 (L.1134). 9, Proximal surface; preparation P145C/1, 29.0 94.9 (L.1135).

Figs. 10, 11. *Densosporites diatretus* nom. nov. 10, Proximal surface; preparation P176A/1, 40.9 95.4 (L.1137). 11, Distal surface; preparation P148/1, 25.0 95.4 (L.1136).

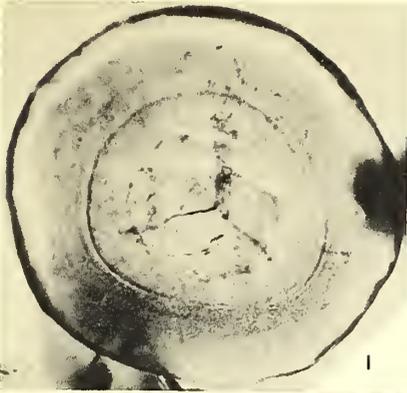
Figs. 12, 13. *Densosporites striatifertus* Hughes and Playford 1961. 12, Proximal surface; preparation P172/3, 25.9 95.5 (L.1145). 13, Proximal surface; preparation P170/1, 23.8 97.2 (L.1144).

Figs. 14, 15. *Densosporites dentatus* (Waltz) Potonié and Kremp 1956. 14, Proximal surface; preparation P148/1, 45.2 95.6 (L.1132). 15, Distal surface; preparation P143B/5, 33.8 106.7 (L.1133).

Figs. 16, 17. *Densosporites aculeatus* sp. nov. 16, Holotype; distal surface. 17, Proximal surface; preparation P201/2, 29.8 102.1 (L.1164).

Fig. 18. *Densosporites* sp. Proximal surface; preparation P167B/13, 38.8 103.0 (L.1166).

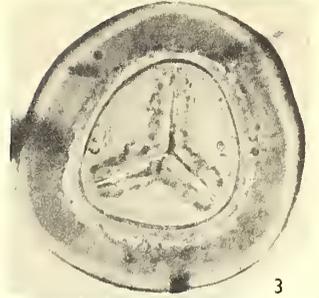
Figs. 19-22. *Densosporites variabilis* (Waltz) Potonié and Kremp 1956. 19, 20, Distal and proximal surfaces respectively; preparation P154/6, 22.7 100.8 (L.1140). 21, Proximal surface; preparation P145B/31, 36.3 102.7 (L.1138). 22, Proximal surface; preparation P158/4, 21.1 93.5 (L.1139).



1



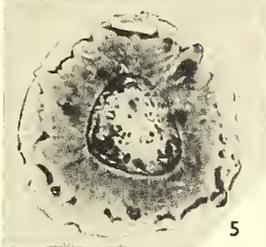
2



3



4



5



6



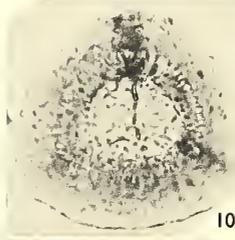
7



8



9



10



11



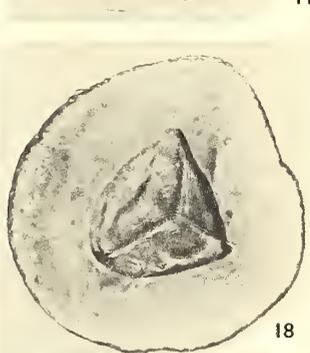
12



13



14



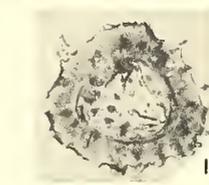
15



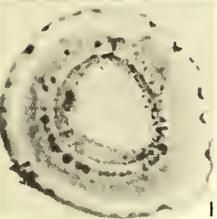
16



17



18



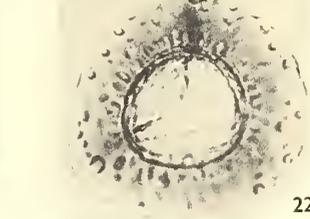
19



20



21



22

Comparison. Some of the spores described by Hoffmeister, Staplin, and Malloy (1955, p. 386; pl. 36, figs. 16, 17) as *Densosporites spinifer*, and subsequently recorded as such by Butterworth and Williams (1958, p. 359; pl. 3, fig. 46) and by Love (1960, p. 109), may be representative of *D. dentatus* (Waltz).

Previous records. Recorded initially by Reinsch (1884) from the Russian Carboniferous. Later and more precisely documented Russian occurrences are from the Lower Carboniferous of the Moscow Basin and of the Kizel, Selizharovo, Voronezh, and Borovichi districts (Luber and Waltz 1938, 1941), and from exclusively Viséan sediments of the Dnieper–Donetz Basin (Ishchenko 1958). Thus this Spitsbergen occurrence is the first reported definitely outside Russia.

Densosporites subcrenatus (Waltz) Potonié and Kremp 1956

Plate 88, figs. 8, 9

1938 *Zonotriletes subcrenatus* Waltz in Luber and Waltz, p. 19; pl. 4, fig. 43.

1956 *Densosporites subcrenatus* (Waltz) Potonié and Kremp, p. 116.

1958 *Hymenozonotriletes subcrenatus* (Waltz) Ishchenko, p. 77; pl. 9, fig. 112.

[non *Tendosporites subcrenatus* (Waltz) Hacquebard and Barss 1957, p. 36; pl. 5, figs. 3, 4.]

Description of specimens. Spores radial, trilete; amb subtriangular, more or less conformable with spore-body outline. Laesurae distinct, simple, straight, length slightly less than body radius. Spore-body exine essentially laevigate, sometimes finely wrinkled; body outline triangular with rounded apices and \pm straight sides. Cingulum laevigate; with crenulate, fringe-like equatorial margin which is often at least partially absent in poorly preserved specimens. Corroded specimens often tend to approach the aspect of *Tripartites*, notably of *T. incisotrilobus* (Naumova; Waltz) Potonié and Kremp 1956 (cf. Waltz in Luber and Waltz 1938, p. 19; Ishchenko 1958, p. 77), although incisement or embayment of the cingulum is not necessarily located interradially.

Dimensions (30 specimens). Overall equatorial diameter 44–65 μ (mean 55 μ); diameter of spore body 26–39 μ (mean 32 μ).

Comparison. The specimens described by Hacquebard and Barss (1957, p. 36; pl. 5, figs. 3, 4) as *Tendosporites subcrenatus* (Waltz) were incorrectly referred to Waltz's species, since they possess a cingulum which is 'irregularly thickened at the periphery'; this is not a feature diagnosed by Waltz or evident from the Spitsbergen representatives. Some of the spores figured by Reinsch (1884, e.g. pl. 3, figs. 38, 41; pl. 17, fig. 41; pl. 19, fig. 41D; pl. 20, fig. 118L) resemble *Densosporites subcrenatus* (Waltz).

Previous records. Previous definite occurrences are confined to the Russian Lower Carboniferous. Luber and Waltz (1938, 1941) record the species from the Moscow Basin and Kizel region, and Ishchenko (1958, stratigraphical range table 3) found it to be restricted to Viséan–Namurian strata of the Dnieper–Donetz Basin.

Densosporites diatretus nom. nov.

Plate 88, figs. 10, 11; text-fig. 9a

1941 *Zonotriletes intermedius* Waltz in Luber and Waltz, pp. 27–28; pl. 5, fig. 68.

1956 *Hymenozonotriletes intermedius* (Waltz) Ishchenko, pp. 64–65; pl. 12, fig. 139.

[non *Densosporites intermedius* Butterworth and Williams, 1958, p. 379; pl. 3, figs. 38, 39.]

Diagnosis. The following is the present writer's translation of the diagnosis given by Waltz (*in* Luber and Waltz 1941): 'Diameter—55–70 μ . Colour brownish yellow. Outline of spore body roundly triangular. Border wide, thick, bearing superficially two types of sculpture. Nearer to the inside edge of the border is an arrangement of short, radial grooves; on the rest of the surface sparsely distributed tuberculate thickenings can be observed. The former type of sculpture comes close to that of *Zonotriletes variabilis* Waltz var. *valleculosus* Waltz, the second shows much similarity to the sculpture of *Zonotriletes polyzonalis* Waltz. The fact that the species described is found in conjunction with the two others mentioned, and also the similarity of morphological features, argues in favour of the existence of a definite link between them. Diameter of spore body 15–25 μ . Width of border 15–30 μ .'

Holotype (here designated). Spore illustrated by Luber and Waltz 1941, pl. 5, fig. 68 (here reproduced as Text-fig. 9a).



TEXT-FIG. 9. a, *Densosporites diatretus* nom. nov., redrawn from Luber and Waltz 1941, pl. 5, fig. 68. b, *Lophozonotriletes rarituberculatus* (Luber) Kedo 1957, redrawn from Luber and Waltz 1941, pl. 5, fig. 76. c. $\times 500$.

Description of specimens. Those observed in the Spitsbergen assemblages conform closely to the above diagnosis, and to the following additional remarks.

Amb varies from convexly subtriangular to triangular (this variation was noted also by Ishchenko 1956, 1958). The radial grooves are confined to the inner margin of the cingulum, and are often much finer and more closely spaced than in the spore illustrated by Waltz (*in* Luber and Waltz 1941; pl. 5, fig. 68) and reproduced herein (text-fig. 9a). The positive sculptural elements on the remainder of the cingulum are usually more strongly developed on the distal surface; in different specimens they range from small coni to larger rod-like thickenings. The cingulum is often rather indistinctly differentiated into an outer light zone and an inner, darker (thicker) zone; this feature was emphasized by Ishchenko (1958, p. 71). Laesurae, apparent only on well-preserved specimens, are distinct, simple, straight to slightly sinuous, length approximately equal to spore-body radius, sometimes extending on to cingulum.

Dimensions (70 specimens). Overall equatorial diameter 55–76 μ (mean 66 μ); diameter of spore body 16–35 μ (mean 25 μ); width of cingulum 14–25 μ (mean 20 μ).

Remarks. This species is included within *Densosporites* (Berry) Potonié and Kremp on the basis of its massive, distinctively sculptured cingulum. Ishchenko (1956, 1958) transferred *Zonotriletes intermedius* Waltz 1941 to *Hymenozonotriletes* Naumova 1937; however, the latter genus as understood by Potonié (1958, p. 29) and evidently by

Naumova (1953) embraces prominently zonate forms having conspicuous spinose sculpture. Thus Ishchenko's assignment of this species is unacceptable.

Comparison. *Densosporites diatretus* nom. nov. shows some resemblance to *Vallatisporites* Hacquebard (1957, p. 312) but lacks the distinct 'groove or rampart-like area' characteristic of that genus. Butterworth and Williams (1958, p. 379) described, from the Scottish Lower Carboniferous, a species which they named *Densosporites intermedius*. These spores are clearly different from those of *Hymenozonotriletes intermedius* (Waltz 1941); hence it is necessary to erect a new trivial epithet for the species on its inclusion in *Densosporites* (ref. articles 55 and 64 of the 1961 International Code of Botanical nomenclature).

Previous records. *Densosporites diatretus* nom. nov. has been recorded previously from Russia only, as follows: Lower Carboniferous of the Moscow Basin and Kizel region (Luber and Waltz 1941); Tournaisian to Middle Viséan only of the western extension of the Donetz Basin (Ishchenko 1956); and Tournaisian, Viséan, and Namurian of the Dnieper-Donetz Basin (Ishchenko 1958).

Densosporites variabilis (Waltz) Potonié and Kremp 1956

Plate 88, figs. 19-22

- 1938 *Zonotriletes variabilis* Waltz in Luber and Waltz, pp. 20-21; pl. 4, figs. 44-46, and pl. A, fig. 16.
 1941 *Zonotriletes variabilis* Waltz var. *foveolatus* Waltz in Luber and Waltz, p. 26; pl. 5, fig. 66a.
 1941 *Zonotriletes variabilis* Waltz var. *fossulatus* Waltz in Luber and Waltz, p. 26; pl. 5, fig. 66b.
 1941 *Zonotriletes variabilis* Waltz var. *valleculosus* Waltz in Luber and Waltz, p. 27; pl. 5, fig. 66c.
 1956 *Densosporites variabilis* (Waltz) Potonié and Kremp, p. 116.
 1956 *Trematozonotriletes variabilis* (Waltz) Ishchenko var. *foveolatus* Waltz; Ishchenko, pp. 102-3; pl. 22, fig. 248.
 1957 *Trematozonotriletes variabilis* (Waltz) Naumova; Byvsheva, p. 1010.
 [non *Densosporites variabilis* (Waltz) Potonié and Kremp; Butterworth and Williams 1958, pp. 380-1; pl. 3, figs. 32-34.]

Description of specimens. Spores radial, trilete; amb roundly subtriangular. Laesurae straight to sinuous, elevated and slightly thickened; frequently not preserved due to delicate spore-body exine. Uniformly thick cingulum prominently sculptured on proximal surface with numerous shallow pits or grooves arranged radially around outer margin of spore body; cavities rarely extend radially beyond centre of cingulum. Additional, irregular pitting on cingulum is often present, and may be attributable to corrosion. Spore body laevigate to granulate; outline more or less conformable with amb. Equatorial margin smooth, undulating, dentate or lobate.

Dimensions (80 specimens). Overall equatorial diameter 41-77 μ (mean 60 μ); diameter of spore body 19-34 μ (mean 26 μ).

Remarks. Three of the four illustrations of *Zonotriletes variabilis* in Luber and Waltz 1938 (pl. 4, figs. 44-46) were reproduced in Luber and Waltz 1941 (pl. 5, fig. 66a-c) and designated infraspecifically as the following varieties: *foveolatus*, *fossulatus*, and *valleculosus*, respectively. However, continuous morphographical variation between these forms

was noted by Waltz and is confirmed abundantly in the present investigation; as such, their infraspecific recognition does not appear warranted.

Comparison. *Densosporites diatretus* resembles *D. variabilis* (Waltz) in possessing similarly disposed radial grooves in the cingulum, which, however, is sculptured additionally with conspicuous tuberculate thickenings. As noted by Waltz (*in* Lubert and Waltz 1941), *D. diatretus* represents a sculptural intermediate between *D. variabilis* and *D. polyzonalis* (Waltz) Potonié and Kremp 1956. In the Spitsbergen assemblages the former two species are commonly although not invariably associated, and are certainly at least morphologically closely related. However, specimens positively identifiable with *D. polyzonalis* have not been observed by the writer.

Although showing similar sculpture to the specimens described above, *Trematizonotriletes variabilis* (Waltz) var. *trigonalis* Ishchenko 1956 (p. 103; pl. 20, fig. 249) possesses a cingulum which is consistently wider about the spore apices, and as such probably represents a distinct species.

Butterworth and Williams (1958) incorrectly assigned to *Densosporites variabilis* (Waltz) a species which they described as being 'abundant throughout' their Scottish Namurian assemblages; these authors implied identity of their specimens with that illustrated by Lubert and Waltz 1938 (pl. 4, fig. 46, subsequently *Zonotriletes variabilis* Waltz var. *valleculosus* Waltz 1941). However, from the description and photographs given by Butterworth and Williams (1958, pp. 380-1; pl. 3, figs. 32-34) and from the study of a slide kindly loaned to the writer by Dr. Butterworth, it is clear that the Scottish specimens differ from *D. variabilis* in the following important respects: (1) the spore body is rather poorly defined; (2) the cingulum shows relatively abrupt equatorial reduction in thickness; (3) the cingulate sculpture consists of irregular, elevated, radial thickenings enclosing equally irregular, and not invariably radially disposed, lumina, which are often imperfectly defined and are not concentrated along the inner margin of the cingulum. In contrast, *D. variabilis* possesses closely spaced, well-defined, pyriform pits, which are radially arranged about the distinct spore body, sharply punctuating an otherwise featureless cingulum of fairly uniform thickness; there is no appearance of the 'radial struts' described by Butterworth and Williams.

Previous records. *Densosporites variabilis* has been reported by numerous authors (Lubert and Waltz 1938, 1941; Ishchenko 1956, 1958; Bludorov and Tuzova 1956; Byvsheva 1957; Kedo 1957, 1958, 1959; Loginova 1959) as an important constituent of Tournaisian, and particularly Viséan-Namurian strata in the U.S.S.R. Recently Love (1960) recorded the species from the Pumpherston Shell Bed (Viséan) of Scotland, and Hughes and Playford (1961) reported its predominance in one sample (S59a) of the Spitsbergen Lower Carboniferous.

Densosporites duplicatus (Naumova) Potonié and Kremp 1956

Plate 89, figs. 6-8

1884 Type 336 of Reinsch, p. 33; pl. 16, fig. 125A.

1884 Type 337 of Reinsch, p. 33; pl. 9, fig. 125.

1938 *Zonotriletes duplicatus* (Naumova) Waltz *in* Lubert and Waltz, p. 21; pl. 4, fig. 53.

1956 *Densosporites duplicatus* (Naumova) Potonié and Kremp, p. 115.

1957 *Labiadensites* cf. *Z. duplicatus* (Naumova; Waltz) Hacquebard and Barss, p. 27; pl. 6, fig. 1.

Description of specimens. Spores radial, trilete; amb roundly subtriangular to sub-circular. Laesurae distinct, straight, length equal to, or slightly less than, spore-body radius; usually accompanied by minor lip development—lips individually about $3\ \mu$ broad, with somewhat irregular outer margins. Spore body concavely or convexly subtriangular to subcircular; laevigate to finely granulate. Outer margin of cingulum strongly and characteristically differentiated into numerous laterally projecting processes which are approximately $10\text{--}15\ \mu$ long, $3\text{--}4\ \mu$ in basal diameter, and are conspicuously expanded and thickened apically into crescentic (mushroom-shaped) caps. These prominent peltate processes are usually very closely packed, often appearing to lie in more than one horizontal plane. Cingulum otherwise laevigate, colour slightly darker than body.

Dimensions (70 specimens). Overall equatorial diameter (including processes) $51\text{--}77\ \mu$ (mean $64\ \mu$); diameter of spore body $26\text{--}39\ \mu$ (mean $32\ \mu$).

Remarks. On the basis of a single specimen, Hacquebard and Barss (1957) proposed the assignment of *Zonotriletes duplicatus* (Naumova) to their new genus *Labiadensites*, which was said to differ from *Densosporites* in its invariable possession of 'a strong trilete and greatly developed lips'. It is evident from the examination of numerous Spitsbergen representatives that lips are only sporadically and never strongly developed in this species; furthermore, the earlier descriptions and illustrations given by Reinsch (1884) and Lubert and Waltz (1938) contain no reference to such laesurate modification. Hence the species seems more suitably included within *Densosporites*, as advocated by Potonié and Kremp (1956, p. 115).

Previous records. *Densosporites duplicatus* was first recorded by Reinsch (1884) from Russian 'Stigmarienkohle' of presumably Lower Carboniferous age. More recently, the species has been reported from Lower Carboniferous deposits of the Moscow Basin and Kizel and Selizharovo regions, U.S.S.R. (Lubert and Waltz 1938, 1941); and from Upper Mississippian coal of the South Nahanni River area, Northwest Territories, Canada (Hacquebard and Barss 1957).

Densosporites striatiferus Hughes and Playford 1961

Plate 88, figs. 12, 13

Dimensions (40 specimens). Overall equatorial diameter $44\text{--}65\ \mu$ (mean $54\ \mu$); diameter of spore body $27\text{--}45\ \mu$ (mean $35\ \mu$); width of cingulum $6\text{--}12\ \mu$ (mean $9\ \mu$).

Densosporites spitsbergensis sp. nov.

Plate 89, figs. 1-5

Diagnosis. Spores radial, trilete; amb subtriangular, more or less conformable with body outline. Laesurae perceptible to distinct, straight or slightly sinuous; extending on to cingulum as thickened, elevated ridges which often attain equatorial margin. Spore body convexly subtriangular, exine often poorly preserved or absent. Cingulum robust, darker in colour than body; slight and gradual equatorial decrease in thickness. Prominent spinose sculpture on distal surface of spores (body and cingulum); spines

crowded and frequently coalescent around inner margin of cingulum, reduced in size and density in equatorial region; length of spines 1.5–5 μ , basal diameter 1–2.5 μ . Proximal surface of spores laevigate to sparsely granulate or spinose.

Dimensions (100 specimens). Overall equatorial diameter 55–80 μ (mean 66 μ); diameter of spore body 23–39 μ (mean 31 μ).

Holotype. Preparation P163/3, 22.2 96.8. L.1146.

Locus typicus. Birger Johnsonfjellet (sample G1089), Spitsbergen; Lower Carboniferous.

Description. Holotype convexly subtriangular, 64 μ overall; spore-body diameter 28 μ ; laesurae distinct, extending to equatorial margin. The species is characterized by its conspicuous distal spinose sculpture, long laesurae, and well-developed cingulum which shows slight reduction in thickness towards the equator; it is a common microfloral constituent of many of the Spitsbergen samples.

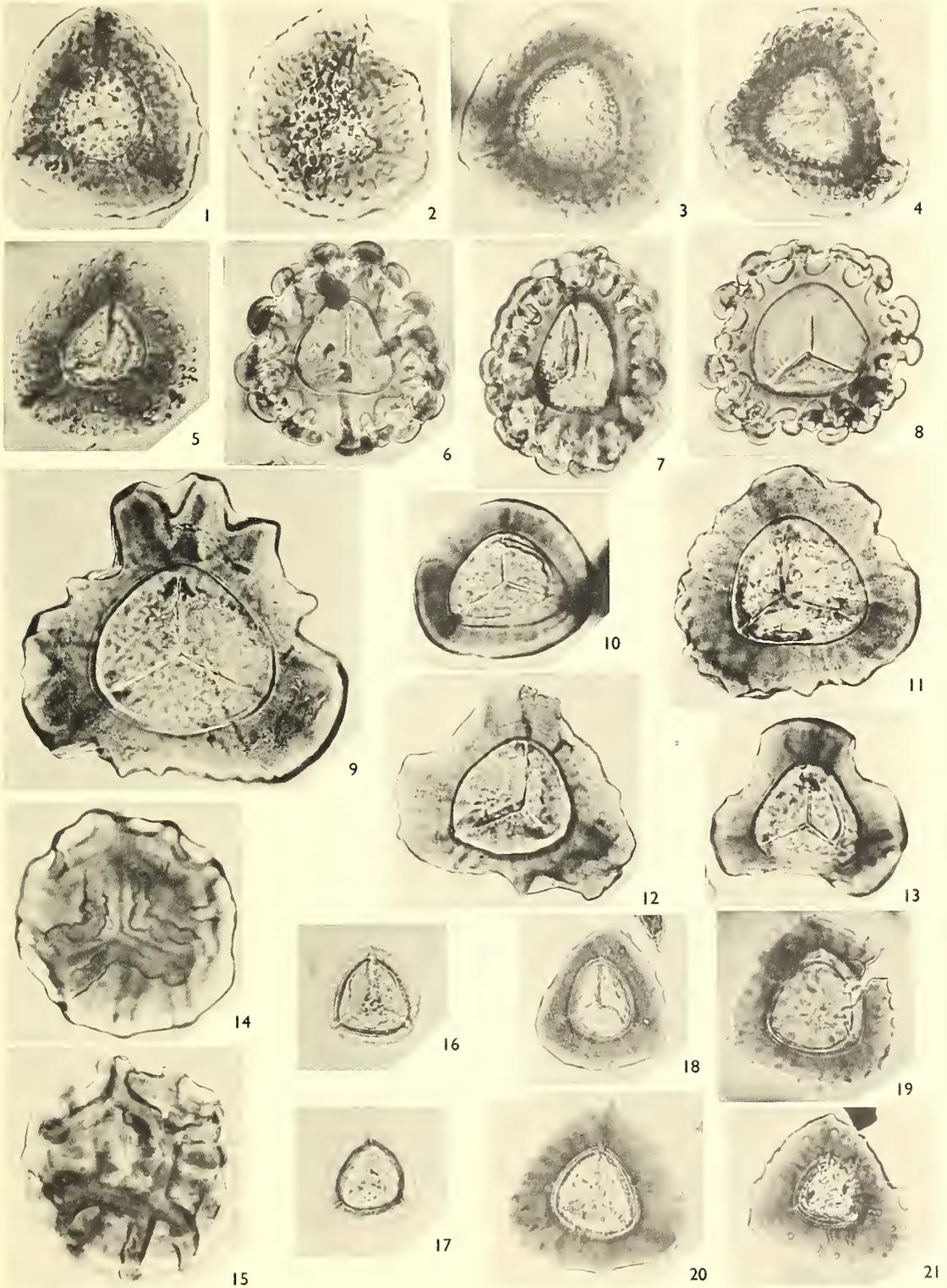
Comparison. *Densosporites pannosus* Knox 1950 (p. 326; pl. 18, fig. 267) is more uniformly and comprehensively spinose and has more prominent, laesurate lips.

Remarks. The *spores dispersae* described above as *Densosporites spitsbergensis* sp. nov. compare closely in all respects with the microspores obtained by Bharadwaj (1959, p. 70; pl. 2, figs. 8–14) from the fructification *Porostrobus zeilleri* Nathorst 1914, which had been collected in 1882 by Nathorst from the Culm (Lower Carboniferous) at Pyramiden, Spitsbergen. Furthermore, representatives occurring in poorly preserved or overmacerated preparations are very similar to the microspores (from *P. zeilleri*) which Bharadwaj had treated with excessive potassium hydroxide. From the widespread occurrence of *D. spitsbergensis* it seems reasonable to assume concomitant widespread distribution of *P. zeilleri* in Spitsbergen during Lower Carboniferous times.

EXPLANATION OF PLATE 89

All figures $\times 500$, and from unretouched negatives.

- Figs. 1–5. *Densosporites spitsbergensis* sp. nov. 1, Holotype; proximal surface. 2, Distal surface; preparation P162/5, 50.7 104.9 (L.1147). 3, Proximal surface; preparation P163/1, 27.0 96.5 (L.1148). 4, Distal surface; preparation P148/4, 44.2 107.3 (L.1149). 5, Proximal surface; preparation P164/2, 42.3 103.2 (L.1150).
- Figs. 6–8. *Densosporites duplicatus* (Naumova) Potonié and Kremp 1956. 6, Proximal surface; preparation P145A/1, 45.0 110.0 (L.1141). 7, Proximal surface; preparation P145B/1, 23.1 104.7 (L.1142). 8, Proximal surface; preparation P145B/27, 26.3 103.2 (L.1143).
- Figs. 9–13. *Densosporites variomarginatus* sp. nov. 9, Proximal surface; preparation P148/56, 39.2 103.7 (L.1153). 10, Proximal surface; preparation P162/6, 30.0 106.4 (L.1154). 11, Holotype; proximal surface. 12, Proximal surface; preparation P148/27, 35.3 104.5 (L.1156). 13, Proximal surface; preparation P163/6, 38.9 101.2 (L.1155).
- Figs. 14, 15. *Knoxisporites cinctus* (Waltz) Butterworth and Williams 1958. Proximal and distal surfaces respectively; preparation P163/7, 30.4 98.9 (L.1170).
- Figs. 16, 17. *Lycospora uber* (Hoffmeister, Staplin, and Malloy) Staplin 1960. 16, Distal surface; preparation P180B/1, 52.8 105.0 (L.1180). 17, Proximal surface; preparation P180B/4, 43.7 106.4 (L.1181).
- Figs. 18–21. *Densosporites rarispinosus* sp. nov. 18, Proximal surface; preparation P180B/1, 51.5 101.5 (L.1159). 19, Distal surface; preparation P145C/2, 34.7 107.3 (L.1160). 20, Holotype; proximal surface. 21, Distal surface; preparation P145B/1, 17.9 96.7 (L.1161).



Densosporites variomarginatus sp. nov.

Plate 89, figs. 9–13

Diagnosis. Spores radial, trilete, subtriangular. Equatorial margin irregular, i.e. smooth, undulating, dentate or lobate. Laesurae distinct, simple, usually straight, almost attaining spore-body margin. Body laevigate, sometimes finely wrinkled; outline subtriangular with rounded apices and convex to slightly concave sides. Cingulum relatively dense, laevigate or with punctations arranged parallel to spore-body outline. Cingulum has perceptibly to distinctly radiating or striated appearance due apparently to an alternation of intrinsic, non-elevated, usually poorly defined radial 'bands' of differing thickness; the breadth of these bands is (collectively) highly variable.

Dimensions (100 specimens). Overall equatorial diameter 44–102 μ (mean 68 μ); diameter of spore body 27–55 μ (mean 39 μ); (maximum) width of cingulum 7–27 μ (mean 15 μ).

Holotype. Preparation P148/62, 40·8 104·9. L.1152.

Locus typicus. Triungen (sample G1472), Spitsbergen; Lower Carboniferous.

Description. Holotype 77 μ overall; spore body microrugulate, outline convexly subtriangular, diameter 43 μ ; cingulum concentrically and finely punctate, width fairly uniform (c. 17 μ), overall distinctly radiating appearance; equatorial margin irregularly undulating.

Despite its generally ill-defined nature (particularly in well-preserved specimens), the radially striated structure of the cingulum is always recognizable. Corrosion, either natural or in preparation, appears to have the effect of emphasizing the structure by embaying the thinner, radial areas, and resulting in an undulating or distinctly lobed equatorial margin. Thus the highly variable nature of the periphery of the cingulum, ranging as a continuous variation from entire to deeply and irregularly incised, is considered to be the result of a concomitant variation in preservation from excellent to poor, respectively. That the margin of the cingulum is highly susceptible to corrosive attack is indicated by the comparative scarcity, even in generally well-preserved assemblages, of specimens possessing an entire, uniformly broad cingulum, and further by the invariable absence of such specimens in poorly preserved assemblages. In some specimens the cingulum appears thickest about the triangular apices of the body.

Comparison. *Densosporites striatus* (Knox 1950, p. 330; pl. 19, fig. 289) Butterworth and Williams 1958 differs from *D. variomarginatus* sp. nov. in having a cingulum that is differentiated into an inner thickened portion and an outer, distinctly thinner zone. The cingulum of *D. subcrenatus* (Waltz) Potonié and Kremp 1956 is marginally crenulate and of essentially uniform, certainly non-striated appearance. *Tendosporites subcrenatus* (non Waltz) Hacquebard and Barss 1957 (p. 36; pl. 5, figs. 3, 4) has shorter laesurae than *D. variomarginatus* and is further distinguished by the irregular peripheral thickening of its cingulum, which is otherwise of approximately the same density as the spore body. *D. heterotomus* (Waltz in Luber and Waltz 1938, pp. 19–20; pl. 2, fig. 28) Potonié and Kremp 1956 may be similar to *D. variomarginatus*. The drawing given by Luber and Waltz depicts a striate cingulum, which is not, however, described as such in the text or evident from type 612 of Reinsch (1884, p. 60; pl. 38, fig. 257) with which Waltz equated her species. Moreover, and in contrast with *D. variomarginatus*, *D. heterotomus* possesses

thickened laesurate lips, is often granulate, and generally much larger (95–120 μ). *D. striatiferus* Hughes and Playford 1961 has much finer and more closely spaced cingulate striations than *D. variomarginatus*.

Densosporites rarispinosus sp. nov.

Plate 89, figs. 18–21; text-fig. 10d

Diagnosis. Spores radial, trilete; amb more or less conformable with convexly sub-triangular spore-body outline. Laesurae simple, perceptible to distinct, straight or sinuous, extending equatorially 2–4 μ beyond body margin. Conspicuous distal sculpture of sparsely and irregularly distributed simple spines, which usually project also from equatorial margin; spinae variable in height (1–6 μ), bases circular or subcircular (diameter 0.5–3 μ); subordinate, small verrucae occasionally additionally present. Apart from this sculpture, spore body and cingulum laevigate to finely punctate (corroded specimens). Cingulum non-tapering, and much darker in colour than spore body.

Dimensions (60 specimens). Overall equatorial diameter 37–67 μ (mean 51 μ); diameter of spore body 18–33 μ (mean 24 μ).

Holotype. Preparation P145C/1, 49.6 98.1. L.1158.

Locus typicus. Triungen (sample G1466), Spitsbergen; Lower Carboniferous.

Description. Holotype 53 μ overall, spore body 27 μ ; irregularly disposed distal spinae 1.5–6 μ long, 1–2.5 μ broad at base, 4–12 μ apart, progressively sparser towards equator; cingulum and body otherwise infrapunctate; sinuous laesurae extending on to cingulum, 2 μ beyond body margin. This distinctive species is characterized by sparse, but conspicuous, spinose distal sculpture, together with consistent slight extension of the laesurae into the cingulum.

Remarks. Smith (1960) has demonstrated the existence of two distinct wall layers in several species of *Densosporites* and *Anulatisporites*—namely an inner membrane (intexine) forming the ‘central body’ and an outer layer (exoexine) which is equatorially expanded and thickened, thus constituting the cingulum. A similar wall construction is evident in *Densosporites rarispinosus* sp. nov.; probably overmacerated specimens (e.g. Pl. 89, fig. 19) show a more or less distinct separation of the two wall layers. The same effect has been discussed and illustrated by Bharadwaj (1959, p. 70; pl. 2, figs. 13, 14) in the case of excessively macerated, *Densosporites*-type microspores of the fructification *Porostrabus zeilleri* Nathorst.

Comparison. *Densosporites spinifer* Hoffmeister, Staplin, and Malloy 1955b (pp. 386–7; pl. 36, figs. 16, 17) differs from *D. rarispinosus* in possessing a coarsely granulate, relatively larger, non-spinose spore body; the spinae of *D. spinifer* are often closely packed and apparently developed on both proximal and distal surfaces of the cingulum. *D. brevispinosus* Hoffmeister, Staplin, and Malloy 1955b (p. 386; pl. 36, fig. 22) is sub-circular and has a variably differentiated, minutely spinose cingulum enclosing a granulate spore body. The spinose sculpture of *D. spinosus* Dybová and Jachowicz 1957 (pp. 164–5; pl. 49, figs. 1–4) is more strongly developed than in *D. rarispinosus*, the cingulum thickness decreases equatorially and the proximal surface is granulate. *D.*

dentatus (Waltz) Potonié and Kremp 1956 has a regularly dentate equatorial margin, but is laevigate or granulate on the proximal and distal surfaces.

Densosporites aculeatus sp. nov.

Plate 88, figs. 16, 17; text-fig. 10e

Diagnosis. Spores radial, trilete; amb conformable with convexly subtriangular outline of spore body. Laesurae indistinct, simple, straight to curved or sinuous, extending to, or just beyond, body margin; frequently not preserved owing to fragility of proximal body wall. Width and thickness of cingulum fairly uniform, colour much darker than spore body. Equatorial margin and whole of distal surface bear numerous, stout, conspicuously tapering, simple spinae, which have \pm circular bases and are variably spaced (but rarely coalescent); length of spines 2.5–9 μ (usually about 5 μ), basal diameter 1.5–5 μ (average 3.5 μ). Apart from spinose sculpture—spore body laevigate to infra-granulate, cingulum laevigate (irregularly punctate in corroded specimens).

Dimensions (36 specimens). Overall equatorial diameter (excluding spinose projections) 31–57 μ (mean 43 μ); diameter of spore body 18–32 μ (mean 26 μ).

Holotype. Preparation P164/3, 22.3 96.9. L.1163.

Locus typicus. Birger Johnsonfjellet (sample G1095), Spitsbergen; Lower Carboniferous.

Description. Holotype roundly subtriangular, 40 μ overall; prominently spinose distally and (particularly) equatorially; spinae 4–7 μ long, 3–4 μ broad at base; cingulum otherwise laevigate, spore body finely granulate; body diameter 28 μ .

Comparison. *Densosporites aculeatus* sp. nov. resembles *D. spinifer* Hoffmeister, Staplin, and Malloy 1955b (pp. 386–7; pl. 36, figs. 16, 17), but differs in bearing spines on the distal surface of the spore body. *Spinozonotriletes*? *exiguus* Staplin 1960 (p. 22; pl. 4, figs. 26–28) is circular and has comparatively short laesurae, but otherwise seems very similar to *D. aculeatus*. Another closely allied species is *D. varispinosus* sp. nov.; this is distinguishable, however, in its much less strongly developed spinose sculpture, and always clearly discernible laesurae.

Densosporites sp.

Plate 88, fig. 18

Description of specimens. Spores radial, trilete; amb roundly subtriangular. Laesurae distinct, simple, straight, extending to spore-body margin. Body subtriangular with straight to slightly convex sides and rounded to somewhat pointed apices; laevigate or faintly punctate, irregularly thickened on distal surface. Broad cingulum of fairly uniform width and similar density to spore body; sculpture irregularly and minutely scabrate to areolate, particularly in equatorial region.

Dimensions (2 specimens). Overall equatorial diameter 77–92 μ ; diameter of spore body 37–40 μ .

Comparison. The only comparable species to have appeared in the literature is *Zonotriletes latizonalis* Waltz (in Luber and Waltz 1941, p. 32; pl. 6, fig. 92); this differs from the specimens described above in its marginally serrate cingulum and smaller spore body (diameter 20–25 μ).

Genus LABIADENSITES Hacquebard and Barss 1957

Type species. *L. attenuatus* Hacquebard and Barss 1957.

Affinity. Unknown.

Labiadensites fimbriatus (Waltz) Hacquebard and Barss 1957

Plate 90, figs. 1-3

1938 *Zonotriletes fimbriatus* Waltz in Luber and Waltz, p. 20; pl. 2, fig. 25.

1956 *Hymenozonotriletes fimbriatus* (Waltz) Ishchenko, p. 63; pl. 12, fig. 133.

1956 *Densosporites fimbriatus* (Waltz) Potonić and Kremp, p. 115.

1957 *Labiadensites fimbriatus* (Waltz) Hacquebard and Barss, p. 28; pl. 4, fig. 2.

Description of specimens. Spores radial, trilete; amb circular to subcircular. Laesurae distinct, straight, almost attaining spore-body margin; flanked by broad, flat lips extending 6-10 μ on either side of laesurae and having undulating outer margins. Spore body laevigate to infrapunctate. Cingulum smooth, dense; encompassed by a more translucent, less robust equatorial border, which has a frilled, rather membranous appearance; boundary between these is usually well defined and conformable with the smooth, circular spore-body margin. Some specimens were observed in which the membranous border overlaps rather irregularly on to the inner part of the cingulum, particularly on its distal surface. Also, the outer portion sometimes shows considerable variation in width on any one specimen (see Pl. 90, fig. 1), in which case the equatorial outline is broadly undulating.

Dimensions (75 specimens). Overall equatorial diameter 90-144 μ (mean 115 μ); diameter of spore body 50-88 μ (mean 69 μ).

Comparison. *Zonotriletes ciliato-marginatus* Waltz (in Luber and Waltz 1941, pp. 21-22; pl. 4, fig. 52) has similar, but less concise, differentiation of the cingulum, the outer portion of which is thickly covered with small projections. Some specimens of *L. fimbriatus* (e.g. Pl. 90, fig. 3), in which the outer membranous border has been partially removed, appear as transitional forms linking this species with *Anulatisporites labiatus* Hughes and Playford 1961, which has a smooth undifferentiated cingulum. Thus the two species may well be closely related.

EXPLANATION OF PLATE 90

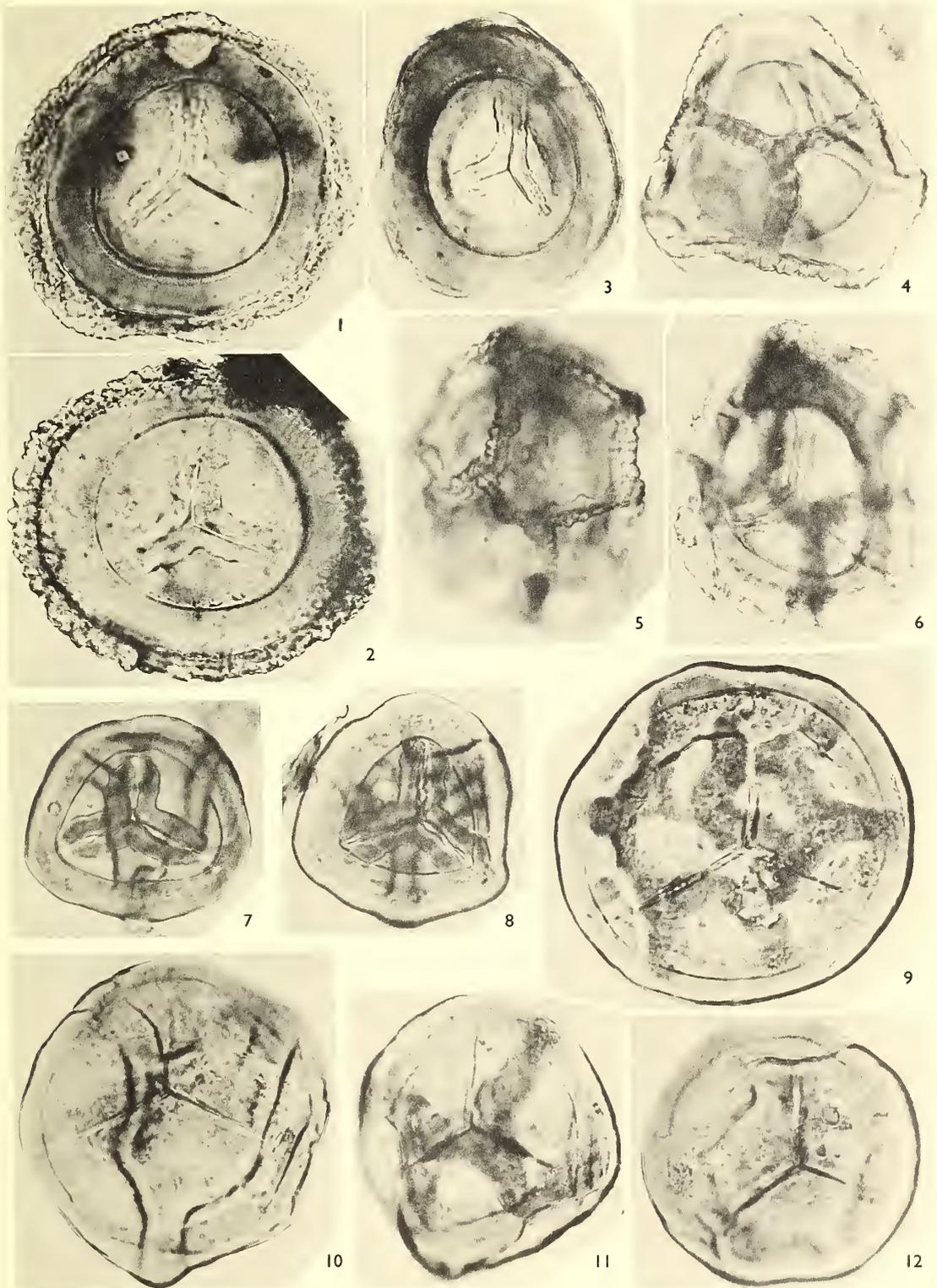
All figures $\times 500$, and from unretouched negatives.

Figs. 1-3. *Labiadensites fimbriatus* (Waltz) Hacquebard and Barss 1957. 1, Distal surface; preparation P148/41, 34.0 106.6 (L.1167). 2, Proximal surface; preparation P148/5, 52.4 108.9 (L.1168). 3, Proximal surface; preparation P163/7, 27.1 111.3 (L.1169).

Figs. 4-6. *Knoxisporites margarethae* Hughes and Playford 1961. 4, Distal surface; preparation P173/1, 20.2 112.5 (L.1171). 5, 6, Distal and proximal surfaces respectively; preparation M811/1, 42.5 110.4 (L.1172).

Figs. 7, 8. *Knoxisporites literatus* (Waltz) comb. nov. 7, Proximal surface; preparation P163/7, 47.7 107.2 (L.1173). 8, Proximal surface; preparation P163/7, 31.4 102.8 (L.1174).

Figs. 9-12. *Knoxisporites hederatus* (Ishchenko) comb. nov. 9, Proximal surface; preparation P181/5, 35.3 95.8 (L.1178). 10, Proximal surface; preparation P148/5, 47.7 112.8 (L.1175). 11, Proximal surface; preparation P148/5, 24.4 100.9 (L.1177). 12, Proximal surface; preparation P148/55, 37.8 105.4 (L.1176).



PLAYFORD, Lower Carboniferous microspores

Previous records. This distinctive species was apparently widespread in the Northern Hemisphere during Lower Carboniferous times, with previous records from the Tournaisian–Viséan of the Moscow Basin and Kizel region (Luber and Waltz 1938, 1941); from the Tournaisian of the western Donetz Basin (Ishchenko 1956); from the Viséan of the Dnieper–Donetz Basin (Ishchenko 1958); and from Upper Mississippian coal of the South Nahanni River area, Northwest Territories, Canada (Hacquebard and Barss 1957).

Genus *KNOXISPORITES* (Potonié and Kremp) Neves 1961

Type species. *K. hageni* Potonié and Kremp 1954.

Discussion. Neves (1961) has emended the diagnosis of *Knoxisporites* Potonié and Kremp 1954, and thereby transferred the genus from the Murornati to the Cingulati. Certainly many of the species (including the type) assigned to *Knoxisporites* appear to be definitely cingulate, in addition to their possession of prominent muri variously arranged on the distal hemisphere. In many instances, however, the distinction between cingulum and equatorially disposed mura would not seem as clear as is implied by Neves (1961).

Knoxisporites may be considered analogous to *Lophozonotriletes* (Naumova) Potonié 1958, differing mainly in sculptural characteristics.

Affinity. Unknown.

Knoxisporites cinctus (Waltz) Butterworth and Williams 1958

Plate 89, figs. 14, 15

1938 *Zonotriletes cinctus* Waltz in Luber and Waltz, p. 22 (no description); pl. 2, fig. 27.

1956 *Annlatisporites cinctus* (Waltz) Potonié and Kremp, p. 111.

1958 *Euryzonotriletes cinctus* (Waltz) Ishchenko, table 3.

1958 *Knoxisporites cinctus* (Waltz) Butterworth and Williams, p. 370; pl. 2, figs. 11–13.

Dimensions (45 specimens). Overall equatorial diameter 58–94 μ (mean 75 μ); diameter of spore body 38–69 μ (mean 54 μ).

Previous records. *Knoxisporites cinctus* (Waltz) has been reported previously (a) from Russia by Luber and Waltz (1938, 1941) from the Lower Carboniferous of the Voronezh and Selizharovo districts, and by Ishchenko (1958) from Namurian rocks of the Dnieper–Donetz Basin; (b) from Scotland by Butterworth and Williams (1958) from the upper part of the Limestone Coal Group (Namurian A); (c) from one sample (B685) of the Lower Carboniferous of Spitsbergen (Hughes and Playford 1961).

Knoxisporites margarethae Hughes and Playford 1961

Plate 90, figs. 4–6

Remarks. Study of numerous additional specimens has indicated that the species is definitely cingulate, with the distal thickened ring developed at or near the cingulum/spore-body margin; and further that the distal extra-reticulum appears to be supported by, although distinct from, the smooth distal muri.

Dimensions (70 specimens). Overall equatorial diameter 64–117 μ (mean 90 μ); diameter of spore body 37–74 μ (mean 53 μ).

Knoxisporites literatus (Waltz) comb. nov.

Plate 90, figs. 7, 8

- 1938 *Zonotriletes literatus* Waltz in Lubert and Waltz, p. 18; pl. 2, fig. 21, and pl. A, fig. 11.
 1956 *Euryzonotriletes literatus* (Waltz) Ishchenko, pp. 52–53; pl. 9, fig. 108.
 1956 *Anulatisporites literatus* (Waltz) Potonié and Kremp, p. 111.
 1957 *Cincturasporites literatus* (Waltz) Hacquebard and Barss, pp. 23–24; pl. 3, figs. 2–5.

Description of specimens. Spores radial, trilete; amb convexly subtriangular, smooth or may show gentle undulation. Laesurae distinct, straight, length equal to, or slightly less than, spore-body radius; bordered by broad, smooth, flat lips which extend approximately 6–10 μ on either side of laesurae. Cingulum broad, usually regular, width 8–19 μ ; inner margin sometimes darker in colour, possibly indicating poleward extension (3–5 μ) over spore body. In some specimens the cingulum is slightly narrower at the apices, so that the amb tends to appear more roundly triangular than the equatorial outline of the spore body. Distal surface has characteristic sculpture of several (usually three or four) smooth, rounded muri, which are rather irregularly disposed and often loosely connected; width of muri 6.5–12 μ . Apart from lips and distal muri, spore body and cingulum laevigate.

Dimensions (75 specimens). Overall equatorial diameter 56–102 μ (mean 76 μ); diameter of spore body 42–74 μ (mean 56 μ). This corresponds closely to the combination of the dimensions reported for the species by Waltz (in Lubert and Waltz 1938), Ishchenko (1956, 1958), and Hacquebard and Barss (1957).

Remarks. This cingulate species, possessing well-developed distal muri, is conformable with *Knoxisporites* Potonié and Kremp as emended by Neves (1961). The 'overlap' of the cingulum on to the spore body is infrequently apparent and it was not mentioned in the original specific diagnosis (Waltz in Lubert and Waltz 1938, p. 18); thus assignment to *Cincturasporites* Hacquebard and Barss 1957 is unacceptable.

Previous records. This characteristically Lower Carboniferous species has been reported previously from the U.S.S.R. (Lubert and Waltz 1938, 1941; Ishchenko 1956, 1958), Canada (Hacquebard and Barss 1957), and Spitsbergen (Hughes and Playford 1961). Probable representatives occur also in the Upper Devonian of Western Australia (Balme and Hassell 1962, p. 11). On the basis of vertical distribution studies in the Dnieper–Donetz Basin, Ishchenko (1958, stratigraphical range table 3) indicates a range from Upper Devonian to Namurian.

Knoxisporites hederatus (Ishchenko) comb. nov.

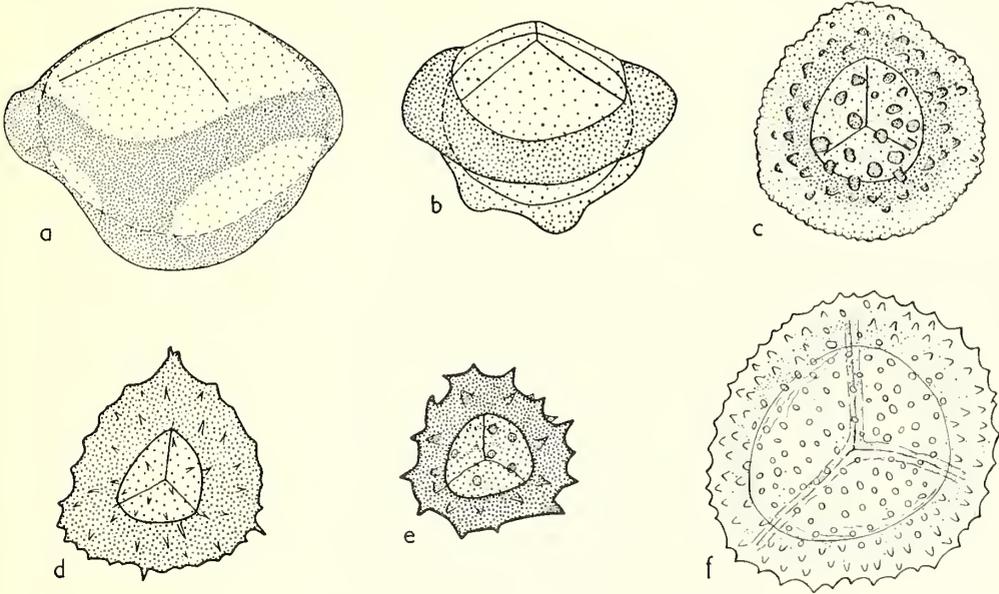
Plate 90, figs. 9–12; text-fig. 10a

- 1956 *Euryzonotriletes hederatus* Ishchenko, pp. 58–59; pl. 10, fig. 121.

Description of specimens. Spores radial, trilete; amb circular to subcircular. Distinct spore body encompassed by more or less conformable cingulum (width 6–16 μ , mean 11 μ). Laesurae distinct, simple, straight, length three-quarters of, to almost equal to, spore-body radius. Distal hemisphere bears conspicuous, widely spaced, relatively low, broad, smooth, rounded muri, which are connected in several places to each other and to the cingulum, but do not form a constant, symmetrical pattern; muri slightly sinuous,

breadth 8–17 μ , height 4–7 μ . Apart from muri, exine laevigate to infrapunctate (oil immersion). Marginal distortion, particularly of muri, common.

Dimensions (40 specimens). Overall equatorial diameter 67–112 μ (mean 86 μ). Thus the Spitsbergen representatives suggest a considerably less restricted size range for the species than that stated by Ishchenko (1956, 1958) as 85–90 μ .



TEXT-FIG. 10. Camera lucida drawings; all magnifications $\times 500$ unless otherwise specified. *a*, *Knoxisporites hederatus* (Ishchenko) comb. nov.; lateral view; preparation P174/2, 41.2–114.2 (L.1179). *b*, *Lophozonotriletes appendices* (Hacquebard and Barss) comb. nov. ($\times 250$); lateral view; preparation P154/5, 53.2–108.7 (L.1190). *c*, *L. variverrucatus* sp. nov.; distal surface; preparation P175/2, 33.9–109.0 (L.1193). *d*, *Densosporites rarispinosus* sp. nov.; distal surface; preparation P145A/1, 25.6–98.0 (L.1162). *e*, *D. aculeatus* sp. nov.; distal surface; preparation P164/2, 43.5–93.3 (L.1165). *f*, *Cristatisporites echinatus* sp. nov.; distal surface; preparation P148/1, 31.9–108.9 (L.1184).

Remarks. This species is included within *Knoxisporites* on the basis of its conspicuous distal sculpture of strongly developed muri together with distinct equatorial girdle. The subgroup *Euryzonotriletes* Naumova 1939 is an unsatisfactory taxon as it embraces many valid genera, and, as noted by Potonié (1956, p. 87), it appears to lack a type species.

Previous records. According to Ishchenko (1956, 1958) this species is confined to sediments of Tournaisian–Lower Viséan age in the western extension of the Donetz Basin; and to Tournaisian–Viséan strata in the Dnieper–Donetz Basin.

Genus LYCOSPORA (Schopf, Wilson, and Bentall) Potonié and Kremp 1954

Type species. *L. micropapillata* (Wilson and Coe) Schopf, Wilson, and Bentall 1944.

Affinity. Schopf, Wilson, and Bentall (1944, p. 54) considered that most of the isolated spores conformable with their genus *Lycospora* represent microspores of arborescent

lepidodendrids. Subsequently, Potonié and Kremp (1954, p. 156) allied the genus with the Lepidophytales, Lepidodendraceae, and Lepidospermales.

Chaloner (1953b) obtained microspores conformable with *Lycospora* from two heterosporous lycopod strobili, *Lepidostrobus dubius* Binney and *L. russelianus* Binney, both of Upper Carboniferous age. In 1958 Sen reported microspores similar to *Lycospora parva* Kosanke 1950 from *Lepidostrobus goldenbergi* Schimper and from *L. variabilis* Lindley and Hutton.

Lycospora uber (Hoffmeister, Staplin, and Malloy) Staplin 1960

Plate 89, figs. 16, 17

- 1938 *Zonotriletes pusillus* (non Ibrahim) Waltz in Luber and Waltz, p. 15; pl. 3, fig. 33, and pl. A, fig. 12.
 1941 *Zonotriletes pusillus* (non Ibrahim) var. *gracilis* Waltz in Luber and Waltz, p. 35; pl. 7, fig. 101b.
 1952 *Hymenozonotriletes pusillus* (non Ibrahim) Ishchenko, p. 50; pl. 13, fig. 122.
 1955 *Cirratiradites uber* Hoffmeister, Staplin, and Malloy, p. 383; pl. 36, fig. 24.
 1957 *Hymenozonotriletes pusillus* (non Ibrahim) Naumova; Byvsheva, p. 1010.
 1960 *Lycospora uber* (Hoffmeister, Staplin, and Malloy) Staplin, p. 20; pl. 4, figs. 13, 17, 18, 20.

Description of specimens. Spores radial, trilete; amb convexly subtriangular, conformable with spore-body outline. Laesurae distinct, straight, length approximately equal to body radius; accompanied by narrow, more or less prominent lips. Spore body subtriangular with convex sides and rounded apices; finely granulate to finely rugulate/verrucate (distal sculpture often coarser); sometimes arcuately folded at periphery. Cingulum ('flange') narrow, laevigate, often diaphanous; equatorial margin smooth in well-preserved specimens.

Dimensions (50 specimens). Overall equatorial diameter 26–39 μ (mean 32 μ); diameter of spore body 19–27 μ (mean 23 μ).

Remarks. The numerous species listed by Staplin (1960, p. 20) as synonymous with *Lycospora uber* (Hoffmeister, Staplin, and Malloy) is a reflection of the variable nature of this species, which is often extremely abundant in the Spitsbergen samples. *L. uber* is undoubtedly conspecific with forms incorrectly assigned by Russian authors (Waltz, Ishchenko, Byvsheva, &c.) to Ibrahim's species, i.e. *L. pusilla* (Ibrahim) Schopf, Wilson, and Bentall. Staplin also lists a number of other species, such as *L. noctuina* Butterworth and Williams 1958 (p. 376; pl. 3, figs. 14, 15), which may well also be representative of *L. uber*. Certainly much specific subdivision of spores in this category has resulted from their susceptibility to corrosion, and consequent somewhat variable appearance, particularly with respect to spore-body sculpture. As noted by Staplin (1960), a detailed reappraisal of the types of all species included within *Lycospora* would seem an essential approach to the problem.

Previous records. This species has been recorded by numerous authors from the Russian Carboniferous (Luber and Waltz 1938, 1941; Ishchenko 1952, 1956, 1958; Byvsheva 1957, &c.) and also from the Upper Mississippian of North America (Hoffmeister, Staplin, and Malloy 1955; Hacquebard and Barss 1957; Staplin 1960). Future proven synonymy may show its presence in the Namurian assemblages described by Dybová and Jachowicz (1957) and Butterworth and Williams (1958). As indicated by Ishchenko

(1958, stratigraphical range table 3), it seems likely that *Lycospora uber* did not appear until early Viséan times; its upper limit of distribution is, however, dependent upon resolution of the taxonomic problems discussed above.

Genus CRISTATISPORITES Potonié and Kremp 1954

Type species. *C. indignabundus* (Loose) Potonié and Kremp 1954.

Discussion. After critical re-examination of the diplotype, and study of other Upper Carboniferous species of *Cristatisporites*, Bhardwaj (1957, p. 105) came to the conclusion that 'the spores are cingulate having a narrow, subequatorial, thickened peripheral region comparable in structure and organisation to the *cingulum* of *Deusosporites* and *Lycospora*'. Richardson (1960, p. 58) followed Bhardwaj in including *Cristatisporites* within the Cingulati, an assignment which is also supported by the Spitsbergen specimens described below.

Affinity. Unknown.

Cristatisporites echinatus sp. nov.

Plate 91, figs. 1-4; text-fig. 10f

Diagnosis. Spores radial, trilete; amb convexly subtriangular. Differentiation into central area and cingulum distinct to obscure; cingulum width approximately 15-25 per cent. of amb diameter. Laesurae prominent, elevated, with thickened lips (individually 2-4.5 μ wide, and up to 4 μ high); extending on to cingulum, often attaining equatorial margin. Conspicuous echinate sculpture restricted to distal hemisphere and equator, comprising small, fairly closely spaced cones or spines, more or less uniformly distributed, and producing serrate equatorial margin. Sculptural elements \pm equal in size on any one specimen, bases circular to oval, apices pointed or slightly rounded, usually discrete, occasionally fused in small groups; basal diameter of cones/spines 1.5-4 μ , length 1.5-5 μ . Proximal hemisphere finely granulate to infrapunctate.

Dimensions (25 specimens). Overall equatorial diameter 63-100 μ (mean 81 μ).

Holotype. Preparation P148/31, 39.7 104.2. L.1182.

Locus typicus. Triungen (sample G1472), Spitsbergen; Lower Carboniferous.

Description. Holotype 92 μ overall, width of cingulum 14-21 μ ; pronounced laesurae (lips 4 μ wide) attaining serrate equatorial margin; proximal hemisphere sparsely and unevenly granulate (grana up to 1 μ in diameter). In some specimens the distal sculpture shows a gradual, almost imperceptible increase in density towards the equator, so that the cones/spines are fairly closely packed equatorially, and comparatively sparsely distributed in the vicinity of the distal pole. Fusion of these sculptural elements, when encountered, is restricted to the equatorial region, with groups of no more than three. The cingulum usually shows some equatorial decrease in thickness which may be gradual or abrupt; in the latter instance (as with the holotype) a dark ring is evident defining the inner margin of the cingulum. The conspicuous triradiate marks usually appear as uniform, slightly roughened, relatively thick ridges in which dehiscence fissures are frequently not visible.

Comparison. One of two illustrations given by Lubert (1955, pl. 5, fig. 111) of *Lepidozonotriletes ciliaris* (Lubert) resembles *Cristatisporites echinatus* sp. nov., but close similarities are not apparent from either the description (p. 46) or the accompanying figure (pl. 5, fig. 112). *Hymenozonotriletes praetervisus* Naumova 1953 (pl. 4, fig. 8) may be similar, but an accurate comparison is not possible from Naumova's illustration and brief description. The subgroup *Hymenozonotriletes* Naumova appears to embrace indiscriminately monosaccate, cingulate, and zonate forms.

Genus LOPHOZONOTRILETES (Naumova) Potonié 1958

Type species. *L. lebedianensis* Naumova 1953.

Affinity. Unknown.

Lophozonotriletes rarituberculatus (Lubert) Kedo 1957

Plate 91, figs. 8, 9; text-fig. 9b

- 1941 *Zonotriletes rarituberculatus* Lubert in Lubert and Waltz, pp. 10, 30; pl. 1, fig. 5, and pl. 5, fig. 76.
 1956 *Euryzonotriletes rarituberculatus* (Lubert) Ishchenko var. *triangulatus* Ishchenko, p. 51; pl. 8, fig. 104.
 1957 *Lophozonotriletes rarituberculatus* (Lubert) Kedo, p. 1166.
 1961 *Lophozonotriletes triangulatus* Hughes and Playford, pp. 35-36; pl. 3, figs. 3-7.

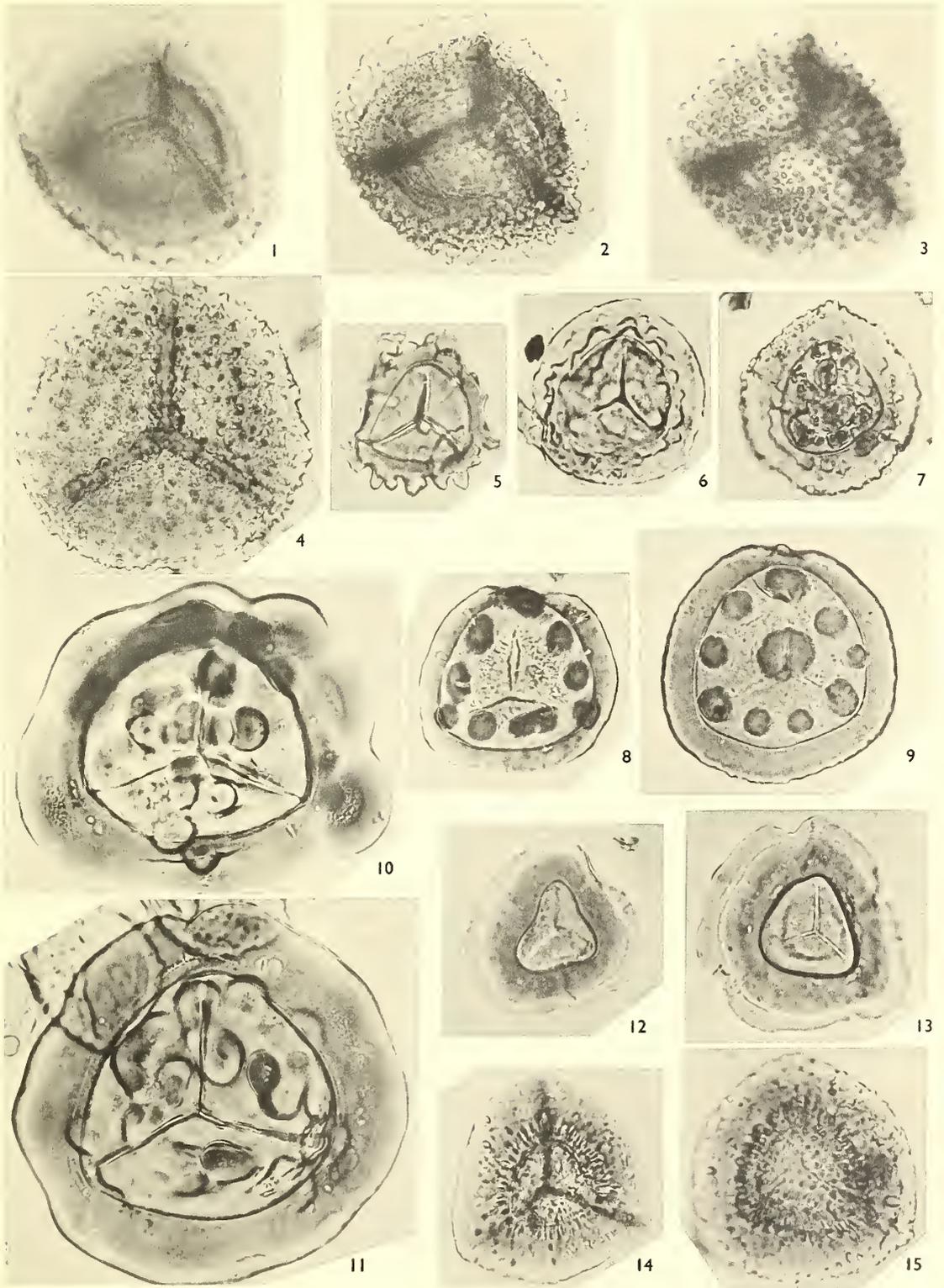
Remarks. In 1956 Ishchenko instituted the infraspecific taxon '*Euryzonotriletes rarituberculatus* (Lubert) comb. nov. var. *triangulatus* var. nov.' Specimens identical to those described by Ishchenko were recorded subsequently from Spitsbergen by Hughes and Playford (1961), who elevated the variety to specific status 'as it occurs alone in considerable numbers in sample B685'. Additional study by the present writer indicates the widespread lateral, and restricted vertical, distribution of this form within Vestspitsbergen.

After the submission (in April 1960) of the Hughes and Playford manuscript, how-

EXPLANATION OF PLATE 91

All figures $\times 500$, and from unretouched negatives.

- Figs. 1-4. *Cristatisporites echinatus* sp. nov. 1-3, Holotype. Proximal view: 1, high focus; 2, central focus; 3, low focus. 4, Distal surface; preparation P175/1, 28.5 113.0 (L.1183).
 Fig. 5. *Lophozonotriletes dentatus* Hughes and Playford 1961. Proximal surface; preparation P226/5, 43.3 113.1 (L.1187).
 Figs. 6, 7. *Lophozonotriletes variverrucatus* sp. nov. 6, Holotype; proximal surface. 7, Distal surface; preparation M811/1, 40.5 99.6 (L.1192).
 Figs. 8, 9. *Lophozonotriletes rarituberculatus* (Lubert) Kedo 1957. 8, Proximal surface; preparation P163/7, 26.2 94.6 (L.1186). 9, Distal surface; preparation P173/10, 30.3 104.2 (L.1185).
 Figs. 10, 11. *Lophozonotriletes appendices* (Hacquebard and Barss) comb. nov. 10, Distal surface; preparation P149A/8, 36.3 104.7 (L.1189). 11, Proximal surface; preparation P149A/1, 17.8 113.9 (L.1188).
 Figs. 12, 13. *Potoniеспores delicatus* sp. nov. 12, Holotype; proximal surface. 13, Proximal surface; preparation P149A/29, 34.0 106.4 (L. 1203).
 Figs. 14, 15. *Tholisporites foveolatus* Hughes and Playford 1961. 14, Proximal surface; preparation P148/40, 36.9 104.0 (L.1200). 15, Distal surface; preparation P172/1, 30.0 104.8 (L. 1201).



PLAYFORD, Lower Carboniferous microspores

ever, the important publication of Luber and Waltz (1941) came to hand, and a detailed comparison of the diagnoses given by Luber (1941, p. 10) for the species, and by Ishchenko (1955, p. 51) for the variety, casts considerable doubt upon the validity of the latter as a distinct morphographical unit. Ishchenko considered his variety distinguishable on the basis of its 'uniformly broad border and regular roundly triangular shape'. However, Luber had clearly described *Zonotriletes rarituberculatus* as being 'roundly triangular', and although noting the margin as somewhat irregular and scallop-like, one of her illustrations (pl. 5, fig. 76: redrawn herein as text-fig. 9b) shows a more or less uniform, entire equatorial margin. It is important to note that Ishchenko included *Z. rarituberculatus* Luber in its entirety within the variety, which must itself, on this basis alone, be considered an unwarranted, superfluous institution.

Of the other illustration given by Luber (1941, pl. 1, fig. 5), which shows an undulating equatorial margin, numerous parallels exist in the Spitsbergen material; these are usually accountable as the result of either folding or corrosion.

Kedo (1957, p. 1166) included *Zonotriletes rarituberculatus* Luber, one of a number of species she listed as characteristic of the Lower Tournaisian of White Russia, within the category of *Lophozonotriletes* Naumova. This assignment remains acceptable under the emendation (by Potonié 1958, pp. 27–28) of Naumova's subgroup (cf. Hughes and Playford 1961, p. 35). *L. rarituberculatus* (Luber) is a highly distinctive species and is undoubtedly of considerable stratigraphical value (see previous records below).

Dimensions (100 specimens). Overall equatorial diameter 50–82 μ (mean 66 μ); diameter of spore body 34–59 μ (mean 47 μ); width of cingulum 5–15 μ (mean 10 μ).

Previous records. Initially described (Luber in Luber and Waltz 1941) from Upper Devonian of the Timan Peninsula and Kizel region and from the lower horizons of the Tournaisian in the southern Moscow Basin and Voronezh region. Ishchenko (1956) found *L. rarituberculatus* to be restricted to Tournaisian strata of the western extension of the Donetz Basin, and Kedo (1957, 1958, 1959) to the Malevka horizon (Lower Tournaisian) of White Russia. Byvsheva (1957, 1960) reported its presence in lowermost Carboniferous from the Melekess and Busuluk deep wells and from the Volga–Ural region. Recently Hughes and Playford (1961) described the species from one sample (B685) of the Spitsbergen Lower Carboniferous, the first-reported occurrence outside the U.S.S.R.

Lophozonotriletes dentatus Hughes and Playford 1961

Plate 91, fig. 5

Dimensions (30 specimens). Overall equatorial diameter 42–69 μ (mean 55 μ); diameter of spore body 28–48 μ (mean 37 μ).

Lophozonotriletes appendices (Hacquebard and Barss) comb. nov.

Plate 91, figs. 10, 11; text-fig. 10b

1957 *Cincturasporites appendices* Hacquebard and Barss, p. 25; pl. 3, figs. 10–12.

Description of specimens. Spores radial, trilete; amb roundly subtriangular. Laesurae distinct, simple, straight, length approximately equal to spore-body radius. Body subtriangular with convex sides and rounded apices. Cingulum uniform or somewhat

variable in width (average $20\ \mu$), laevigate to finely punctate, often exhibiting narrow concentric furrows; inner margin sometimes darker and well defined, probably indicating poleward 'overlap' ($3\text{--}5\ \mu$) on spore body. Prominent distal sculpture consisting of from four to twenty-two large, smooth, rounded projections (verrucae) disposed rather irregularly on spore body and sometimes additionally on inner margin of cingulum; occasional sparse development on infrapunctate proximal surface of spore body. Verrucae subcircular to oval in surface view, basal diameter $8\text{--}27\ \mu$, height $6\text{--}10\ \mu$; rarely coalescent, most strongly developed around distal pole. Equatorial margin smooth to undulating.

Dimensions (44 specimens). Overall equatorial diameter $110\text{--}170\ \mu$ (mean $137\ \mu$); diameter of spore body $69\text{--}117\ \mu$ (mean $90\ \mu$).

Remarks. Although generally conformable, the above description diverges slightly from the original diagnosis of *Cincturasporites appendices* Hacquebard and Barss 1957. The latter authors evidently did not encounter specimens in which the projections are developed proximally as well as (and much more strongly and abundantly) on the distal surface. Furthermore, many of the Spitsbergen representatives possess projections in excess of the 'three to ten' stated by Hacquebard and Barss.

As discussed previously, *Cincturasporites* Hacquebard and Barss 1957 appears to be an unsatisfactory taxon of doubtful validity; certainly the 'overlap' diagnostic of the genus is recognizable in rather less than half of the specimens described above. On the other hand, the cingulate and conspicuously verrucate nature of the species is in accordance with *Lophozonotriletes* Naumova as emended by Potonié (1958, pp. 27–28).

Previous records. From Upper Mississippian coal of the South Nahanni River area, Northwest Territories, Canada (Hacquebard and Barss 1957).

Lophozonotriletes variverrucatus sp. nov.

Plate 91, figs. 6, 7; text-fig. 10c

Diagnosis. Spores radial, trilete; amb convexly subtriangular, finely dentate to almost smooth. Laesurae distinct, simple, straight or slightly sinuous, almost attaining spore-body margin. Spore body usually somewhat lighter in colour than cingulum, which may show gradual, indistinct, equatorial decrease in thickness. Prominent distal sculpture of verrucae and, less commonly, baculae, distributed rather irregularly on both spore body and cingulum. Projections usually discrete, but bases sometimes fused, particularly around inner margin of cingulum; reduced or absent on equatorial region. Projections rather variable in size, shape, and disposition; range $1\text{--}7\ \mu$ long, $2\text{--}12\ \mu$ broad. Proximal hemisphere laevigate or infrapunctate.

Dimensions (30 specimens). Overall equatorial diameter $42\text{--}68\ \mu$ (mean $55\ \mu$); diameter of spore body $23\text{--}36\ \mu$ (mean $30\ \mu$); width of cingulum $9\text{--}16\ \mu$ (mean $12\ \mu$).

Holotype. Preparation P175/3, 48-6 94-0. L.1191.

Locus typicus. Citadellet (sample G1450), Spitsbergen; Lower Carboniferous.

Description. Holotype $56\ \mu$ overall, diameter of spore body $34\ \mu$, width of cingulum $11\ \mu$; proximal surface of spore body infrapunctate, of cingulum laevigate; whole distal hemisphere, excepting outer margin of cingulum, bearing numerous verrucae, some

baculae; sculpturing elements 2–7 μ long, 2–12 μ broad, frequently fused at bases in vicinity of spore body/cingulum junction; equatorial margin practically smooth.

Remarks. This cingulate species is included within *Lophozonotriletes* on the basis of its conspicuously developed verrucate/baculate sculpture. It is distinct from *L. varituberculatus* (Luber), which has less numerous, more regular distal projections.

Genus MONILOSPORA (Hacquebard and Barss) Staplin 1960

Type species. *M. moniliformis* Hacquebard and Barss 1957.

Discussion. The emendation of the genus *Monilospora* Hacquebard and Barss 1957 by Staplin (1960, p. 28) is here accepted, since it somewhat clarifies the morphological features, particularly in light of the effects of corrosion. The present writer is in agreement with Staplin's statement that three of the species in Hacquebard and Barss 1957—*Monilospora moniliformis*, *Tendosporites subcrenatus* (*non* Waltz), and *Densosporites subserratus*—perhaps represent different manifestations, due to variable preservation, of the same species.

It seems unfortunate that the terms 'capsula' and 'patella' introduced and utilized by Staplin (1960) in relation to the structure of this and other genera (*Monilospora*, *Tendosporites*) are not illustrated or defined in any detail, and are without reference to the layers of the spore wall; in their present form the use of such terms would only add to the confusion at present prevailing in palynological terminology. As understood by the present writer, Staplin's 'outer hull' or 'capsula' in fact refers to the envelopment of the intexine by the exoexine, which may be equatorially expanded and/or thickened, whereas 'patella' (cf. 'patina' of *Tholiosporites* Butterworth and Williams 1958, pp. 381–2; text-fig. 3) implies predominantly distal thickening of the exoexine.

Affinity. Unknown.

Monilospora trimgensis sp. nov.

Plate 92, figs. 2, 3

Diagnosis. Spores radial, trilete; amb subtriangular. Laesurae distinct, simple, straight, length approximately three-quarters to four-fifths spore-body radius. Spore body laevigate; subtriangular with broadly rounded apices and concave to almost straight sides. Broad cingulum showing gradual and slight equatorial decrease in thickness which is emphasized by corrosion; irregularly scalloped in outer part. Scalloping may be confined to outermost region or, if coarser, may extend about half-way towards spore-body margin.

Dimensions (30 specimens). Overall equatorial diameter 80–117 μ (mean 97 μ); diameter of spore body 38–66 μ (mean 52 μ).

Holotype. Preparation P145B/36, 38.0 100.9. L.1194.

Locus typicus. Triungen (sample G1466), Spitsbergen; Lower Carboniferous.

Description. Holotype 92 μ overall; cingulum width 19 μ , outer margin almost entirely scalloped (indented as much as 10 μ), otherwise laevigate; spore body 53 μ in diameter, laevigate. The species is characterized by its large size and distinctive cingulum.

It is possible that the often highly irregular, scallop-like indentations of the cingulum are the result of corrosive action. However, it is important to note in this connexion that the other microfloral elements, contained in both samples (G1466, G636) from which *Monilospora triungensis* sp. nov. has been recovered, appear exceptionally well preserved.

Comparison. This species resembles *Monilospora mutabilis* Staplin 1960 (p. 28; p. 6, figs. 1-7, 9) but is consistently larger.

Monilospora dignata sp. nov.

Plate 92, figs. 4, 5

Diagnosis. Spores radial, trilete; amb subtriangular to oval. Laesurae distinct, simple, straight, length almost equal to body radius. Spore body subtriangular with straight to convex sides and rounded apices; laevigate to infrapunctate. Cingulum of somewhat variable width (mean $14\ \mu$); including well-defined, continuous, thickened equatorial region, which is elevated, rounded in cross-section, and superficially either laevigate or finely wrinkled; width of marginal thickening typically variable on any given specimen, about $5-10\ \mu$. Cingulum otherwise smooth.

Dimensions (30 specimens). Overall equatorial diameter $48-64\ \mu$ (mean $56\ \mu$); diameter of spore body $25-36\ \mu$ (mean $30\ \mu$).

Holotype. Preparation P145B/18, 41.0 101.4. L.1197.

Locus typicus. Triungen (sample G1466), Spitsbergen; Lower Carboniferous.

Description. Holotype $62\ \mu$ overall; laesurae almost attain spore-body margin; body laevigate, subtriangular with straight to convex sides; cingulum $12-17\ \mu$ broad; prominent, elevated, smooth, marginal thickening ($5-9\ \mu$ in width) appearing to encroach irregularly upon undifferentiated inner part of cingulum.

Comparison. *Monilospora dignata* sp. nov. is distinguishable from *M. moniliformis* Hacquebard and Barss 1957 (p. 38; pl. 5, figs. 8, 9) in possessing a smaller spore body, longer laesurae, and continuous marginal thickening. *Knoxisporites carnosus* (Knox) Butterworth and Williams 1958 (p. 369; pl. 2, figs. 8-10) is larger than *M. dignata* and its spore body is prescribed by a pronounced zone of cingulate thickening.

EXPLANATION OF PLATE 92

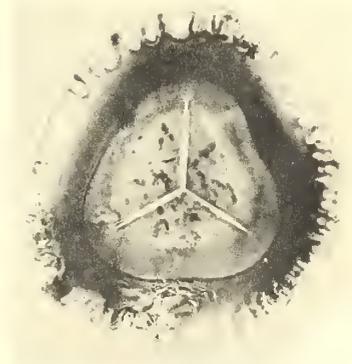
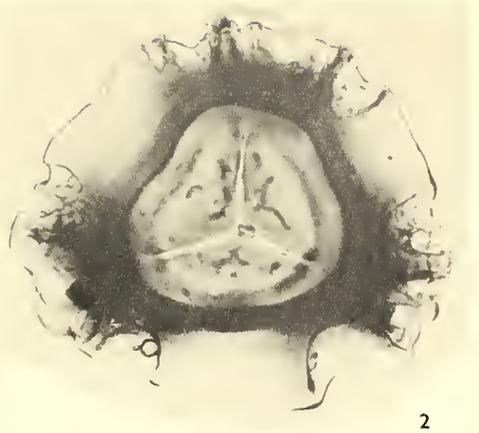
All figures $\times 500$, and from unretouched negatives.

Fig. 1. *Cirratiradites solaris* Hacquebard and Barss 1957. Proximal surface; preparation P155/15, 40.3 102.8 (L.1206).

Figs. 2, 3. *Monilospora triungensis* sp. nov. 2, Proximal surface; preparation P145B/34, 34.0 108.5 (L.1195). 3, Holotype; proximal surface.

Figs. 4, 5. *Monilospora dignata* sp. nov. 4, Holotype; proximal surface. 5, Proximal surface; preparation P145B/1, 46.7 99.8 (L.1198).

Figs. 6, 7. *Cirratiradites elegans* (Waltz) Potonié and Kremp 1956. 6, Proximal surface; preparation P149A/41, 46.2 100.4 (L.1207). 7, Proximal surface; preparation P149A/2, 45.6 95.2 (L.1208).



Infraturma *PATINATI* Butterworth and Williams 1958
Genus *THOLISPORITES* Butterworth and Williams 1958

Type species. *T. scoticus* Butterworth and Williams 1958.

Affinity. Unknown.

Tholisporites foveolatus Hughes and Playford 1961

Plate 91, figs. 14, 15

Dimensions (75 specimens). Overall equatorial diameter 52–77 μ (mean 64 μ); diameter of proximal central area 24–37 μ (mean 31 μ).

Comparison. *Densosporites intermedius* (Waltz) comb. nov. shows some general resemblance, but is non-patinate and has different sculpture in the equatorial region.

Infraturma *ZONATI* Potonié and Kremp 1954
Genus *POTONIESPORES* Artüz 1957

Type species. *P. bizonales* Artüz 1957.

Discussion. In her diagnosis of *Potoniespores*, Artüz (1957, p. 254) refers to the presence of a single V-shaped indentation of the equatorial margin. However, this feature may well prove merely a secondary (preservation) effect and hence its significance as a diagnostic characteristic is doubtful. Concise differentiation of the equatorial girdle into an inner thickened portion and an outer membranous zone permits the discrimination of *Potoniespores* from *Murospora* (*al. Simozonotriletes*).

Affinity. Unknown.

Potoniespores delicatus sp. nov.

Plate 91, figs. 12, 13

Diagnosis. Spores radial, trilete; amb subtriangular, conformable with spore-body outline. Laesurae distinct, simple, straight, length slightly less than spore-body radius. Spore body laevigate to infrapunctate; subtriangular with rounded apices and markedly concave to slightly convex sides. Equatorial girdle entirely laevigate; abruptly and uniformly differentiated into a prominent, dark, thickened, inner part and a thin, outer, diaphanous zone which is frequently folded and torn. Approximately half to two-thirds of the total girdle width is occupied by the inner thickened portion.

Dimensions (35 specimens). Overall equatorial diameter 50–69 μ (mean 58 μ); diameter of spore body 23–33 μ (mean 27 μ).

Holotype. Preparation P180B/4, 24.7 95.1. L.1202.

Locus typicus. Birger Johnsonfjellet (sample G1102), Spitsbergen; Lower Carboniferous.

Description. Holotype 54 μ overall; body concavely subtriangular, 24 μ in diameter, infrapunctate; equatorial girdle 15 μ broad, (inner) two-thirds occupied by dark, thickened portion, outer membranous zone with one conspicuous fold.

Comparison. *Potoniespores bizonales* Artüz 1957 (p. 254; pl. 6, fig. 47) differs from

P. delicatus sp. nov. in possessing longer laesurae and a relatively broader outer membranous zone. *Hymenozonotriletes concavus* Ishchenko 1956 (p. 63; pl. 12, fig. 134) has a much larger spore body together with somewhat irregular differentiation of the equatorial girdle.

Genus *CIRRATRIRADITES* Wilson and Coe 1940

Type species. *C. saturni* (Ibrahim) Schopf, Wilson, and Bentall 1944.

Affinity. Microspores showing close resemblance to *Cirratriradites anulatus* Kosanke and Brokaw (*in* Kosanke 1950) have been recovered from the herbaceous, heterosporous lycopod *Selaginellites suissei* Zeiller (Chaloner 1954), and also from the detached, heterosporous strobilus *S. crassicinctus* Hoskins and Abbott (1956).

Cirratriradites solaris Hacquebard and Barss 1957

Plate 92, fig. 1

Description of specimens. Spores radial, trilete; amb convexly subtriangular, conformable with spore-body outline. Laesurae distinct, straight, length approximately equal to body radius; bordered by strongly developed lips individually 3–4 μ wide. Spore-body wall very thick (5–9 μ), irregularly punctate to microreticulate. Membranous zona relatively thin, supported by numerous, radially disposed, anastomosing ribs, which tend to be emphasized by corrosion. Well-preserved specimens uncommon.

Dimensions (25 specimens). Overall equatorial diameter 117–252 μ (mean 189 μ); diameter of spore body 55–100 μ (mean 78 μ). This agrees closely with the combination of the size ranges observed by Hacquebard and Barss (1957) and Staplin (1960).

Comparison. *Hymenozonotriletes aurantiacus* Naumova (Ishchenko 1956, p. 67; pl. 13, fig. 144), recorded also as *Zonotriletes aurantiacus* (Naumova) Waltz (*in* Luber and Waltz 1938, p. 16; pl. 3, fig. 40), is undoubtedly a closely related species. It is distinguishable from *C. solaris* in its smaller size and in possessing shorter, indistinct, apparently simple laesurae.

Previous records. This species has been reported previously from the Upper Mississippian of Canada (Hacquebard and Barss 1957; Staplin 1960).

Cirratriradites elegans (Waltz) Potonié and Kremp 1956

Plate 92, figs. 6, 7

1938 *Zonotriletes elegans* Waltz *in* Luber and Waltz, p. 15; pl. 3, fig. 32.

1956 *Cirratriradites elegans* (Waltz) Potonié and Kremp, p. 126.

1958 *Hymenozonotriletes elegans* (Waltz) Ishchenko, p. 67; pl. 7, fig. 88.

Description of specimens. Spores radial, trilete; amb convexly subtriangular, conformable with spore-body outline. Laesurae distinct, straight; extending on to zona, frequently reaching equator; accompanied by conspicuous, smooth, elevated, thickened lips, having maximum development on spore body, extending 4–6 μ on either side of laesurae. Spore body scabrate; non-foveolate. Zona much lighter in colour than spore body, more or less smooth, often folded, shows equatorial decrease in thickness; radially pitted or channelled in corroded specimens.

Dimensions (45 specimens). Overall equatorial diameter 70–128 μ (mean 102 μ); diameter of spore body 44–63 μ (mean 53 μ).

Previous records. *Cirratiradites elegans* has been known hitherto only from the U.S.S.R. Waltz (*in* Luber and Waltz 1938) described it initially from Viséan strata of the Moscow Basin, and a recent report is from Viséan to Namurian rocks of the Dnieper–Donetz Basin (Ishchenko 1958).

Genus CAMPTOZONOTRILETES Staplin 1960

Type species. *C. vermiculatus* Staplin 1960.

Affinity. Unknown.

Camptozonotriletes velatus (Waltz) comb. nov.

Plate 93, figs. 1–3

1938 *Zonotriletes velatus* Waltz *in* Luber and Waltz, p. 14; pl. 3, fig. 35, and pl. A, fig. 18.

1955 *Reticulatisporites velatus* (Waltz) Potonié and Kremp, p. 112.

1958 *Hymenozonotriletes velatus* (Waltz) Ishchenko, p. 75; pl. 8, fig. 105.

Description of specimens. Spores radial, trilete; amb roundly subtriangular to sub-circular. Laesurae distinct, straight, equal to or slightly less than body radius; simple, or bordered by narrow, thickened, elevated lips which often extend, and diverge markedly, immediately beyond radial termini of laesurae, thus appearing rather ‘spanner-like’ in polar view. Equatorial zone (‘flange’) uniform, lighter in colour than spore body; outer margin smooth or undulating (due to folding), more or less conformable with spore-body equator. Distal surface marked by development of a variable number of dark, thickened ridges of irregular length and disposition, particularly characteristic of spore body but often extending on to zona. Ridges 4–8 μ wide, simple or divided equally by a narrow longitudinal channel; sometimes connected to form an irregular, wide-meshed reticulum; rarely present on proximal surface.

Dimensions (100 specimens). Overall equatorial diameter 57–116 μ (mean 84 μ); diameter of spore body 33–88 μ (mean 57 μ). This extends considerably the size ranges quoted by Waltz (*in* Luber and Waltz 1938) and Ishchenko (1958).

Remarks. The spores described above occur abundantly in the upper horizons of the Lower Carboniferous of Spitsbergen; they conform closely to the descriptions given by Waltz (*in* Luber and Waltz 1938) and by Ishchenko (1958) of respectively *Zonotriletes velatus* and *Hymenozonotriletes velatus*. The assignment of the species to *Reticulatisporites* (Ibrahim) by Potonié and Kremp (1955, p. 112) is clearly incorrect. It is here included within *Camptozonotriletes* Staplin 1960 on the basis of structure (spore with an equatorial flange) and prominent distal sculpture (irregular muri).

Previous records. *Camptozonotriletes velatus* (Waltz) comb. nov. has been recorded hitherto exclusively from the U.S.S.R. Luber and Waltz (1938, 1941) report its occurrence in Lower Carboniferous strata of the Moscow Basin and Selizharovo and Voronezh regions. According to the work of Ishchenko (1958) the species is present in Upper Devonian and Viséan rocks of the Dnieper–Donetz Basin, but apparently absent in the Tournaisian.

Genus *DIATOMOZONOTRILETES* (Naumova) emend.

1939 *Diatomozonotriletes* Naumova, p. 355; fig. 1.

1956 *Reinschospora* Schopf, Wilson, and Bentall, β section *Diatomozonotriletes* (Naumova) Potonié and Kremp, pp. 131–2.

1961 *Diatomozonotriletes* (Naumova) Potonié and Kremp 1956; Hughes and Playford, p. 40.

Emended diagnosis. Microspores radial, trilete; spore body triangular or subtriangular in equatorial outline. Laesurae usually well defined and long; simple or accompanied by lips. Spore body almost entirely encompassed by prominent zona (corona) consisting of numerous, strongly developed, mainly discrete saetae (fimbriae) emanating radially from equatorial margin of spore body. Saetae are particularly well developed in central interrational equatorial regions, characteristically exhibiting a gradual diminution in size towards the triangular apices of the spore, where they may be either absent or considerably reduced. Saetae pointed or blunt; sometimes fused, at least in part, but always remain recognizable individually within the corona as distinct structural entities. Spore body often sculptured, particularly on distal surface.

Type species (here designated). *Diatomozonotriletes saetosus* (Hacquebard and Barss 1957, p. 41; pl. 6, fig. 3) Hughes and Playford 1961.

Other species. The following species are now included within *Diatomozonotriletes* (Naumova) emend.

1. *Diatomozonotriletes* (al. *Reinschospora*) *cervicornutus* (Staplin 1960, p. 24; pl. 5, figs. 1–3) comb. nov. Occurrence: Canada (after Staplin 1960)—Golata formation, Alberta; Upper Mississippian.

2. *Diatomozonotriletes* (al. *Zonotriletes*) *curiosus* (partim) (Waltz in Luber and Waltz 1938, pl. 4, fig. 49; non pl. A, fig. 13) Ishchenko 1956. Occurrence: U.S.S.R. (after Luber and Waltz 1941)—Moscow Basin, Kizel, Selizharovo, and Voronezh regions; Lower Carboniferous. U.S.S.R. (after Ishchenko 1956, 1958)—western Donetz Basin, Dnieper–Donetz Basin; Viséan.

3. *Diatomozonotriletes hughesii* sp. nov.

4. *Diatomozonotriletes* (al. *Reinschospora*) *jubatus* (Staplin 1960, p. 23; pl. 5, figs. 7, 8) comb. nov. Occurrence: Canada (after Staplin 1960)—Golata formation, Alberta; Upper Mississippian.

5. *Diatomozonotriletes* (al. *Reinschospora*) *nahannensis* (Hacquebard and Barss 1957, p. 41; pl. 6, figs. 1, 2) comb. nov. Occurrence: Canada (after Hacquebard and Barss 1957)—South Nahanni River area, Northwest Territories; Upper Mississippian.

6. *Diatomozonotriletes* (al. *Reinschospora* sect. *Diatomozonotriletes*) *radforthi* (Potonié 1956, p. 69; pl. 9, fig. 90) comb. nov. Occurrence: Canada (after Radforth and McGregor 1954, p. 605)—Wabumun Lake; age uncertain (see Radforth and McGregor 1956, footnote on pp. 27–28).

7. *Diatomozonotriletes rarus* sp. nov.

8. *Diatomozonotriletes trilinearis* sp. nov.

9. *Diatomozonotriletes ubertus* Ishchenko 1956, p. 100; pl. 19, fig. 242. Occurrence: U.S.S.R. (after Ishchenko 1956, 1958)—western Donetz Basin, Dnieper–Donetz Basin; Viséan to Lower Namurian.

10. *Diatomozonotriletes* (al. *Zonotriletes*) *vesicarius* (Waltz in Luber and Waltz 1941, p. 30; pl. 5, fig. 78) comb. nov. Occurrence: U.S.S.R. (after Luber and Waltz 1941)—Selizharovo region; Lower Carboniferous.

Discussion. In anticipation of the possible eventual recognition of *Diatomozonotriletes* Naumova as a distinct form-genus, Potonié and Kremp (1956a, pp. 131–2) proposed its subgeneric ('sectional') status within the category of *Reinschospora* Schopf, Wilson, and Bentall. Subsequently, Hughes and Playford (1961) incorrectly attributed generic rank to *Diatomozonotriletes* (Naumova) Potonié and Kremp 1956 (in Potonié 1956, p. 69), which lacks the designation of a type species.

Species recorded recently (by Ishchenko 1956, 1958; Hacquebard and Barss 1957; Staplin 1960; Hughes and Playford 1961), together with those described below, indicate the consistent presence in the Lower Carboniferous of a distinct group of *Reinschospora*-like spores possessing coronae of relatively coarse, strongly developed saetae. On the other hand, Upper Carboniferous representatives of

Reinschospora, for example the type species *R. speciosa* (Loose), are characterized by more delicate coronae consisting of a dense aggregation of much finer fimbriae. Such, indeed, is the criterion upon which Potonié and Kremp (1956a) based their sectional subdivision of *Reinschospora*. Thus the separation of *Diatomozonotriletes* from *Reinschospora* is warranted on morphographical grounds and appears also to have definite stratigraphical significance.

Comparison. Some species of *Anapiculatisporites* Potonié and Kremp 1954, for example *A. serratus* sp. nov., possess a strongly spinose equatorial margin which may simulate the zona of *Diatomozonotriletes*. In such cases, however, the sculpture visible at the margin represents an equatorial development of the predominantly distal, spinose sculpture of *Anapiculatisporites*. In *Diatomozonotriletes*, distal sculpture is subordinate and quite distinct from the structural components of its encompassing zona.

The present writer is in agreement with Potonié (1960, p. 60) concerning the 'problematical' nature of *Procoronaspora* Butterworth and Williams 1958. This genus appears to overlap the connotations of several previously instituted genera, such as *Lycospora*, but future work may possibly justify its recognition as a discrete form-genus. *Procoronaspora* is undoubtedly closely related to *Diatomozonotriletes* (Naumova) emend., but the 'fine grade' of its diverse sculpture ('grains, verrucae, spines, baculae, &c.') serves to distinguish it from the latter genus. As noted by Potonié (1960, p. 60), Butterworth and Williams's assignment of *Diatomozonotriletes curiosus* (Waltz) is incorrect.

Affinity. Unknown.

Diatomozonotriletes saetosus (Hacquebard and Barss) Hughes and Playford 1961

Plate 93, figs. 4-7

- 1938 *Zonotriletes speciosus* (non Loose) Waltz in Luber and Waltz, pp. 14-15; pl. 4, fig. 48, and pl. A, fig. 9.
 1956 *Diatomozonotriletes speciosus* (non Loose) Ishchenko, pp. 99-100; pl. 19, figs. 239-41.
 1957 *Reinschospora saetosus* Hacquebard and Barss, pp. 41-42; pl. 6, fig. 3.
 1961 *Diatomozonotriletes saetosus* (Hacquebard and Barss) Hughes and Playford, p. 40; pl. 4, figs. 14, 15.

Description of specimens. Spores radial, trilete; spore body subtriangular with concave sides and rounded to truncated apices. Laesurae distinct, straight, extending almost to equatorial margin; simple or bordered by narrow, slightly thickened lips. Prominent corona comprising nine to fifteen discrete, typically pointed saetae projecting laterally from each interradial portion of the spore-body equator. Saetae 2.5-5 μ broad at base, 3-22 μ long; attain maximum length in central interradial region, diminishing uniformly towards smooth triangular apices. Spore body usually entirely laevigate, occasionally finely granulate on distal surface. Exine thick (2-4 μ), often distinctly thinner at apices.

Dimensions (85 specimens). Equatorial diameter of spore body 36-63 μ (mean 49 μ).

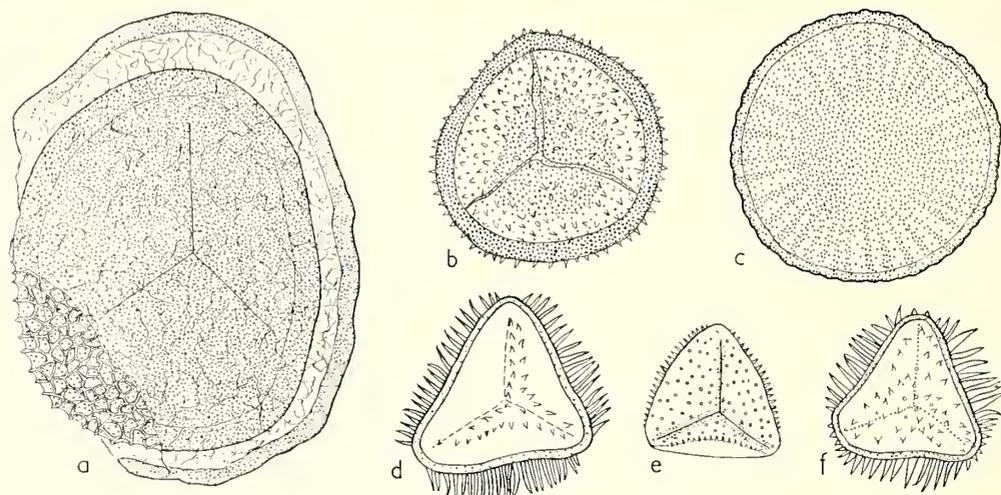
Holotype. As designated by Hacquebard and Barss (1957, p. 42).

Locus typicus. South Nahanni River area, Northwest Territories, Canada (after Hacquebard and Barss 1957); Upper Mississippian.

Previous records. *Diatomozonotriletes saetosus* has been recorded extensively from the U.S.S.R., as follows: Lower Carboniferous of the Moscow Basin and of the Selizharovo, Borovichi, and Kizel regions (Luber and Waltz 1938, 1941); Lower Viséan only of the

western Donetz Basin (Ishchenko 1956); Lower Carboniferous of the Melekes and Busuluk deep wells (Byvsheva 1957); Viséan–Namurian of the Dnieper–Donetz Basin (Ishchenko 1958); Yasnopolyansky substage (Lower Viséan) of the Saratov–Stalingrad Volga area (Loginova 1959); and Lower Carboniferous of the Volga–Ural region (Byvsheva 1960). Note that these Russian authors invariably incorrectly assign this species to Loose's species, i.e. *Reinschospora speciosa* (Loose) Schopf, Wilson, and Bentall.

Hacquebard and Barss (1957) described the species from the Upper Mississippian of



TEXT-FIG. 11. Camera lucida drawings; all magnifications $\times 500$. *a*, *Velosporites microreticulatus* sp. nov.; proximal surface; preparation P163/7, 49.6–110.7 (L.1236). *b*, *Spinozonotriletes balteatus* sp. nov.; proximal surface; preparation P149A/3, 42.4–105.8 (L.1244). *c*, *Radialetes costatus* gen. et sp. nov.; preparation P159/5, 48.0–112.5 (L.1252). *d*, *Diatomozonotriletes trilinearis* sp. nov.; distal surface; preparation P149A/2, 26.9–108.5 (L.1227). *e*, *D. rarus* sp. nov.; distal surface; preparation P145B/2, 43.6–110.9 (L.1230). *f*, *D. hughesii* sp. nov.; distal surface; preparation P149B/1, 44.6–104.5 (L.1223).

Canada (see above), and Hughes and Playford (1961) reported some specimens from the Lower Carboniferous (sample B609) of Spitsbergen.

Diatomozonotriletes hughesii sp. nov.

Plate 93, figs. 8–11; text-fig. 11f

Diagnosis. Spores radial, trilete; amb subtriangular with rounded apices and concave to almost straight sides. Laesurae perceptible to distinct, simple, more or less straight, almost attaining equatorial margin. Well-developed corona consisting of eleven to seventeen large, mutually dissociated, uniformly tapering saetae projecting laterally from each side of the triangular amb, and having pointed, rarely divided apices. Saetae reach maximum size on centres of sides (up to $16\ \mu$ long and $4\ \mu$ in basal diameter); absent or commonly reduced to small coni on triangular apices of spore body. Distal surface of spore body distinctly echinate, bearing scattered, somewhat irregularly distributed

spines (length 2–6 μ); bases of spines rather bulbous (diameter 1–2 μ). Proximal surface laevigate. Exine 1.5–2 μ thick.

Dimensions (80 specimens). Equatorial diameter of spore body 30–47 μ (mean 39 μ).

Holotype. Preparation P149B/1, 47.3 107.6. L.1218.

Locus typicus. Triungen (sample G1470), Spitsbergen; Lower Carboniferous.

Description. Holotype body diameter 46 μ ; saetae (interradial) 5–15 μ long; triangular apices of amb each bearing four to five conii, 2–3 μ long, 1.5 μ broad at base; distal spinae congregated in polar region, relatively sparse elsewhere, average length 5 μ ; exine 2 μ thick. This species is characterized by distinctly echinate distal sculpture, together with frequent development of small conii on the radial corners of the spore body.

Comparisou. *Diatomozonotriletes curiosus* (Waltz) Ishchenko (1956, pp. 100–1; pl. 19, fig. 243) and '*Reinschospora* sp. A' of Staplin (1960, p. 24; pl. 5, fig. 18) have finer, more numerous saetae.

Diatomozonotriletes trilinearis sp. nov.

Plate 93, figs. 12–14; text-fig. 11d

Diagnosis. Spores radial, trilete; amb subtriangular with straight to slightly concave sides, and rounded to truncated apices. Laesurae distinct, simple, straight, almost reaching equatorial margin. Seventeen to twenty-six closely spaced saetae project radially from sides of spore body amb constituting prominent corona, which is not developed at triangular apices. Saetae pointed, occasionally divided, mutually dissociated, basal diameter 1.5–2 μ , longest in central interradian region (up to 14 μ), exhibiting a slight, gradual reduction in size towards smooth apices of spore body. Distal surface bearing sharply tapered spinae, 2–4 μ long, 1.5–2 μ broad at base, characteristically congregated in a Y-shaped area, the orientation and radial extent of which conforms with that of the trilete mark on the opposite surface. Each limb of the 'Y' often consists of two parallel lines of spinae. Apart from this restricted spinose sculpture, spore body laevigate. Exine 1.5–2.5 μ thick.

Dimensions (45 specimens). Equatorial diameter of spore body 35–56 μ (mean 45 μ).

Holotype. Preparation P149A/2, 33.5 95.6. L.1224.

Locus typicus. Triungen (sample G1470), Spitsbergen; Lower Carboniferous.

Description. Holotype body diameter 50 μ ; coronal saetae 4–13 μ long, less than 1 μ apart; constituent spinae of Y-shaped, distal, sculptured area are less closely spaced in polar region.

Comparison. Type 63 of Reinsch (1884, p. 7; pl. 2, fig. 27) from the Russian (?Lower) Carboniferous may be conspecific with *Diatomozonotriletes trilinearis* sp. nov.

Diatomozonotriletes rarus sp. nov.

Plate 93, figs. 15, 16; text-fig. 11e

Diagnosis. Spores radial, trilete; amb subtriangular with slightly convex to slightly concave sides and rounded apices. Laesurae distinct, straight, length three-quarters of,

to almost equal to, spore-body radius; bordered by thickened, slightly elevated lips, individually about $2\ \mu$ wide. Equatorial corona consisting of discrete, closely spaced, pointed saetae attaining maximum size interradially ($3.5\text{--}5\ \mu$ long, $1.5\text{--}2\ \mu$ in basal diameter) and diminishing gradually and uniformly towards the smooth triangular apices. Proximal surface of spore body laevigate; distal surface echinate, with numerous, small, fairly evenly distributed coni, $1.5\text{--}2\ \mu$ long, $1\text{--}1.5\ \mu$ broad at base, and $1.5\text{--}4\ \mu$ apart. Exine (excluding sculpture) up to $1\ \mu$ thick.

Dimensions (15 specimens). Equatorial diameter of spore body $37\text{--}48\ \mu$ (mean $42\ \mu$).

Holotype. Preparation P145B/19, 38.3 103.4. L.1228.

Locus typicus. Triungen (sample G1466), Spitsbergen; Lower Carboniferous.

Description. Holotype body diameter $39\ \mu$; distal coni reduced in size and density in equatorial region; laesurae conspicuously labiate. This distinctive but very rare species is characterized by relatively short, pointed, equatorial saetae, distal echinate sculpture, together with marked lip development.

Comparison. *Diatomozonotriletes rarus* sp. nov. is similar to *D. curiosus* (Waltz in Luber and Waltz 1938, pl. 4, fig. 49) Ishchenko 1956, which is distinguishable, however, in possessing longer saetae and simple laesurae.

Anteturma POLLENITES R. Potonié 1931

Turma SACCITES Erdtman 1947

Subturma MONOSACCITES (Chitaley) Potonié and Kremp 1954

Infraturma TRILETESACCITI Leschik 1955

Subinfraturma INTRORNATI Butterworth and Williams 1958

Discussion. Butterworth and Williams's (1958) suprageneric subdivision of monosaccate grains on the basis of predominantly either internal or external sculpture is

EXPLANATION OF PLATE 93

All figures $\times 500$, and from unretouched negatives.

Figs. 1–3. *Camptozonotriletes velatus* (Waltz) comb. nov. 1, Proximal surface; preparation P164/15, 32.2 101.5 (L.1210). 2, Distal surface; preparation P149A/27, 38.7 104.4 (L.1211). 3, Proximal surface; preparation P157/4, 23.6 113.6 (L.1212).

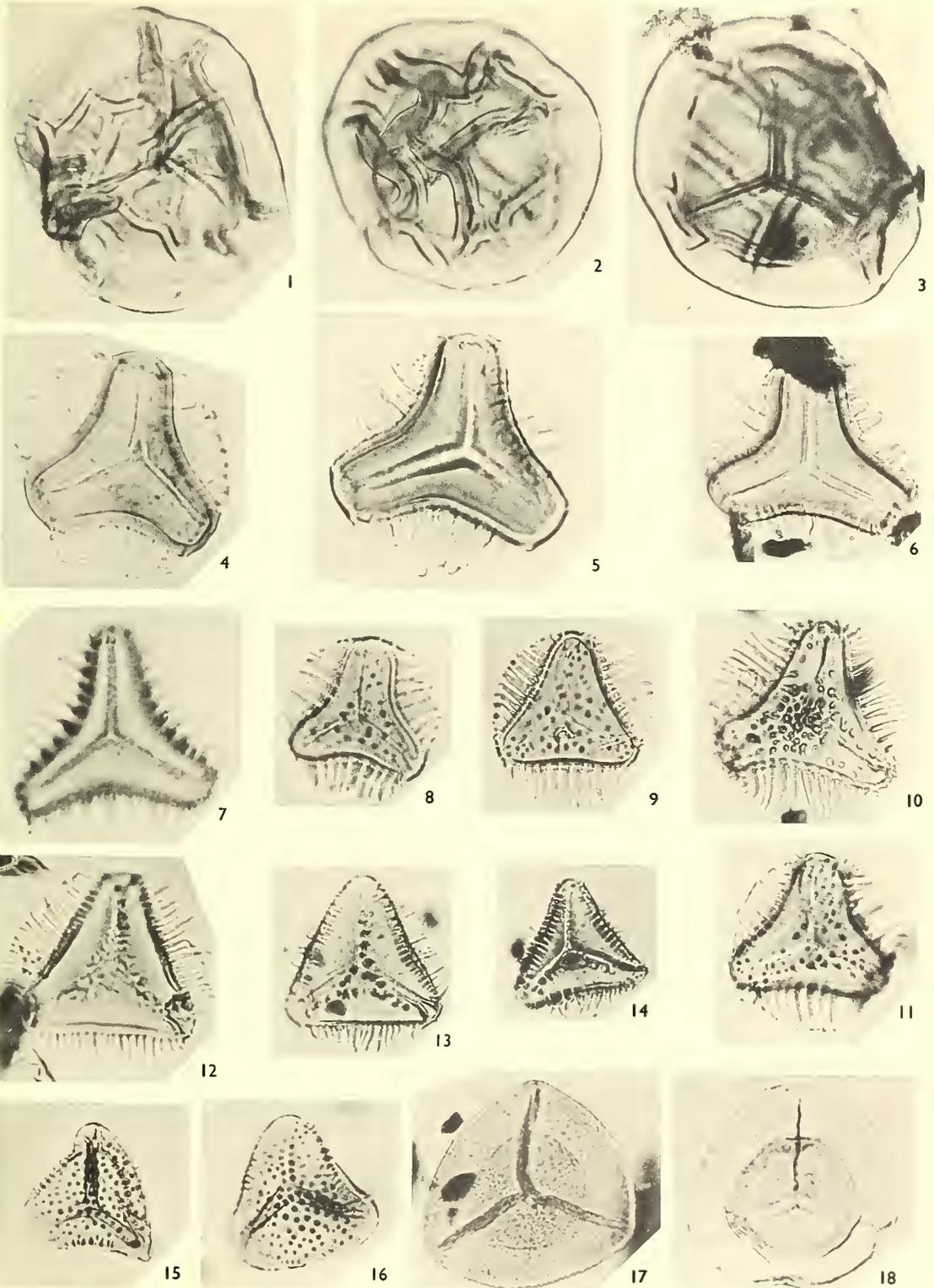
Figs. 4–7. *Diatomozonotriletes saetosus* (Hacquebard and Barss) Hughes and Playford 1961. 4, Proximal surface; preparation P167B/10, 35.9 104.0 (L.1215). 5, Proximal surface; preparation P167B/4, 35.5 100.7 (L.1214). 6, Proximal surface; preparation P167A/2, 25.3 110.3 (L.1216). 7, Proximal surface; preparation P127/3, 53.7 96.9 (L.1217).

Figs. 8–11. *Diatomozonotriletes hughesii* sp. nov. 8, Proximal surface; preparation P149A/1, 28.2 113.3 (L.1219). 9, Proximal surface; preparation P149A/35, 32.7 102.0 (L.1220). 10, Holotype; distal surface. 11, Distal surface; preparation P157/2, 18.9 108.5 (L.1222).

Figs. 12–14. *Diatomozonotriletes trilinearis* sp. nov. 12, Holotype; proximal surface. 13, Distal surface; preparation P149B/1, 15.5 99.8 (L.1225). 14, Proximal surface; preparation P149B/2, 38.5 97.4 (L.1226).

Figs. 15, 16. *Diatomozonotriletes rarus* sp. nov. 15, Holotype; proximal surface. 16, Distal surface; preparation P145C/1, 30.3 106.6 (L.1229).

Figs. 17, 18. *Endosporites micromanifestus* Hacquebard 1957. 17, Proximal surface; preparation P145B/2, 24.5 94.3 (L.1232). 18, Proximal surface; preparation P174/2, 25.5 112.0 (L.1231).



PLAYFORD, Lower Carboniferous microspores

undoubtedly of morphographical significance. However, in many cases the distinction is not readily ascertainable. Although Butterworth and Williams (1958) assigned their genus *Remysporites* to the Extrornati, Potonié (1960, p. 72) included it within the Intrornati since he considered that the often 'externally microreticulate' bladder appearance of this genus may well be due to the development of infrareticulate structure rather than to external sculpture of the exoexine. According to Potonié similar manifestation of internal bladder structure is evident in other genera (*Endosporites*, *Wilsonia*, *Guthörlisporites*, *Microsporites*). Hence, *Velosporites* Hughes and Playford 1961, which shows 'fine external sculpture' of the saccus, is also probably more correctly included within the Intrornati.

Genus ENDOSPORITES Wilson and Coe 1940

Type species. *E. ornatus* Wilson and Coe 1940.

Discussion. Richardson (1960, p. 49) has with justification drawn attention to the overlapping connotations of *Auroraspora* Hoffmeister, Staplin, and Malloy 1955 and *Endosporites* Wilson and Coe 1940. However, Richardson's statement that *Auroraspora* 'differs from *Endosporites* in the absence of a limbus' is questionable, since the original diagnosis of the latter genus (Wilson and Coe 1940, p. 184), which is still accepted unemended, and a recent morphological amplification of the type species (Wilson 1960) contain no reference to an equatorial bladder thickening (limbus). Admittedly, some authors (Potonié and Kremp 1954; Bhardwaj 1957; Chaloner 1953*a*, 1958*b*) have noted the characteristic presence of a limbus in representatives of *Endosporites*, and it is undoubtedly an important morphographical feature which may well have generic significance. However, there are many species included within *Endosporites*, and presently recognized as such, which appear to lack the development of a limbus. In all, therefore, a complete reappraisal of the type species of this and other related monosaccate genera (particularly *Auroraspora*) would seem advisable. Pending this, the present writer considers it preferable at this stage to retain the original generic assignment of the two species instituted by Hacquebard (1957), *E. micromanifestus* and *E. macromanifestus*, both of which Richardson (1960) transferred to *Auroraspora*.

Perhaps the least unsatisfactory distinction between *Auroraspora* and *Endosporites* was expressed by Hoffmeister, Staplin, and Malloy (1955*b*, p. 381) on the basis of relative thicknesses of bladder and body walls. According to these authors *Auroraspora* possesses a central body having a 'moderately thick wall' enclosed by a 'transparent and very thin bladder'; whereas in *Endosporites* the body wall 'approximates the bladder in thickness' (cf. Wilson 1960, pl. 1, fig. 5—explanation p. 31). As Richardson (1960, p. 49) implies, little diagnostic importance can be attached to actual or relative colour which is partially dependent upon preservation and maceration procedures.

Wilson (1960) has demonstrated conclusively that in *Endosporites ornatus* the central body is attached to the bladder on the proximal side only; this method of attachment was interpreted earlier by Potonié and Kremp (1954, p. 149; fig. 81).

Affinity. Chaloner (1953*a*, 1958*b*) has reported the occurrence of microspores very similar to *Endosporites globiformis* (Ibrahim) Schopf, Wilson, and Bentall 1944 in the lycopod cone *Polysporia mirabilis* Newberry 1873 (syn. *Lepidostrobis zea* Chaloner 1953*a*). Earlier, Schopf, Wilson, and Bentall (1944, p. 45) stated that '*Endosporites* is

related to some of the Pennsylvanian Cordaitaleans' because of the presence of *E. pelucidus*-type spores within the strobilus *Cordaitanthus shuleri* Darrah 1940. This attribution of *Endosporites* has been discounted by Wilson (1960, p. 31) because he has shown that *E. pelucidus* is more correctly assigned to the genus *Florinites* (see Wilson 1958).

Endosporites micromanifestus Hacquebard 1957

Plate 93, figs. 17, 18

1956 *Hymenozonotriletes* aff. *variabilis* Naumova; Ishchenko, p. 62; pl. 11, figs. 129, 130.

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

1960 *Auroraspora micromanifestus* (Hacquebard) Richardson, p. 51.

Description of specimens. Spores radial, trilete; amb convexly subtriangular. Laesurae distinct, accompanied by elevated, rather irregular, flange-like lips that frequently extend to the equator. Central body thin, smooth, well defined; outline more or less conformable with amb. Bladder thin, often folded, infragranulate.

Dimensions (50 specimens). Overall equatorial diameter 42–95 μ (mean 67 μ); diameter of central body 28–65 μ (mean 44 μ).

Previous records. Described initially by Hacquebard (1957) from lowermost Mississippian strata of Nova Scotia, this species has been recorded subsequently from the Scottish Viséan by Love (1960) and from one sample (B685) of the Lower Carboniferous of Spitsbergen (Hughes and Playford 1961). It evidently occurs also throughout the Tournaisian–Viséan–Namurian succession of the western extension of the Donetz Basin (Ishchenko 1956, p. 62).

GENUS REMYSPORITES Butterworth and Williams 1958

Type species. *R. magnificus* (Horst) Butterworth and Williams 1958.

Discussion. Contrary to the statement of Butterworth and Williams (1958, p. 386), the saccus in this genus is now considered to envelop the central body entirely (see discussion herein of *Velosporites*).

Affinity. Affinity with the Cycadofilices is suggested by the similarity between the type species and the spores borne by *Paracalathiops stachei* (Stur) Remy 1953 (see Butterworth and Williams 1958, p. 387; Potonié 1960, p. 72).

Remysporites albertensis Staplin 1960

Plate 94, fig. 3

Description of specimens. Spores radial, trilete; amb and body outline subcircular to circular. Smooth central body completely enveloped by loosely fitting bladder; both commonly folded, and probably attached at conspicuous proximal polar (contact) area. Contact area convexly subtriangular, distinctly sculptured with mixed rugulae and verrucae; bladder surface otherwise smooth. Central body and bladder walls both thin (about 1–1.5 μ). Laesurae distinct, simple, straight, length half to two-thirds central body radius.

Dimensions (25 specimens). Overall equatorial diameter 146–205 μ (mean 178 μ); diameter of central body 113–150 μ (mean 130 μ).

Comparison. The specimens conform closely with the diagnosis given by Staplin (1960, p. 35), except that they extend the size range considerably. However, Staplin does not state the number of specimens he measured, and in any case it seems likely that such large monosaccate species exhibit considerable size diversity, dependent probably upon mode of preservation and/or maceration (cf. Butterworth and Williams 1958, p. 388).

Previous records. From the Golata formation (Upper Mississippian) of Alberta, Canada (Staplin 1960).

Genus VELOSPORITES Hughes and Playford 1961

Type species. *V. echinatus* Hughes and Playford 1961.

Discussion. This genus includes large monosaccate spores (as diagnosed by Hughes and Playford 1961, p. 42) characterized by relatively minor but distinctive body-wall sculpture. It is also important to state that a limbus may or may not be present.

According to Butterworth and Williams (1958, p. 386) the genus *Remysporites* is characterized by 'bladder enveloping central body except on proximal side'; and it was principally on this basis that Hughes and Playford (1961) decided to erect the genus *Velosporites* to incorporate a species rather similar to *Remysporites magnificus* (Horst) Butterworth and Williams but possessing comprehensive bladder envelopment. Recently, however, through the courtesy of Drs. M. A. Butterworth and A. H. V. Smith of the National Coal Board, the opportunity has been taken of examining the material from which Butterworth and Williams diagnosed *Remysporites*. As a result the present writer came to the conclusion—jointly with Dr. Butterworth—that the bladder in *R. magnificus* (the type species) does, in fact, envelop the central body entirely. This is substantiated further by a more recently described representative of *Remysporites*, *R. albertensis* Staplin 1960 (p. 35; pl. 8, figs. 8, 10), which is also recorded herein. The characteristic sculpture and relatively thick wall of the central body, exhibited by the two species recorded below, is, however, considered sufficient to justify the continued recognition of *Velosporites* as a distinct form-genus.

Affinity. Unknown.

Velosporites echinatus Hughes and Playford 1961

Plate 94, fig. 1

Remarks. The surface of the central body characteristically bears minute, sparsely distributed conical or very low, mound-like elevations, which are often evident only under oil immersion. The bladder is commonly folded on both large and small scale, the latter resulting in a microrugulate effect.

Dimensions (80 specimens). Overall equatorial diameter 102–194 μ (mean 140 μ); diameter of central body 70–128 μ (mean 100 μ).

Velosporites microreticulatus sp. nov.

Plate 94, fig. 2; text-fig. 11a

Diagnosis. Spores radial, trilete; monosaccate; amb circular to oval, more or less entire. Laesurae simple, straight, length approximately four-fifths central body radius, not evident on bladder. Central body distinct, circular to subcircular, thick-walled (4–9 μ); distinct, finely reticulate sculpture of very narrow, pointed muri up to 1.5 μ high, enclosing small, polygonal lumina which are 1.5–7 μ broad (average 3.5 μ); surrounded completely by thin, transparent bladder. Bladder extending 9–27 μ beyond central body margin; definite equatorial thickening (limbus) 3–6.5 μ wide, smooth, imposing comparative rigidity to bladder. Bladder often densely microrugulate or vermiculate, frequently corroded or torn, thickness about 0.5 μ .

Dimensions (16 specimens). Overall equatorial diameter 100–140 μ (mean 118 μ); diameter of central body 73–102 μ (mean 88 μ).

Holotype. Preparation P163/7, 22.3 94.7. L.1235.

Locus typicus. Birger Johnsonfjellet (sample G1089), Spitsbergen; Lower Carboniferous.

Description. Holotype 120 μ overall, subcircular; central body 92 μ in diameter, 5 μ in thickness, circular, colour much darker than bladder; bladder partially removed thereby revealing detail of conspicuous microreticulate sculpture of central body; limbus 6 μ wide.

Subturma POLYSACCITES Cookson 1947

Genus ALATISPORITES Ibrahim 1933

Type species. *A. pustulatus* Ibrahim 1933.

Affinity. Unknown.

Alatisporites tessellatus Staplin 1960

Plate 95, fig. 10

Description of specimens. Spores radial, trilete. Central body circular, finely and densely rugulate. Laesurae indistinct, simple, straight, length half to two-thirds body radius. Approximately seven to eight thin, overlapping, frequently strongly folded bladders are prominent equatorially but attached to distal surface of body.

Dimensions (17 specimens). Overall equatorial diameter 75–109 μ (mean 87 μ); body diameter 52–61 μ (mean 56 μ).

EXPLANATION OF PLATE 94

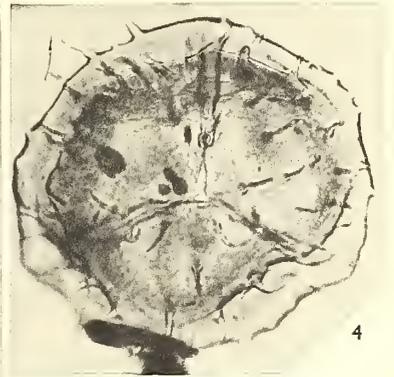
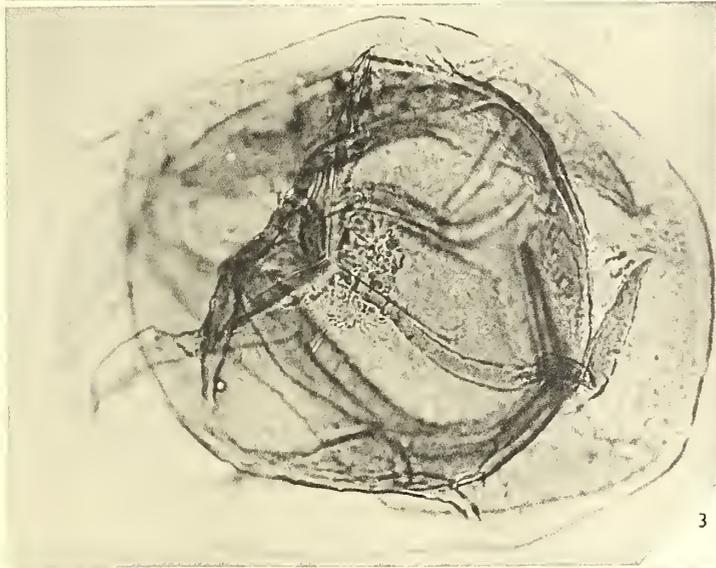
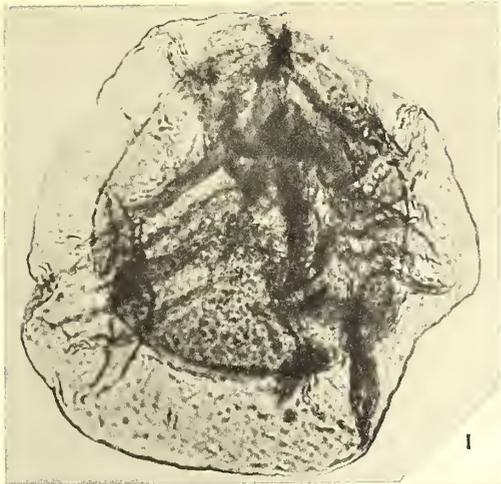
All figures $\times 500$, and from unretouched negatives.

Fig. 1. *Velosporites echinatus* Hughes and Playford 1961. Proximal surface; preparation M811/5, 58.2 108.9 (L.1234).

Fig. 2. *Velosporites microreticulatus* sp. nov. Holotype; proximal surface.

Fig. 3. *Remysporites albertensis* Staplin 1960. Proximal surface; preparation P149A/15, 40.4 100.1 (L.1233).

Figs. 4–6. *Spinozonotriletes uncatu*s Hacquebard 1957. 4, Proximal surface; preparation P175/2, 42.8 108.9 (L.1238). 5, Proximal surface; preparation P148/5, 38.8 93.0 (L.1240). 6, Distal surface; preparation P148/51, 39.1 107.0 (L.1237).



Remarks. Apart from extending the range of overall size, the Spitsbergen specimens conform very closely to the diagnosis given by Staplin (1960, p. 31; pl. 7, fig. 10).

Previous records. Described initially from the Golata formation (Upper Mississippian) of Alberta, Canada (Staplin 1960).

Turma ALETES Ibrahim 1933
Subturma AZONALETES (Luber) Potonié and Kremp 1954
Infraturma RETICULONAPITI (Erdtman) Vimal 1952
Genus RETIALETES Staplin 1960

Type species. *R. radforthii* Staplin 1960.

Discussion. In his diagnosis of this genus, Staplin (1960, p. 6) states: 'spores alete, but sometimes split along a few fine grooves that originate at one end and parallel the long axis'. Similar but usually more extensive splitting has been observed in certain Mesozoic microspores, e.g. *Schizosporis* Cookson and Dettmann 1959 and *Psophosphaera* Naumova (in Bolkhovitina 1959). In *Retialetes*, rupturing, when present, is always longitudinally situated, and suggests a possible mechanism for germination.

Affinity. Unknown.

Retialetes radforthii Staplin 1960

Plate 95, figs. 1-3

Description of specimens. Spores alete, ellipsoidal. Comprehensive reticulate sculpture comprised of rounded or flat-topped, low, smooth muri (1-3 μ high, 1-2.5 μ broad) enclosing subcircular to polygonal lumina 4-22 μ in longest diameter (usually about 8 μ). Exine (excluding muri) 3-5 μ thick; often split along one, occasionally two or more, narrow grooves that parallel the long axis of the spore.

Dimensions (25 specimens). 102-182 μ (mean 144 μ) by 66-107 μ (mean 84 μ).

Previous records. This distinctive species was originally described by Staplin (1960) from the Upper Mississippian Golata formation of Alberta, Canada.

Genus RADIALETES gen. nov.

Type species. *R. costatus* sp. nov.

Diagnosis. Microspores radial, alete. Outline circular or subcircular. Distinctive sculpture consisting of radially disposed muri or incipient thickenings which thus give the spores an overall radiating appearance. Muri sometimes considerably diminished towards central portions of spores.

Comparison. The spore illustrated by Hoffmeister, Staplin, and Malloy (1955a, pl. 3, fig. 7) as '*Radiaspora*' sp. has similar, albeit exclusively distal, sculpture but differs from *Radialetes* gen. nov. in being distinctly trilete. As noted by Potonié (1956, p. 42), *Radiaspora* has yet to be validated as a generic name. *Radialetes* is distinct from *Aumancisporites* Alpern 1958 (p. 84), which is sculptured with more or less parallel grooves disposed transversely with respect to the long axis of the spore. *Undulatasporites* Leschik 1955 (p. 28) has irregular rugulate sculpture.

Affinity. Unknown.

Radialetes costatus sp. nov.

Plate 95, figs. 7-9; text-fig. 11c

Diagnosis. Spores radial, alete. Outline circular to subcircular; commonly distorted due to folding. Both surfaces sculptured with more or less distinct, low, non-anastomosing, radially disposed muri which attain maximum development at the margin, and may be lacking or considerably diminished centrally; muri 1.5-5 μ broad, 1-3 μ apart, up to 2 μ high. Folding of exine usually results in marked apparent discordance of muri on opposing surfaces producing an overall 'cross-hatched' effect. Exine (including sculpture) 2-6 μ thick; apart from muri, laevigate to finely granulate or punctate.

Dimensions (50 specimens). Diameter 42-117 μ (mean 70 μ).

Holotype. Preparation P145B/38, 40.7 105.9. L.1249.

Locus typicus. Triungen (sample G1466), Spitsbergen; Lower Carboniferous.

Description. Holotype 48 μ , circular; conspicuous radial muri 1.5-3 μ broad, 1-1.5 μ high, 1.5-3 μ apart; muri do not extend to central portion of either surface; exine otherwise laevigate, total thickness 2 μ .

Remarks. This distinctive, alete species, characterized by simple, radially disposed muri, has not been recorded in available literature. It shows considerable size variation, but is otherwise morphographically constant. *R. costatus* sp. nov. occurs in many of the Spitsbergen Lower Carboniferous samples, but is always a minor constituent.

INCERTAE SEDIS

Genus SPINOZONOTRILETES Hacquebard 1957

Type species. *S. uncatu*s Hacquebard 1957.

Discussion. This and several other genera were instituted by Hacquebard (1957, pp. 314-15) as convenient subdivisions of the broad subgroup *Archaeozonotriletes* Naumova 1953. Both Naumova and Hacquebard used the term 'perispore' to denote the usually strongly developed, often conspicuously sculptured outer membrane which encloses and frequently almost obscures the central body of many of the spores embraced by the subgroup. It is, however, highly questionable whether a true perispore (perine), as usually understood (cf. Erdtman 1952; Harris 1955), is represented.

Potonié (1960, p. 42) suggested that the 'central body' seen in *Spinozonotriletes* may be a mesospore, a feature which, according to Potonié (1958, p. 21), is present also in the type species of *Grandispora* Hoffmeister, Staplin, and Malloy 1955.

From text-figs. 5, 6c of Richardson (1960) it is evident that his genus *Ancyrospora* shows wall features similar to those of *Spinozonotriletes*. Richardson (p. 55) applied the term 'bladder' to the thick, strongly sculptured, outer membrane (which he regarded as the exoexine) enveloping the central body (intexine), and thus assigned *Ancyrospora* to the Monosaccites. There seems to be considerable doubt, however, as to whether the outer enveloping layer of the exine in these spores is truly comparable to the exoexine (bladder) of typical Palaeozoic monosaccate types (e.g. *Endosporites*, *Remysporites*, *Velosporites*). Thus until further work is done on the structure of such forms as *Spinozonotriletes*, their non-committal suprageneric assignment seems preferable.

Grandispora was described by Hoffmeister, Staplin, and Malloy (1955) as possessing a 'central body wall only slightly thicker than the bladder wall', a feature which together with its constantly subcircular amb permits clear discrimination from *Spinozonotriletes*.

Affinity. Unknown.

*Spinozonotriletes uncatu*s Hacquebard 1957

Plate 94, figs. 4-6

Description of specimens. Spores radial, trilete; amb convexly subtriangular. Laesurae with prominent, folded, flange-like lips (up to $5\ \mu$ wide and $7\ \mu$ high) extending to equator. Exoexine conspicuously sculptured with large, simple spines which are particularly frequent around the equatorial regions, less abundant in the polar areas; some specimens were noted in which the spines were reduced or absent on finely granulate contact areas. Spines have broad, circular bases ($2-6\ \mu$ wide) which often appear rather bulbous in lateral view; length $4-19\ \mu$. This wide variation in spine dimensions is between specimens rather than within specimens, which individually bear spines of markedly uniform size. Exoexine thickness $3-5.5\ \mu$ (exclusive of spines); commonly folded. Intexine rather indistinct, more or less conformable with equatorial outline, diameter roughly three-quarters overall diameter.

Dimensions (66 specimens). Overall equatorial diameter (exclusive of spines) $74-150\ \mu$ (mean $104\ \mu$). This is closely conformable with the size range stated by Hacquebard (1957, p. 316).

Comparison. *Spinozonotriletes uncatu*s may be conspecific with *Acanthozonotriletes senticosus* Ishchenko 1956 (p. 87; pl. 16, fig. 200), which is somewhat smaller ($67-70\ \mu$), but is otherwise very similar.

Previous records. From the Horton group (lowermost Mississippian) of Nova Scotia, Canada (Hacquebard 1957). The possibly identical species *Acanthozonotriletes senticosus* is confined to Tournaisian strata of the western Donetz Basin (Ishchenko 1956).

Spinozonotriletes balteatus sp. nov.

Plate 95, figs. 4-6; text-fig. 11b

Diagnosis. Spores radial, trilete; amb roundly subtriangular to oval. Laesurae obscured by elevated, narrow, membranous, flange-like lips, frequently contorted due to compression and extending to limbate equatorial margin. Intexine indistinct to perceptible, roundly subtriangular. Distal surface of exoexine densely and uniformly sculptured with small, simple spinae which sometimes coalesce to form a rugulate pattern; spines usually evident at equator, sparsely scattered to absent on proximal surface. Spines have rounded to polygonal bases (diameter $0.5-2.5\ \mu$); length $1-2\ \mu$. Equatorial margin of exoexine marked by well-defined limbus $3.5-7\ \mu$ broad in polar view.

Dimensions (40 specimens). Overall equatorial diameter $51-102\ \mu$ (mean $73\ \mu$); diameter prescribed by intexine $30-59\ \mu$ (mean $42\ \mu$).

Holotype. Preparation P149A/3, 30.5 97.5. L.1241.

Locus typicus. Triungen (sample G1470), Spitsbergen; Lower Carboniferous.

Description. Holotype 77 μ overall, irregularly roundly subtriangular; sinuous laesurate lips extend to conspicuously limbate margin; intexine perceptible, 44 μ in diameter; distal surface of exoexine covered with small, crowded spinae which are often coalescent at their bases; apart from spines, exoexine laevigate. Obliquely compressed specimens common; in such cases the limbus appears as a well-defined, dark, transgressive band, marking the true equatorial margin.

Remarks. This species, characterized by the presence of a limbus and of predominantly distal spinose sculpture, appears unparalleled in available literature. On the basis of its exoexinal sculpture and somewhat obscure intexine, the species finds suitable inclusion within *Spinozonotriletes* Hacquebard.

Genus TETRAPORINA Naumova 1939 ex Naumova 1950

Type species. *T. antiqua* Naumova 1950 (designated by Potonié 1960, p. 130).

Discussion. This genus, recently validated by Potonié (1960), was instituted by Naumova (1939, p. 357) as a subgroup of her group *Tetraporosa*, which she included within the class *Porosa* Naumova. The original diagnosis of *Tetraporina* stated 'pollen with four pores, without folds', and according to Naumova the class *Porosa* 'belongs exclusively to the *Angiospermae*'. Subsequently, Naumova (1950) and Teteriuk (1956) have described a number of Russian Lower Carboniferous species of *Tetraporina*, and reaffirmed their belief in the angiospermous affinity of such forms. More recently, the names *Azonotetraporina* and *Zonotetraporina* were introduced by Teteriuk (1958, pl. 1 explanation) merely as captions to some drawings of further Lower Carboniferous *Tetraporina*-like spores, and must therefore at this stage be considered *nomina nuda*. Thus Staplin's (1960, p. 6) usage of *Azonotetraporina* as a valid generic entity is unacceptable. Furthermore, from the figures given by Teteriuk (1958) it seems likely that the forms were differentiated only on the basis of wall thickness.

Tetraporina Naumova is rather an unsatisfactory taxon in that the supposedly diagnostic four 'pores' are often either incompletely or not developed; this is apparent from both Naumova's and Teteriuk's illustrations and also from the Spitsbergen specimens described below. These latter represent an interesting new Lower Carboniferous occurrence, but are insufficient basis for the seemingly necessary, comprehensive reappraisal of the genus, the most significant feature of which appears to be constantly quadrangular shape.

Affinity. The angiospermous attribution (Naumova 1939, 1950; Teteriuk 1956, 1958) of *Tetraporina* has been regarded doubtfully by many subsequent authors (Staplin 1960, p. 6; Scott, Barghoorn, and Leopold 1960, p. 287; Hughes 1961, p. 89). Certainly the brief descriptions and line drawings of the Russian forms are inadequate for a critical assessment of botanical affinity. The possible algal affinity of the genus was discussed recently by Scott *et al.* (1960, p. 287), who noted its close morphological similarity with species of the unicellular green alga *Tetraëdron*. Valuable support in this connexion is apparent from a paper by Churchill (1960), who figured a number of Cainozoic and living unicellular algae and aplanospores; of his illustrations, fig. 1, nos. 3, 4, 6, 8, 11, 12, and 13 show striking superficial resemblance to *Tetraporina*. Moreover, Dr. Churchill

has kindly examined the specimens described below and he considers that there is little doubt of their algal affinity.

Tetraporina incrassata Naumova 1950

Plate 95, figs. 12, 13

Description of specimens. Spores aleate; outline quadrangular with distinctly concave sides and rounded corners. Exine scabrate to almost smooth, generally about $2\ \mu$ thick; locally \pm conspicuously thickened at corners, which may occasionally show aperture-like perforations.

Dimensions (12 specimens). Diagonal length 46–70 μ (mean 60 μ).

Previous records. From the Lower Carboniferous of the Moscow Basin (Naumova 1950).

Tetraporina glabra Naumova 1950

Plate 95, fig. 11

Description of specimens. Spores aleate; outline quadrangular with concave sides and rounded angles. Exine uniformly thick (3 μ), laevigate. In the figured specimen one minute perforation is present in the vicinity of each corner; the other specimens encountered appear non-perforate.

Dimensions (3 specimens). Diagonal length 50–54 μ .

Previous records. From Lower Carboniferous deposits of the Moscow Basin (Naumova 1950).

Tetraporina horologia (Staplin) comb. nov.

Plate 95, figs. 14, 15

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

Description of specimens. Spores aleate; outline quadrangular with concave to almost straight sides and rounded corners. Exine thin, hence readily folded and distorted; surface finely granulate to slightly roughened. Apertures rarely evident, but often simulated by arcuate folds at the corners.

Dimensions (14 specimens). Diagonal length 44–71 μ (mean 56 μ).

Remarks. As discussed above, *Azonotetraporina* Teteriuk is not a valid genus and in any case appears to be a misconceived subdivision of *Tetraporina* Naumova. Accordingly Staplin's species, which was questionably referred to *Azonotetraporina*, is here transferred to *Tetraporina*.

Comparison. *Tetraporina glabra* Naumova 1950 (pl. 1, figs. 5, 28) is thicker-walled, but otherwise similar to *T. horologia* (Staplin) comb. nov.

Previous records. From the Golata formation (Upper Mississippian) of Alberta, Canada (Staplin 1960).

MICROFLORAL ASSEMBLAGES AND STRATIGRAPHICAL
APPLICATIONS

The primary object of this section is to assess the stratigraphical significance of the microfossil elements, described above, of the Lower Carboniferous succession of Spitsbergen. It will be shown below that two distinct, successive, microfossil suites (assemblages) are distinguishable, each characterized by a number of distinctive microspore species of restricted stratigraphical ranges and hence of considerable correlative value both within and outside Spitsbergen. Evidence will be adduced as to the age of these assemblages, with reference to the standard European stage subdivisions of the Carboniferous, on the admittedly indirect basis of Russian and North American microfossil parallelism.

As noted previously, the microfossils examined in the present study have been recovered from a wide variety of lithologies (especially clastic rock types), and are thus probably fairly representative of the overall contemporary flora. Collecting has been insufficiently detailed, however, to permit palaeoecological inferences based upon quantitative/qualitative studies of the microfossils observed throughout a limited stratigraphical succession (cf. Neves 1958).

Delineation of microfossil assemblages

Detailed study of microfossils contained in samples collected from the three successions, at Birger Johnsonfjellet, Triungen, and Citadellet (see text-fig. 2), has given an overall picture, as comprehensive as sampling intervals permit, of the microfossil succession in the Spitsbergen Lower Carboniferous. Tables 1 and 2 list all the microspore species present in the samples from these localities; in the preparations of most samples, abundance and sufficiently good preservation of the microfossil elements has permitted representation on a quantitative basis, resulting from a count of 250 specimens per sample. It will be evident from these Tables that, whilst many species are ubiquitous, a fairly large number possess restricted vertical distribution. A more or less uniform microfossil suite occurs in samples from the lower parts of the Birger Johnsonfjellet and Triungen sections and in the entire collected Citadellet section (see Table 1). This distinctive suite is here conveniently designated as the *Rarituberculatus* Assemblage. The

EXPLANATION OF PLATE 95

All figures $\times 500$, and from unretouched negatives.

Figs. 1-3. *Retialetes radforthii* Staplin 1960. 1, Preparation P155/7, 36.0 106.0 (L.1246). 2, Showing longitudinal rupture; preparation P155/13, 33.9 105.2 (L.1247). 3, Preparation P155/10, 36.9 103.3 (L.1248).

Figs. 4-6. *Spinozonotriletes balteatus* sp. nov. 4, Holotype; distal surface. 5, Tetrad; preparation P149A/1, 26.4 100.4 (L.1243). 6, Proximal surface; preparation P145B/1, 17.9 95.6 (L.1242).

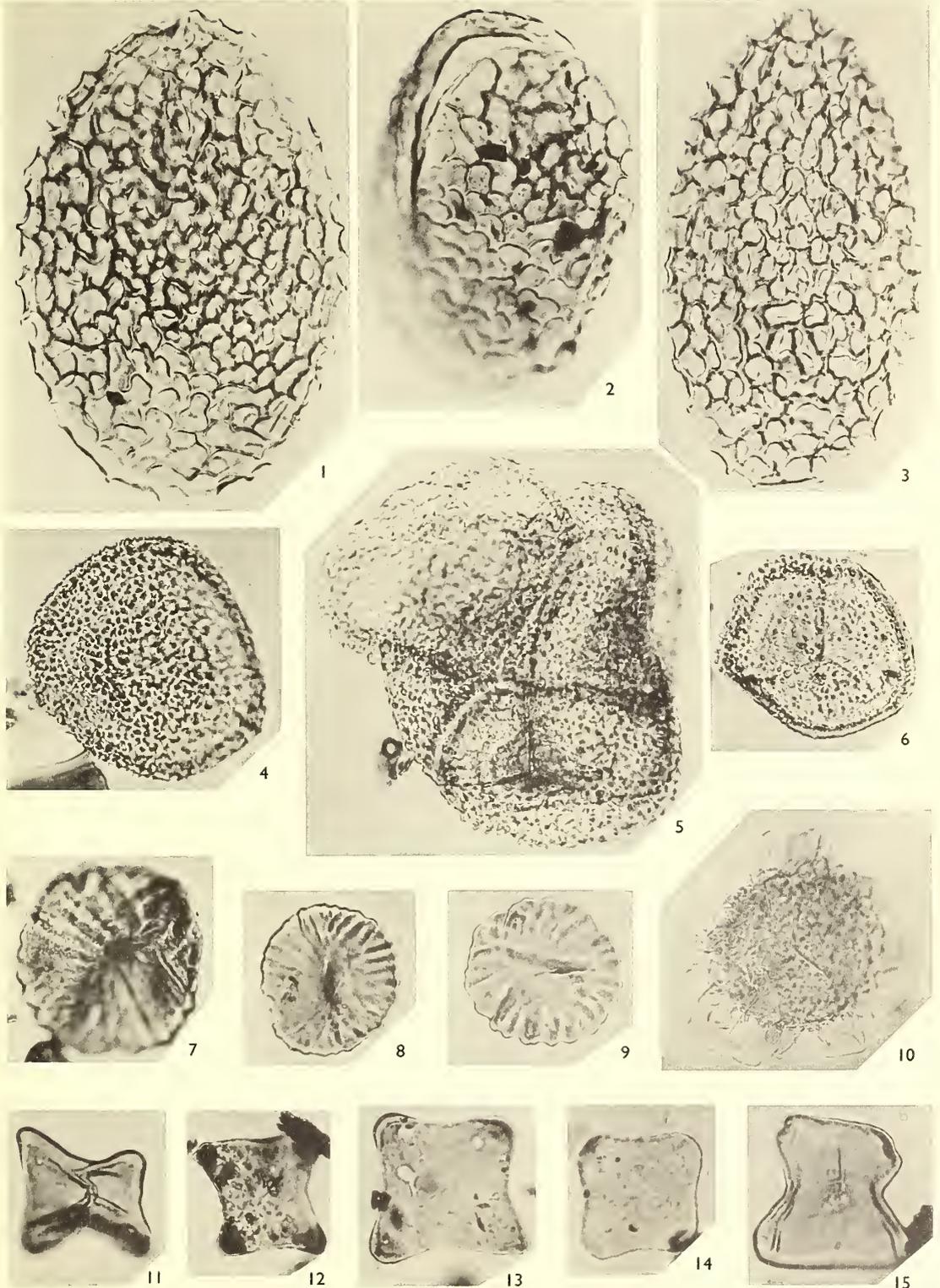
Figs. 7-9. *Radialetes costatus* gen. et sp. nov. 7, Preparation P163/1, 38.7 107.9 (L.1250). 8, Preparation P145B/7, 35.2 106.0 (L.1251). 9, Holotype.

Fig. 10. *Alatisporites tessellatus* Staplin 1960. Proximal surface; preparation P163/2, 40.4 113.5 (L. 1245).

Fig. 11. *Tetraporina glabra* Naumova 1950. Preparation P145B/5, 35.5 104.2 (L.1255).

Figs. 12, 13. *Tetraporina incrassata* Naumova 1950. 12, Preparation P139/4, 30.1 103.6 (L.1253). 13, Preparation P145A/1, 44.7 102.6 (L.1254).

Figs. 14, 15. *Tetraporina horologia* (Staplin) comb. nov. 14, Preparation P181/3, 32.1 105.5 (L.1256). 15, Preparation P202/3, 31.9 97.7 (L.1257).



PLAYFORD, Lower Carboniferous microspores

microspore species	BIRGER JOHNSONFJELLET					TRIUNGEN		CITADELLET						
	G1086	G1087	G1088	G1089	G1090	G1091	G1473	G1472	G1445	G1446	G1448	G1450	G1451	G1453
<i>Chaetosphaerites pollenisimilis</i>								x						
<i>Leiotriletes inermis</i>	x	2.0	0.4	x	x	3.6	1.2	2.4	4.4	1.6	4.4	5.2	2.4	4.4
<i>L. subintortus</i> var. <i>rotundatus</i>		x	1.6	2.8	x	x	x	x	x	1.2	2.0	2.0	1.6	4.4
<i>L. ornatus</i>	x		x	0.4	x	1.6		x	0.8	0.4	0.8	1.6	0.8	1.6
<i>L. microgranulatus</i>								x			x	0.8	0.8	4.0
<i>Punctatisporites glaber</i>	x	3.6	2.8	2.8	x	3.6	0.4	1.6	5.6	6.4	7.2	10.0	5.6	8.8
<i>P. pariverruculatus</i>	x			2.0		1.6		x	0.4	0.4	x	2.0	0.8	0.8
<i>P. labiatus</i>				0.4				x			0.4	1.6		
<i>P. pseudobeus</i>								0.4						
<i>Calamospora micromagosa</i>	x	2.4	2.0	1.2		0.8	1.2	0.8	3.2	2.8	3.6	3.2	4.0	2.8
<i>Phyllothecotrilletes rigidus</i>			x				x		1.2		0.8	x	2.8	2.8
<i>Granulatisporites planiuaculus</i>	x													
<i>Cyclogranisporites lasius</i>	x	2.4	0.4			0.4		0.4	3.2	1.6	5.6	5.2	2.8	2.4
<i>C. flexuosus</i>								0.8	x	0.8	0.8	1.6	0.8	1.2
<i>Verrucosporites gobbettii</i>				x	x			x			0.4	1.2	1.2	1.2
<i>Lophotriletes coniferus</i>						x			4.4	1.2	x	0.4	x	x
<i>Apiculatisporia macrurus</i>				0.4			3.2	0.4			0.4	0.8		
<i>Acanthotriletes multisetus</i>				x				0.8	2.4	11.2	12.0	6.4	5.2	4.8
<i>A. mirus</i>								x					x	
<i>Convolutispora tuberculata</i>				3.6	x	0.4	0.8	0.8	1.6	1.2	4.4	2.8	1.6	1.6
<i>C. vermiformis</i>	x	4.8	0.4	2.0			6.8	0.4	3.6	3.2	1.6	1.6	0.8	0.4
<i>C. harlandii</i>		3.2	0.8	2.0	x	1.2		2.8	0.4	0.8	0.4	0.4	1.6	0.4
<i>C. crassa</i>				0.4		0.4		0.4		x	x	0.8	x	
<i>Microreticulatisporites lunatus</i>				0.8		0.4	0.8	0.4			1.6	2.8	2.0	0.8
<i>Dictyotriletes caperatus</i>			x	0.4				2.8	0.8	1.2	0.8			
<i>Reticulatisporites cancellatus</i>			0.8	4.8	x	0.8		12.8		0.8	0.8	x	2.8	1.2
<i>R. planus</i>		0.4	0.4	0.8	x	x		0.4	0.8	0.4	x			
<i>Perotriletes perinatus</i>		2.0	0.4	1.2	x	0.4	0.4	0.4	1.2	1.6	1.2	1.2	0.4	0.4
<i>P. magnus</i>	x	4.4	0.4	x			0.8	0.4	x	1.2	1.2	x	0.8	0.8
<i>Triquitrites batillatus</i>				x		1.6								
<i>Tripartites incisotrilobus</i>				19.2	x	2.8		2.8			0.4	1.2	2.8	7.6
<i>Stenozonotriletes stenozonalis</i>						x		x	x	x	x			
<i>S. facillis</i> var. <i>praecrassus</i>			x	0.4				x	2.4	0.8	0.4			
<i>S. simplex</i>	x	2.0	3.2	x			1.6	x	0.8	1.6				
<i>S. inductus</i>	x	x						x	x					
<i>S. clarus</i>	x			0.8			0.4	0.8	0.4	0.4				
<i>S. perforatus</i>				x		x	2.0		0.8	2.0				
<i>S. cf. spetcanus</i>								x	x			x	x	
<i>Murospora intorta</i>	x					x			x	x				
<i>M. conduplicata</i>		2.0		3.6		1.6		0.8	0.8	x	0.4	4.4	x	1.6
<i>M. sublobata</i>				x		x					2.0	0.8	0.8	0.8
<i>Anulatisporites anulatus</i>					x	6.4	10.8	x	2.4	5.2	2.4	3.2	2.4	2.4
<i>A. labiatus</i>			3.2	3.2	x	1.6	3.6	8.0	18.8	8.4	2.8	0.4	5.2	0.8
<i>A. orbiculatus</i>					x			x	0.8		0.8	x	x	x
<i>A. canaliculatus</i>			0.8	x	x	x	0.8	0.4	0.4	1.2	0.8	0.8	x	x
<i>Densosporites dentatus</i>				2.4	x	36.0	30.4	1.6			4.0	4.8	6.4	4.8
<i>D. intermedius</i>				2.4	x	3.2		0.4			0.8	1.2	5.0	6.4
<i>D. variabilis</i>				x				1.2					3.2	3.2
<i>D. striatiferus</i>		21.2							x	0.4				
<i>D. spitsbergensis</i>			2.8	4.0	x	8.0		1.6			3.6	3.6	5.6	10.8
<i>T. variomarginatus</i>			8.4	16.8	x	4.8		10.8		1.2	10.0	6.4	16.8	
<i>Labiadensites fimbriatus</i>				1.2				0.4					x	0.4
<i>Knoxiosporites cinctus</i>				x		x			1.6	0.8			x	x
<i>K. margarethae</i>		0.8		0.8		0.8	0.4	x	2.8	6.0	x	x	x	x
<i>K. literatus</i>				1.6		1.6		0.4	0.4			0.4	0.4	0.8
<i>K. hederatus</i>				x				x			0.4	0.8	0.8	0.8
<i>Cristatisporites echinatus</i>								x				x	x	x
<i>Lophozonotriletes rarituberculatus</i>	x	7.2	1.2	2.8	x	0.8	0.4	x	4.4	2.8	0.8	0.8	0.8	0.8
<i>L. dentatus</i>									1.6	2.4				
<i>L. variverrucatus</i>	x							0.4	1.2	x	x	0.4	0.4	x
<i>Tholisporites foveolatus</i>		3.6	43.6	2.4			14.8	26.0	18.4	22.0	2.0	0.8	0.8	
<i>Endosporites micromanifestus</i>			0.4	0.4				x	0.8	0.8	4.4	5.2	1.2	2.4
<i>Velosporites echinatus</i>		0.4	0.4	0.8		0.4	6.0	x	x	0.8	0.4	x	0.4	x
<i>V. microreticulatus</i>				0.4				x			x			
<i>Spinozonotriletes uncatatus</i>				x			0.4	1.2		x	x	1.2	0.4	1.2
<i>Alatisporites tessellatus</i>				0.4										x
<i>Radiales costatus</i>			0.4	x			x	x	x	0.8	0.4		x	0.4
<i>Tetraporina incrassata</i>						x								x
<i>T. horologia</i>														

TABLE 1. Microspore distribution in samples from the Citadellet succession and from the lower parts of the sections exposed at Birger Johnsonfjellet and Triungen. In most samples, constituent species are recorded as percentages, which are based upon individual counts of 250 specimens. Indeterminable specimens in each case comprise the percentage complementary to that of specifically determinable specimens. 'x' indicates observed presence in a particular sample, but not in actual count. Relatively sparse and poorly preserved spores were recovered from samples G1086 and G1090, and hence neither was considered suitable for quantitative specific estimation. Correction: for *Densosporites intermedius* read *D. diatretus* (see p. 623).

microspore species	BIRGER JOHNSONFJELLET									TRIUNGEN					
	G1092	G1093	G1095	G1096	G1098	G1099	G1101	G1102	G1471	G1470	G1469	G1468	G1467	G1466	G1465
<i>Chaetosphaerites pollenisimilis</i>	0.4	1.2		2.4	1.2	x		0.4		0.4		x	x	3.6	
<i>Leiotrilletes inermis</i>	1.6	0.8	1.6	2.4	2.0	x		0.8		0.8	x	x	1.6	0.4	x
<i>L. subintortus</i> var. <i>rotundatus</i>	0.4	x	1.6	1.2		x	x	1.6	x	0.4		x	0.4	0.4	
<i>L. ornatus</i>					x			0.4	x				x	0.4	
<i>L. curiosus</i>								0.4		0.8				x	
<i>Punctatisporites glaber</i>	0.8	0.4	1.2	3.2	1.2	x		2.4	x	5.6	x	1.2	2.0	0.8	
<i>P. parvivermiculatus</i>															
<i>P. pseudobesius</i>			1.6							4.8			2.0		
<i>P. stabilis</i>	1.2	0.4	x	0.4									x	2.0	
<i>Calamospora microrugosa</i>	0.8	0.4	0.8	2.4	0.4		x	0.4	x	2.8		2.0	2.4	1.2	
<i>Phyllotheocetrilletes rigidus</i>	x	x	x		x	x		x	x	0.4		x	0.4	x	
<i>Waltzispora lobophora</i>					x			x		x			x	0.4	
<i>W. albertensis</i>				x				0.8					x	6.4	
<i>W. sagittata</i>								x							
<i>Cyclogranisporites lasius</i>	x	x		0.8							x	5.2	0.8	x	
<i>C. flexuosus</i>	x		0.4		x	x		0.4					x	x	
<i>Verrucosiporites eximius</i>					x	x				0.8			0.4	x	
<i>Anapiculatisporites concinnus</i>			0.4					1.2		0.8				8.8	
<i>A. serratus</i>										1.2	x			2.4	
<i>Acanthotrilletes multisetus</i>												0.4			
<i>Hystricosporites</i> sp.			x												
<i>Convolutispora tuberculata</i>	x		2.0		x		x			0.4	x	38.0	2.4	x	
<i>C. clavata</i>												0.8	x		
<i>C. harlandii</i>	2.0	0.4	0.8												
<i>C. crassa</i>	x	x													
<i>C. labiata</i>	0.4														
<i>C. usitata</i>	1.2			0.4	x					0.8	x		x		
<i>Microreticulatisporites lunatus</i>	x		0.4		x					x	x				
<i>Reticulatisporites rudis</i>										x				x	
<i>R. cancellatus</i>	4.4	2.0	2.8	2.4	0.4	x		2.0		0.8	x	x	x	0.4	
<i>R. variolatus</i>	1.6		0.8		x			x		0.4	x	x	x	x	
<i>R. peltatus</i>			x	1.6	x		x	x	x	0.4			x	x	
<i>R.?</i> sp.														x	
<i>Foveosporites insculptus</i>			0.4		0.4	x		x	x	4.4	x	0.8	4.0	x	
<i>Perotrilletes perinatus</i>	x		x						x						
<i>P. magnus</i>	x	0.4	0.8						x	x					
<i>Triquitrites trivalvis</i>					0.8	x	x	0.8						0.4	0.4
<i>T. batillatus</i>	5.6	1.2	0.8	0.4	x					0.4			0.4	x	
<i>Tripartites incisotrilobus</i>	1.2		0.4		2.8	x	x	0.8		0.8		1.2	0.8	1.2	0.4
<i>T. complanatus</i>					x			x		x				0.4	
<i>Stenozonotrilletes clarus</i>	x						x						0.4	0.4	
<i>S. facilis</i> var. <i>praecrassus</i>	0.4		x							x				x	
<i>S. perforatus</i>		0.4											x		
<i>S. cf. spetcaudus</i>			x												
<i>Murospora intorta</i>	0.8	0.4	0.4	0.4	0.8	x	x	0.8	x	x			x	0.8	
<i>M. aurita</i>	12.8	24.8	4.8	4.4	28.0	x	x	7.2	x	1.2		0.4	0.4	5.2	x
<i>M. conduplicata</i>		0.4	1.2	0.4	x	x	x	0.4	x	0.4	x	0.8	0.4	2.0	x
<i>M. sublobata</i>	x		x		0.4	x	x	x	x	0.4		x	x	1.2	x
<i>M. dupla</i>						x									
<i>M. strigata</i>					x									0.4	
<i>M. tripulvinata</i>					x										
<i>M. friendii</i>		2.0			x	x				0.4		0.4	0.4	0.4	
<i>Anulatisporites anulatus</i>	1.2	0.8	4.8	2.0	0.4	x		0.4	x	2.0		1.2	4.0	0.8	x
<i>A. labiatus</i>	1.6	0.4	0.4		x	x	x		x	0.4	x	0.8	x	x	
<i>Densosporites bialatus</i>			18.4	1.6	0.8	x		1.2	x			0.8	0.8	1.2	
<i>D. dentatus</i>	3.2	2.0	12.0	2.0	4.0	x		4.0	x	8.4	x	0.8	12.4	1.2	
<i>D. subcrenatus</i>					x	x	x	x	x	x	x	x	0.4	0.8	
<i>D. intermedius</i>	3.6	6.8	4.2	1.2	2.0			0.4	x	3.6	x		2.0	1.2	
<i>D. variabilis</i>	26.4	23.6	16.8	6.4	4.0	x	x	1.6	x	12.8	x	0.8	46.0	6.4	
<i>D. duplicatus</i>			0.4		0.8			0.4	x	x		0.8	x	x	
<i>D. spitzbergensis</i>	10.0	13.2	3.6	2.0	0.8					1.2	x		0.8	2.4	
<i>D. rarispinosus</i>								4.4	x	x	x		0.8		
<i>D. aculeatus</i>			2.4	x		x		x	x	0.8	x		0.8		
<i>D. sp.</i>					x							x			
<i>Labiadensites fimbriatus</i>	5.6	0.8	0.8	x	0.4	x	x	x	x			6.4	2.0	0.4	
<i>Knoxisporites cinctus</i>			1.2												
<i>K. margarethae</i>	x														
<i>K. literatus</i>	6.4	11.2	2.4		x	x	x	0.8			x	0.4		0.4	
<i>Lycospora uber</i>			2.0	56.8	43.2	x	x	61.2	x	5.6	x	2.4	2.4	32.4	
<i>Lophozonotrilletes appendicea</i>								x		0.4	x		0.4	1.6	
<i>Monilospora triungensis</i>														0.4	
<i>M. dignata</i>								x						0.8	
<i>Potoniespores delicatus</i>			x		1.2	x		0.4		x			0.4	x	
<i>Cirratiradites solaris</i>								x						x	
<i>C. elegans</i>	x		0.8	x						0.4					
<i>Camptozonotrilletes velatus</i>	2.4	0.4	2.0					x	x	1.6	x	0.4	1.2	x	
<i>Diatomozonotrilletes saetosus</i>			x		1.6	x	x	0.4					0.8	x	
<i>D. hughesii</i>			x	x		x	x	0.8	x	6.0		0.8	0.8	2.4	
<i>D. trilinearis</i>									x	4.0		4.4	0.8	0.4	
<i>D. rarus</i>									x					x	
<i>Endosporites micromanifestus</i>	x		0.4	x	x	x	x	0.4						x	
<i>Remysporites albertensis</i>										x			x		
<i>Velosporites microreticulatus</i>	x														
<i>Spinozonotrilletes balteatus</i>										13.6	x	21.6	0.8	2.8	
<i>Alatisporites tessellatus</i>				0.4				x							
<i>Retialetes radforthii</i>														x	
<i>Radialetes costatus</i>		1.2	0.4						x	x		0.4	x	x	
<i>Tetraporina incrassata</i>														x	
<i>T. glabra</i>														x	
<i>T. horologia</i>										x				0.4	x

TABLE 2. Microspore distribution in Birger Johnsonfjellet and Triungen samples succeeding those documented in Table 1. In most samples, constituent species are recorded as percentages, which are based upon individual counts of 250 specimens. Indeterminable specimens in each case comprise the percentage complementary to that of specifically determinable specimens. 'x' indicates observed presence in a particular sample, but not in actual count. Counting was precluded in samples G1099, G1101, G1471, G1469, and G1465, owing to sparse occurrence and/or poor preservation of the recovered spores. Correction: for *Densosporites intermedius* read *D. diatretus* (see p. 623).

younger microfloral suite, termed the Aurita Assemblage, is present in samples from Birger Johnsonfjellet and Triungen, immediately succeeding those documented in Table 1. It includes many species unknown from the Rarituberculatus Assemblage and lacks a considerable number characteristic of the latter. The detailed microfloral analysis of the samples from Birger Johnsonfjellet and Triungen which contain the Aurita Assemblage is presented in Table 2. This microfloral subdivision is not intended to suggest finality, as it is recognized that subsequent work on more detailed collections may well provide a more precise microflorally based zonation.

In the Birger Johnsonfjellet section, the change in microspore content occurs stratigraphically between samples G1091 and G1092, at respectively 128 metres and 138 metres above base. At Triungen the change occurs between samples G1472 and G1471, at respective heights above base of 100 metres and 132 metres. The apparent abruptness of this 'change' would possibly be in fact reduced to a transition if intermediate samples from both sections were available. It is important to note, however, that none of the samples from other localities contains evidence of a mixture of the diagnostic representatives of the two assemblages discussed below.

The Rarituberculatus Assemblage. The older assemblage, which is named from the most consistently occurring species (see Table 1), is characterized diagnostically by the following microspore species:

- Lophozonotriletes rarituberculatus* (Luber) Kedo 1957
- Verrucosporites gobbettii* sp. nov.
- Lophotriletes coniferus* Hughes and Playford 1961
- Convolutispora vermiformis* Hughes and Playford 1961
- Dictyotriletes caperatus* sp. nov.
- Reticulatisporites planus* Hughes and Playford 1961
- Stenozonotriletes inductus* Ishchenko 1956
- Anulatisporites canaliculatus* sp. nov.
- Densosporites striatiferus* Hughes and Playford 1961
- Densosporites variomarginatus* sp. nov.
- Knoxisporites hederatus* (Ishchenko) comb. nov.
- Cristatisporites echinatus* sp. nov.
- Lophozonotriletes dentatus* Hughes and Playford 1961
- Lophozonotriletes variverrucatus* sp. nov.
- Tholisporites foveolatus* Hughes and Playford 1961
- Velosporites echinatus* Hughes and Playford 1961
- Spinozonotriletes uncatatus* Hacquebard 1957

Other species apparently exclusive to the older assemblage, but of less common occurrence, are: *Punctatisporites labiatus* sp. nov., *Leiotriletes microgranulatus* sp. nov., *Acanthotriletes mirus* Ishchenko 1956, and *Stenozonotriletes stenozonalis* (Waltz) Ishchenko 1958.

The following species are common but not diagnostic components of the Rarituberculatus Assemblage: *Cyclogranisporites flexuosus* sp. nov., *Convolutispora tuberculata* (Waltz) Hoffmeister, Staplin, and Malloy 1955, *Reticulatisporites cancellatus* (Waltz) comb. nov., *Perotriletes perinatus* Hughes and Playford 1961, *P. magnus* Hughes and Playford 1961, *Tripartites incisotrilobus* (Naumova) Potonié and Kremp 1956, *Stenozonotriletes clarus* Ishchenko 1958, *Murospora conduplicata* (Andrejeva) comb. nov., *M. sublobata* (Waltz) comb. nov., *Anulatisporites anulatus* (Loose) Potonié and Kremp 1954, *A. labiatus* Hughes and Playford 1961, *Densosporites dentatus* (Waltz)

Potonié and Kremp 1956, *D. diatretus* nom. nov., *D. spitsbergensis* sp. nov., *Knoxisporites cinctus* (Waltz) Butterworth and Williams 1958, *K. margarethae* Hughes and Playford 1961, *K. literatus* (Waltz) comb. nov., *Endosporites micromanifestus* Hacquebard 1957, and *Radialetes costatus* gen. et sp. nov.

The Aurita Assemblage. From a comparison of Tables 1 and 2 it is evident that this assemblage comprises an even more diverse microflora than that represented by the *Rarituberculatus* Assemblage. In particular, zonate forms (*Cirratiradites*, *Camptozonotriletes*, *Potoniespores*, *Diatomozonotriletes*) appear significantly; the older assemblage appears to be entirely devoid of zonate (*s. str.*) spores. Other striking generic introductions are *Lycospora*, *Anapiculatisporites*, *Waltzisporea*, *Monilospora*, *Foveosporites*, *Remysporites*, and *Retialetes*. Furthermore, the genera *Reticulatisporites*, *Convolutispora*, *Densosporites*, and *Murospora* are represented prolifically by numerous species in this younger assemblage. Especially significant is the total absence of *Lophozonotriletes rarituberculatus* (Luber), the 'index' species of the older microfloral suite.

The following microspore species are considered diagnostic components of the *Aurita* Assemblage, and have not been observed in the older assemblage:

- Murospora aurita* (Waltz) comb. nov., emend.
- Waltzisporea lobophora* (Waltz) Staplin 1960
- Waltzisporea albertensis* Staplin 1960
- Waltzisporea sagittata* sp. nov.
- Verrucosisporites eximius* sp. nov.
- Anapiculatisporites concinnus* sp. nov.
- Reticulatisporites variolatus* sp. nov.
- Reticulatisporites peltatus* sp. nov.
- Foveosporites insculptus* sp. nov.
- Triquirites trivalvis* (Waltz) Potonié and Kremp 1956
- Murospora friendii* sp. nov.
- Densosporites bialatus* (Waltz) Potonié and Kremp 1956
- Densosporites subcrenatus* (Waltz) Potonié and Kremp 1956
- Densosporites duplicatus* (Naumova) Potonié and Kremp 1956
- Densosporites rarispinosus* sp. nov.
- Densosporites aculeatus* sp. nov.
- Lycospora uber* (Hoffmeister, Staplin, and Malloy) Staplin 1960
- Lophozonotriletes appendices* (Hacquebard and Barss) comb. nov.
- Potoniespores delicatus* sp. nov.
- Cirratiradites elegans* (Waltz) Potonié and Kremp 1956
- Camptozonotriletes velatus* (Waltz) comb. nov.
- Diatomozonotriletes saetosus* (Hacquebard and Barss) Hughes and Playford 1961
- Diatomozonotriletes hughesii* sp. nov.
- Spinozonotriletes balteatus* sp. nov.

The Assemblage name is based upon the species *Murospora aurita* (Waltz), which is almost invariably present, often as the predominating species (see Table 2).

Other species which are much rarer than those of the foregoing list, but which nevertheless appear similarly restricted to the younger assemblage, are as follows: *Leiotriletes curiosus* sp. nov., *Anapiculatisporites serratus* sp. nov., *Convolutispora clavata* (Ishchenko) Hughes and Playford 1961, *Reticulatisporites rudis* Staplin 1960, *Reticulatisporites?* sp., *Tripartites complanatus* Staplin 1960, *Murospora dupla* (Ishchenko) comb. nov., *M. strigata* (Waltz) comb. nov., *M. tripulvinata* Staplin 1960, *Monilospora triungensis* sp. nov., *M. dignata* sp. nov., *Cirratiradites solaris* Hacquebard and Barss 1957, *Diatomo-*

zonotriletes trilinearis sp. nov., *D. rarus* sp. nov., *Remysporites albertensis* Staplin 1960, and *Retialetes radforthii* Staplin 1960.

The following species, which are also components of the Rarituberculatus Assemblage, are often present in significant proportions: *Chaetosphaerites pollenisimilis* (Horst) Butterworth and Williams 1958, *Convolutispora tuberculata* (Waltz) Hoffmeister, Staplin, and Malloy 1955, *Reticulatisporites cancellatus* (Waltz) comb. nov., *Triquitrites batillatus* Hughes and Playford 1961, *Tripartites incisotrilobus* (Naumova) Potonié and Kremp 1956, *Murospora intorta* (Waltz) comb. nov., *M. conduplicata* (Andrejeva) comb. nov., *M. sublobata* (Waltz) comb. nov., *Anulatisporites anulatus* (Loose) Potonié and Kremp 1954, *A. labiatus* Hughes and Playford 1961, *Densosporites dentatus* (Waltz) Potonié and Kremp 1956, *D. diatretus* nom. nov., *D. variabilis* (Waltz) Potonié and Kremp 1956, *D. spitsbergensis* sp. nov., *Labiadensites fimbriatus* (Waltz) Hacquebard and Barss 1957, *Knoxisporites literatus* (Waltz) comb. nov., *Endosporites micromanifestus* Hacquebard 1957, and *Radialetes costatus* gen. et sp. nov.

The Birger Johnsonjellet and Triungen samples, from which the Aurita Assemblage has been recovered, are lithologically more diverse than those from which the older assemblage has been studied. It seems relevant, therefore, to consider the general relationships observed between rock-type and contained microfloral elements, although, as noted previously, detailed palaeoecological inferences are not possible. For this purpose a series of histograms (text-fig. 12) has been constructed to represent the relative proportions of common microfloral constituents observed in five lithological types, all of which contain the Aurita Assemblage. The microflora of the dull coal (E363) and of the highly carbonaceous (coaly) shale (R38) are notably restricted in comparison with those of the other sediments represented on text-fig. 12. In E363 the predominating forms are species of *Densosporites*, and *Reticulatisporites cancellatus* (Waltz) is also an important constituent. The microflora of R38 is marked by an extremely high percentage of *Murospora aurita* (Waltz). In the fine-grained sandstone (G1102) and the two carbonaceous shales (G1098, G1466) the microfloras exhibit considerable diversity, with *Lycospora uber* (Hoffmeister, Staplin, and Malloy) as the most abundant component. By contrast this species is comparatively rare in E363 and R38. These spore associations are probably representative of a more or less contemporary flora as preserved in sediments which accumulated in different ecological situations; possible botanical implications will be discussed subsequently in this paper.

A summary compilation of the species characteristic of the two microfloral assemblages is presented on Table 5.

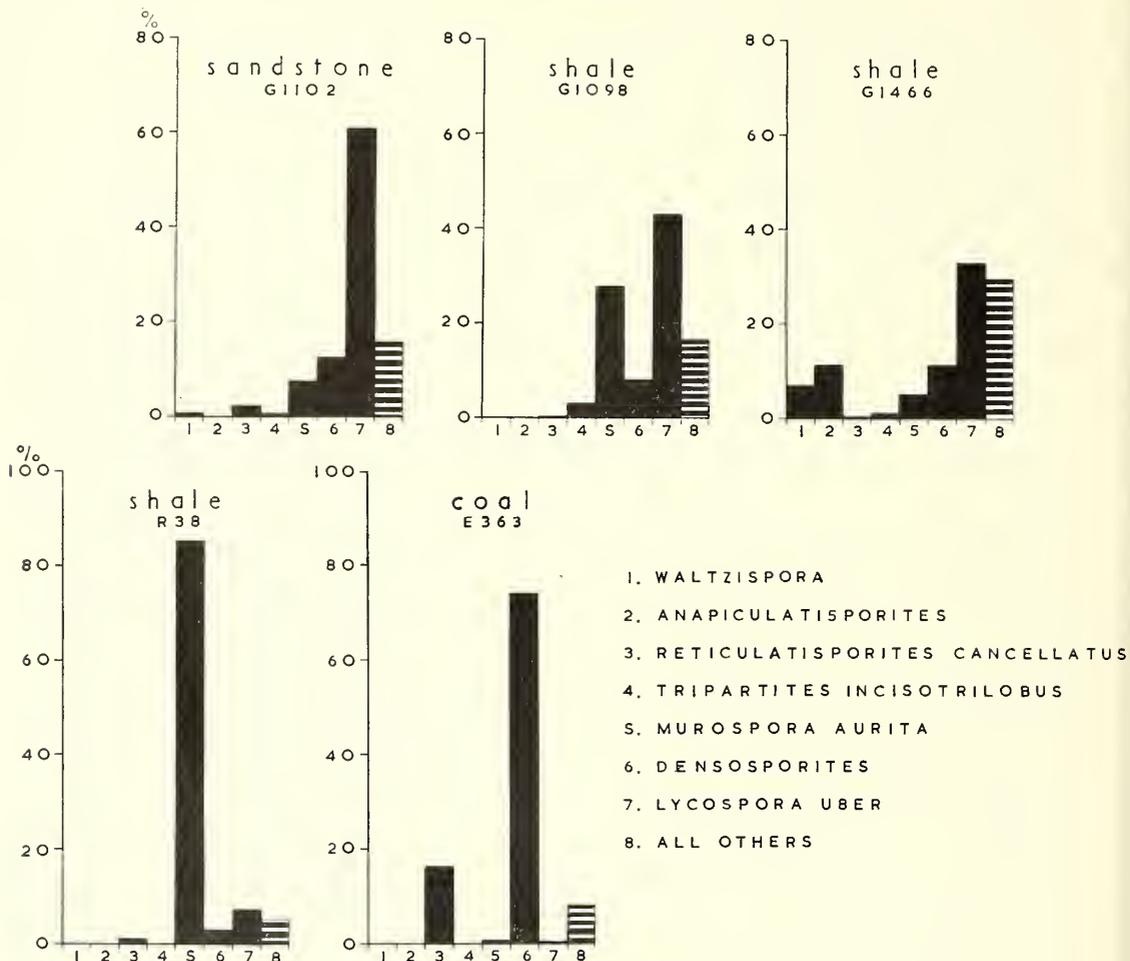
Age of the microfloral assemblages

The Rarituberculatus Assemblage. The 'index' species of this assemblage, *Lophozonotriletes rarituberculatus* (Luber), is a characteristic constituent of Russian strata of Tournaisian age (Luber and Waltz 1941; Ishchenko 1956; Kedo 1957, 1958, 1959; Byvsheva 1957, 1960). It has not been recorded from Viséan or younger rocks, but was reported by Luber and Waltz (1941) from allegedly Upper Devonian sediments of the Timan Peninsula and Kizel region. However, more recent Russian work (as cited above) seems to suggest that *L. rarituberculatus* is an exclusively Tournaisian form.

Another significant species is *Spinozonotriletes uncatius* Hacquebard, which has been described from the lowermost Mississippian of Canada. Its possible Russian equivalent,

Acanthozonotriletes senticosus Ishchenko, is confined to Tournaisian deposits of the western Donetz Basin. Two other species described by Ishchenko (1956), *Stenozonotriletes inductus* and *Acanthotriletes mirus*, have similar vertical restriction.

Convolutispora vermiformis Hughes and Playford occurs in Canadian strata of lowest Mississippian and of probable Upper Devonian age.



TEXT-FIG. 12. Histograms showing microspores present in different rock-types containing the Aurita Assemblage.

Numerous other components of the Rarituberculatus Assemblage, most of which are also present in the younger assemblage, are unknown from pre-Tournaisian strata. These are: *Chaetosphaerites pollenisimilis* (Horst), *Acanthotriletes multisetus* (Luber), *Microreticulatisporites lunatus* Knox, *Tripartites incisotrilobus* (Naumova), *Stenozonotriletes facilis* Ishchenko var. *praecrassus* Ishchenko, *Murospora intorta* (Waltz), *M. conduplicata* (Andrejeva), *M. sublobata* (Waltz), *Zonotriletes macrodiscus* Waltz (probable Russian equivalent of *Anulatisporites labiatus* Hughes and Playford), *Anulati-*

sporites orbiculatus (Waltz), *Densosporites dentatus* (Waltz), *D. diatretus*, *D. variabilis* (Waltz), *Labiadensites fimbriatus* (Waltz), *Knoxisporites cinctus* (Waltz), *K. hederatus* (Ishchenko), and *Endosporites micromanifestus* Hacquebard.

From the above evidence it is concluded that the Rarituberculatus Assemblage is of Tournaisian age.

The Aurita Assemblage. The younger assemblage is marked by the absence of the characteristic Tournaisian species cited above and especially notable is the sudden disappearance of *Lophozonotriletes rarituberculatus* (Luber).

Murospora aurita (Waltz), the 'index' species of the Aurita Assemblage, was described initially (Luber and Waltz 1938, 1941) from Russian strata, the age of which was not specified more precisely than 'Lower Carboniferous'. Subsequent investigations (Hacquebard and Barss 1957; Staplin 1960) indicate its presence in Canadian deposits of Upper Mississippian age. These latter occurrences, together with evidence from the present study of the complete absence of *M. aurita* in the older assemblage, suggest strongly that the species is post-Tournaisian. It is noteworthy also that *M. aurita* is unknown in rocks definitely assignable to the Namurian stage.

Numerous other Russian, Canadian, and British species are important constituents of this assemblage. *Convolutispora clavata* (Ishchenko), *Murospora dupla* (Ishchenko), *M. strigata* (Waltz), and *Triquitrites trivalvis* (Waltz) have been recorded as exclusively Viséan species in the U.S.S.R., although the latter species is known also from Namurian A coals of Scotland (Butterworth and Williams 1958). *Waltzispora sagittata* sp. nov. occurs in the Scottish Viséan (Love 1960).

The following species are unknown from Namurian or younger strata of the U.S.S.R.: *Reticulatisporites cancellatus* (Waltz), *Stenozonotriletes clarus* Ishchenko, *Murospora conduplicata* (Andrejeva), *Densosporites dentatus* (Waltz), *Labiadensites fimbriatus* (Waltz), and *Camptozonotriletes velatus* (Waltz).

Densosporites subcrenatus (Waltz), *Cirratiradites elegans* (Waltz), and *Diatomozonotriletes saetosus* (Hacquebard and Barss) are apparently confined in Russia to rocks of Viséan and Namurian age.

Lycospora uber (Hoffmeister, Staplin, and Malloy), which is often an extremely abundant constituent of the assemblage, appears from previous records to range from lowest Viséan to at least Westphalian A.

The following species have been reported hitherto from strata ranging in age from Tournaisian to Namurian: *Convolutispora tuberculata* (Waltz), *Tripartites incisotrilobus* (Naumova), *Stenozonotriletes facilis* Ishchenko var. *praecrassus* Ishchenko, *Densosporites intermedius* (Waltz), *D. variabilis* (Waltz), *Knoxisporites literatus* (Waltz), and *Endosporites micromanifestus* Hacquebard. *Densosporites bialatus* (Waltz) is also known to be similarly long-ranging, but appears to be especially abundant in Russian strata of Viséan–Namurian age.

A number of species, confined to the Aurita Assemblage, are common to the coal microflora described by Hacquebard and Barss (1957), which is probably equivalent in age to the Middle Chester series of the United States. These comprise: *Waltzispora albertensis* Staplin, which is present also in the Russian Lower Carboniferous (Reinsch 1884) and was formally described by Staplin (1960); *Cirratiradites solaris* Hacquebard and Barss, also recorded by Staplin (1960); *Densosporites duplicatus* (Naumova),

initially reported by Lubert and Waltz (1938) from the Russian Lower Carboniferous; and *Lophozonotriletes appendices* (Hacquebard and Barss).

The microflora described by Staplin (1960) is from the Golata formation of Canada, which is equivalent in age to the Lower Chester series of the United States and is thus probably slightly older than the coal investigated by Hacquebard and Barss (1957). The following species, all described for the first time by Staplin (1960), are restricted in Spitsbergen to the Aurita Assemblage: *Reticulatisporites rudis*, *Tripartites complanatus*, *Murospora tripulvinata*, *Remysporites albertensis*, and *Retialetes radforthii*. In particular, the latter species appears to be confined at Birger Johnsonfjellet and Triungen to the stratigraphically highest beds containing the younger assemblage.

Very little obvious similarity exists between the Aurita Assemblage and the Namurian microfloras described by Horst (1955), Dybová and Jachowicz (1957), Butterworth and Williams (1958), and Neves (1961). Indeed, the only species in common are those which are known from the work of other authors to occur also in strata of greater age, i.e. at least Viséan. Furthermore, none of the definitely post-Viséan Russian species, as documented by Ishchenko (1956, 1958), is present in the assemblage.

It is evident that the Aurita Assemblage conforms closely at specific level with microfloras reported by numerous authors from Viséan strata of the U.S.S.R. Significant correlation can also be made with Lower-Middle Chester microfloras of Canada. As noted previously in this paper, the European equivalence of the Chester series is somewhat uncertain, but more recent goniatite and conodont studies suggest correlation of the lower part of the series with the Upper Viséan rather than with the Namurian A.

Collectively, the above evidence strongly indicates that the Aurita Assemblage is of Viséan age, although a possible extension into the older Namurian is not precluded. Definite pronouncement in this latter respect must necessarily await more conclusive palaeontological evidence concerning the European equivalence of the Chester series, coupled with further palynological investigation of the North American Mississippian, the microfloras of which are as yet only sparsely known (see text-fig. 4).

As discussed previously, the two microfloral assemblages are represented successively in the sections at Birger Johnsonfjellet and Triungen. Thus the Billefjorden Sandstones as developed at these localities incorporate strata ranging in age from Tournaisian to Viséan, possibly to lowest Namurian. Certainly the presence (in the stratigraphically highest beds) of *Retialetes radforthii*, together with a number of other forms described by Staplin (1960) and Hacquebard and Barss (1957), seems to indicate an upper age limit of either topmost Viséan or alternatively lowest Namurian.

Samples from the Citadellet succession contain exclusively the Rarituberculatus Assemblage, hence indicating a Tournaisian age. However, the uppermost part of this section has not been sampled (see text-fig. 2) and it is possible therefore that beds of Viséan age are represented at Citadellet. *In situ* samples were unobtainable from basal Billefjorden Sandstones of the three reference successions; thus the precise age of the lowermost part of the series at Birger Johnsonfjellet, Triungen, and Citadellet is unknown.

Correlation within Svalbard

The microfloral assemblages delineated above have been observed in preparations of samples from various other localities in Vestspitsbergen and from Nordkapp, Bjørnøya.

Thus the rocks exposed at these localities (listed below) may be correlated with the palynologically documented successions at Birger Johnsonfjellet, Triungen, and Citadellet. Two comprehensive check lists (Tables 3 and 4) record the microspore species present in samples from localities other than those of the three successions. Table 3 incorporates samples containing the Rarituberculatus Assemblage, whilst the younger assemblage is represented (in a relatively large number of samples) in Table 4.

Citation is made below of some of the more stratigraphically significant constituent species of each sample which, in containing one or other of the microfloral assemblages, is referable implicitly to appropriate portions of the reference successions. The localities are shown on text-fig. 1; data on their stratigraphy have already been presented.

Vestspitsbergen

1. *Citadellet*. Samples B685 (studied earlier by Hughes and Playford 1961) and B687 both contain prolific microfloras representative of the Rarituberculatus Assemblage, and as such are conformable with the other Citadellet samples recorded palynologically in Table 1. Age—Tournaisian.

2. *Triungen*. Sample G1461 contains an abundant and well-preserved microflora which is typical of the Aurita Assemblage. In particular, the presence of the rare forms *Reticulatisporites? sp.* and *Retialetes radforthii* suggests a similar horizon to that of sample G1466 of the known Triungen succession. Age—Upper Viséan, or possibly lowermost Namurian.

3. *Ebbadalen (north side)*. Sample B706 yielded a fairly well-preserved microflora including the following diagnostic representatives of the younger assemblage: *Murospora aurita*, *Waltzispota albertensis*, *Reticulatisporites peltatus*, *Densosporites bialatus*, *Lycospora uber*, *Camptozonotriletes velatus*, *Diatomozonotriletes saetosus*, &c. Age—Viséan.

Sample W860 contains a somewhat poorly preserved microflora recognizably conformable with the Aurita Assemblage. Significant species present include *Murospora aurita*, *Convolutispora clavata*, *Reticulatisporites peltatus*, *Densosporites bialatus*, *Lycospora uber*, *Diatomozonotriletes saetosus*, and *Camptozonotriletes velatus*. The additional presence of *Convolutispora harlandii* suggests correlation with a horizon

LOCALITY	A		B
	B 685	B 687	B 680
<i>Leiotriletes inermis</i>	x	x	x
<i>L. subintortus</i> var. <i>rotundatus</i>	x	x	
<i>L. ornatus</i>	x	x	
<i>L. microgranulatus</i>		x	x
<i>Punctatisporites glaber</i>	x	x	x
<i>P. parvivermiculatus</i>		x	
<i>P. labiatus</i>			x
<i>Calamospora microrugosa</i>	x	x	x
<i>Phyllothecotriletes rigidus</i>	x		
<i>Cyclogranisporites lasius</i>	x		
<i>C. flexuosus</i>		x	
<i>Verrucosisporites gobettii</i>		x	x
<i>Lophotriletes confusus</i>	x	x	
<i>Acanthotriletes multisetus</i>		x	
<i>A. mirus</i>		x	
<i>Convolutispora vermiformis</i>	x	x	x
<i>C. harlandii</i>		x	
<i>Microreticulatisporites lunatus</i>	x	x	
<i>Dictyotriletes caperatus</i>		x	x
<i>Reticulatisporites cancellatus</i>		x	x
<i>R. planus</i>	x	x	
<i>Ferotriletes perinatus</i>	x	x	
<i>F. magnus</i>		x	
<i>Tripartites incisotrilobus</i>	x		
<i>Stenozonotriletes stenozonialis</i>		x	
<i>S. inductus</i>		x	
<i>S. clarus</i>		x	
<i>S. perforatus</i>		x	
<i>S. cf. spetcaudus</i>		x	
<i>Murospora conduplicata</i>	x	x	
<i>Anulatisporites anulatus</i>		x	x
<i>A. labiatus</i>	x	x	x
<i>A. orbiculatus</i>		x	
<i>A. canaliculatus</i>		x	x
<i>Densosporites dentatus</i>		x	x
<i>D. intermedius</i>		x	x
<i>D. variabilis</i>		x	
<i>D. striatiferus</i>	x		
<i>D. variomarginatus</i>		x	x
<i>Labiadensites fimbriatus</i>		x	
<i>Enoxisporites cinctus</i>	x		
<i>K. margarethae</i>	x	x	x
<i>Lophozonotriletes rarituberculatus</i>	x	x	x
<i>L. dentatus</i>	x	x	
<i>L. variverrucatus</i>	x	x	x
<i>Tholisporites foveolatus</i>	x	x	
<i>Endosporites micromanifestus</i>	x	x	
<i>Velosporites echinatus</i>	x	x	x
<i>Spinozonotriletes uncatatus</i>	x		
<i>Radialetes costatus</i>	x		

TABLE 3. Check list of microspore species, representative of the Rarituberculatus Assemblage, present in samples other than those documented in Table 1. Locality index—A, Citadellet; B, Odellfjellet. Correction: for *Densosporites intermedius* read *D. diatretus* (see p. 623).

comparable with that of G1095 in the Birger Johnsonfjellet succession. Age—Viséan.

Both these samples are from near the base of the Billefjorden Sandstones, suggesting that Culm sedimentation commenced at this particular locality relatively late in the Lower Carboniferous.

4. *Ebbadalen (south side)*. Samples B609 (recorded in Hughes and Playford 1961), B604, F531, F774, G332, G334, G366, and G382 are all from the same horizon, which is well above the base of the Culm. None yielded a well-preserved microflora. The following are some of the species, indicative of the Aurita Assemblage, which were observed in these complementary samples: *Murospora aurita*, *Anapiculatisporites concinnus*, *Reticulatisporites peltatus*, *Foveosporites insculptus*, *Triquitrites trivalvis*, *Tripartites complanatus*, *Murospora friendii*, *Densosporites bialatus*, *D. duplicatus*, *D. rarispinosus*, *Lycospora uber*, *Potoniespores delicatus*, *Cirratriradites solaris*, *Diatomozonotriletes saetosus*, *Remysporites albertensis*, and *Retialetes radforthii*. Age—Upper Viséan, or possibly lowermost Namurian.

5. *Wordiekammen (north side)*. The coal S59a (studied by Hughes and Playford 1961) contains a rather restricted microflora including such representatives of the younger assemblage as: *Murospora aurita*, *Convolutispora clavata*, *Lycospora uber*, and *Spinozonotriletes balteatus*. Age—Viséan.

6. *Adolfbukta (north shore)*. A particularly well-preserved microflora, typical of the Aurita Assemblage, was obtained from sample W217. Species present include: *Murospora aurita*, *Leiotriletes curiosus*, *Waltzispora lobophora*, *W. albertensis*, *Verrucosporites eximius*, *Triquitrites trivalvis*, *Tripartites complanatus*, *Densosporites bialatus*, *D. duplicatus*, *Lycospora uber*, *Lophozonotriletes appendices*, *Cirratriradites solaris*, *Diatomozonotriletes saetosus*, *D. hughesii*, *D. rarus*, and *Retialetes radforthii*. Age—Upper Viséan, or possibly lowermost Namurian.

7. *De Geerfjellet*. Samples G636 and T269, which are from the same outcrop and horizon, both yielded well-preserved microfloras characteristic of the Aurita Assemblage. Stratigraphically important species include: *Murospora aurita*, *Waltzispora albertensis*, *W. sagittata*, *Anapiculatisporites serratus*, *A. concinnus*, *Reticulatisporites? sp.*, *R. rudis*, *R. peltatus*, *Tripartites complanatus*, *Triquitrites trivalvis*, *Murospora tripulvinata*, *Densosporites bialatus*, *D. duplicatus*, *Lycospora uber*, *Monilospora triungensis*, *Cirratriradites solaris*, *Diatomozonotriletes saetosus*, *D. hughesii*, *D. trilinearis*, *D. rarus*, *Spinozonotriletes balteatus*, and *Retialetes radforthii*. Age—Upper Viséan, or possibly lowermost Namurian.

8. *Ragnarbreen*. A somewhat restricted microflora was obtained from the coal R38 (see text-fig. 12). Constituent species include the following, all representative of the younger assemblage: *Murospora aurita*, *Waltzispora albertensis*, *Reticulatisporites peltatus*, *Triquitrites trivalvis*, *Murospora friendii*, *Densosporites bialatus*, *Lycospora uber*, *Camptozonotriletes velatus*, *Diatomozonotriletes saetosus*, &c. Age—Viséan.

9. *Anservika*. The microfloras obtained from samples R5, F20, D120, G1283, G1280, G1278, and G1276 are specifically similar and, as they were collected from approximately the same horizon, may be considered here collectively. The Aurita Assemblage is represented by such forms as *Murospora aurita*, *Waltzispora albertensis*, *W. sagittata*, *Verrucosporites eximius*, *Convolutispora clavata*, *Reticulatisporites variolatus*, *R. peltatus*, *Foveosporites insculptus*, *Murospora friendii*, *Densosporites bialatus*, *D. dupli-*

catus, *D. rarispinosus*, *Lycospora uber*, *Lophozonotriletes appendices*, *Cirratriradites solaris*, &c. Age—Viséan.

10. *Carronella*. Sample G1080 contains a very sparse microflora, which, in containing *Murospora aurita*, *M. tripulvinata*, and *Lycospora uber*, is referable to the Aurita Assemblage. Age—Viséan.

11. *Gerritella*. Sample 353 yielded a sparse microflora, including the following species diagnostic of the younger assemblage: *Murospora aurita*, *M. tripulvinata*, *Densosporites rarispinosus*, *Lycospora uber*, *Lophozonotriletes appendices*, *Diatomozonotriletes saetosus*, and *Monilospora dignata*. In particular, the presence of the latter species suggests correlation with the stratigraphically highest sample (G1102) of the Birger Johnsonfjellet succession. Age—Upper Viséan, or possibly lowermost Namurian.

More abundant and diverse assemblages were recovered from samples 390 and 391. The following forms, diagnostic of the Aurita Assemblage, were identified from both samples: *Murospora aurita*, *Reticulatisporites peltatus*, *Lycospora uber*, and *Cirratriradites solaris*. Age—Viséan.

12. *Margaretbreen*. Sample G1339 contains a diverse and well-preserved microflora with many species characteristic of the younger assemblage. These include: *Murospora aurita*, *M. friendii*, *Triquitriles trivalvis*, *Densosporites bialatus*, *D. duplicatus*, *D. aculeatus*, *Lycospora uber*, *Camptozonotriletes velatus*, *Diatomozonotriletes saetosus*, and *Spinozonotriletes balteatus*. Age—Viséan.

A much less abundant microflora was obtained from sample G1344. Although *Murospora aurita* was not identified, the Aurita Assemblage is represented by such forms as *Lycospora uber*, *Camptozonotriletes velatus*, and *Retialetes radforthii*. The latter species suggests correlation with the uppermost parts of the successions at Triungen and Birger Johnsonfjellet. Age—Upper Viséan, or possibly lowermost Namurian.

13. *Svenbreen*. Sample E363, from just above the base of the Billefjorden Sandstones, includes the following representatives of the younger assemblage: *Murospora aurita*, *Reticulatisporites variolatus*, *Densosporites bialatus*, *D. rarispinosus*, *Lycospora uber*, *Cirratriradites elegans*, *Camptozonotriletes velatus*, and *Diatomozonotriletes hughesii*. Also present is *Convolutispora harlandii*, which, together with the above species, suggests correlation of this sample with approximately the same horizon as sample G1095 of the Birger Johnsonfjellet succession. Age—Viséan.

14. *Odelfjellet*. Sample B680 yielded a well-preserved microflora. The Rarituberculatus Assemblage is represented diagnostically by such forms as *Lophozonotriletes rarituberculatus*, *L. variverrucatus*, *Punctatisporites labiatus*, *Verrucosporites gobbettii*, *Dictyotriletes caperatus*, *Anulatisporites canaliculatus*, and *Velosporites echinatus*. Age—Tournaisian.

From stratigraphically higher beds, samples B624 and H267 yielded diverse microfloras referable to the Aurita Assemblage. Species common to both samples include: *Murospora aurita*, *Reticulatisporites peltatus*, *Densosporites aculeatus*, *Lycospora uber*, *Lophozonotriletes appendices*, *Cirratriradites elegans*, and *Camptozonotriletes velatus*. Age—Viséan.

15. *Ålandvatnet*. Comparatively poorly preserved microfloras were recovered from samples B616 and B619. Both contained the following species, which are diagnostic of the younger assemblage: *Murospora aurita*, *Densosporites bialatus*, *Lycospora uber*, *Cirratriradites elegans*, and *Camptozonotriletes velatus*. Age—Viséan.

16. *Lemströinfjellet*. Sample B443 contains a sparse microflora, including the following characteristic representatives of the Aurita Assemblage: *Murospora aurita*, *Anapiculatisporites concinnus*, and *Lycospora uber*. Age—Viséan.

17. *Blårevbreen*. Prolific and closely similar microfloras were recovered from samples M365, Q55, and Q56. Amongst the forms, common to all or at least two of these samples, and diagnostic of the Aurita Assemblage, are: *Murospora aurita*, *M. friendii*, *M. strigata*, *Waltzispota albertensis*, *Reticulatisporites variolatus*, *R. peltatus*, *Triquitrites trivalvis*, *Densosporites bialatus*, *D. duplicatus*, *D. rarispinosus*, *Lycospora uber*, *Cirratriradites elegans*, *Camptozonotriletes velatus*, *Diatomozonotriletes saetosus*, *D. hughesii*, *Remysporites albertensis*, and *Retialetes radfordii*. This spore association is very similar to that encountered in the stratigraphically highest samples from Triungen and Birger Johnsonfjellet. Age—Viséan, or possibly lowermost Namurian.

Bjornoya

1. *Nordkapp*. A few species only were positively identifiable in the poorly preserved microfloras recovered from samples P702 and P725. Sample P702 contains the following stratigraphically significant forms: *Densosporites bialatus*, *Lycospora uber*, and *Diatomozonotriletes saetosus*. Sample P725 includes *Anapiculatisporites concinnus*, *Lycospora uber*, and *Spinozonotriletes balteatus*. Although neither sample appears to contain the 'index' species *Murospora aurita*, their microfloras are clearly referable to the Aurita Assemblage. Age—Viséan.

From the above it is evident that the majority of the samples may be correlated with the upper parts of the Birger Johnsonfjellet and Triungen successions, by virtue of their content of representatives of the Aurita Assemblage. Moreover, the fact that many of these younger samples—specifically those from Ebbadalen (north side), Svenbreen, and Blårevbreen—are from basal beds suggests that in some places Culm deposition may have commenced relatively late in the Lower Carboniferous.

Apart from the localities of the three reference successions, only one sample (from Odellfjellet) contained the Rarituberculatus Assemblage. In addition two samples from higher in the Odellfjellet section yielded the younger assemblage. Thus this section is comparable in age (Tournaisian–Viséan) to those of Birger Johnsonfjellet and Triungen.

BOTANICAL RELATIONSHIPS

The outstandingly successful stratigraphical applications of dispersed-spore studies over the past two decades have tended to transcend the fundamentally botanical nature of palynology. Indeed, the botanical origin of many Carboniferous spore genera is at present unknown. Such workers as Chaloner (1953*a, b*; 1954; 1958*a, b*), W. and R. Remy (1957), and Sen (1958) have contributed considerably to our knowledge of the botanical affinities of some of the more characteristic *spores dispersae* of Carboniferous age. As a result it is now possible to deduce the existence of certain plant groups solely on the basis of dispersed-spore evidence.

As listed by Nathorst (1914) and Forbes *et al.* (1958), the macroflora of the Spitsbergen Culm consists predominantly of arborescent lycopods including numerous representatives of *Lepidodendron* and *Bothrodendron*. The presence of *Lepidodendron* is almost certainly reflected in the microflora by the abundance of *Lycospora* (occurring as

MICROFLORAL ASSEMBLAGE	R A R I T U B E R C U L A T U S	A U R I T A
S U G G E S T E D A G E	T O U R N A I S I A N	V I S É A N, possibly to NAMURIAN A
Leiotriletes microgranulatus		
Punctatisporites labiatus		
Verrucosisporites gobbettil		
Lophotriletes coniferus		
Acanthotriletes mirus		
Convolutispora vermiformis		
Dictyotriletes caperatus		
Reticulatisporites planus		
Stenozonotriletes stenozonalis		
Stenozonotriletes inductus		
Anulatisporites canaliculatus		
Densosporites striatiferus		
Densosporites variomarginatus		
Knoxisporites hederatus		
Cristatisporites echinatus		
Lophozonotriletes rarituberculatus		
Lophozonotriletes dentatus		
Lophozonotriletes variverrucatus		
Tholisporites foveolatus		
Velosporites echinatus		
Spinozonotriletes uncatius		
Cyclogranisporites flexuosus		
Convolutispora tuberculata		
Reticulatisporites cancellatus		
Tripartites incisotrilobus		
Stenozonotriletes clarus		
Anulatisporites labiatus		
Densosporites dentatus		
Densosporites intermedius		
Densosporites spitsbergensis		
Labiadensites fimbriatus		
Knoxisporites literatus		
Endosporites micromanifestus		
Radialetes costatus		
Waltzisporea lobophora		
Waltzisporea albertensis		
Verrucosisporites eximius		
Reticulatisporites variolatus		
Reticulatisporites peltatus		
Foveosporites insculptus		
Triquitrites trivalvis		
Tripartites complanatus		
Murospora aurita		
Murospora friendii		
Densosporites bialatus		
Densosporites duplicatus		
Densosporites rarispinosus		
Densosporites aculeatus		
Lycospora uber		
Lophozonotriletes appendices		
Potoniespores delicatus		
Cirratriradites solaris		
Cirratriradites elegans		
Camptozonotriletes velatus		
Diatomozonotriletes saetosus		
Diatomozonotriletes hughesii		
Spinozonotriletes balteatus		

TABLE 5. Summary compilation of important constituent species of the two Microfloral Assemblages delineable in the Lower Carboniferous of Spitsbergen. The indicated probable age of each Assemblage is discussed in detail in the text. Correction: for *Densosporites intermedius* read *D. diatretus* (see p. 623).

a single species, *Lycospora uber*), since this spore genus has been found associated elsewhere only with various species of the cone *Lepidostrobus* (see Chaloner 1953b; Sen 1958). In view of the total absence of *Lycospora uber* in the older microfloral assemblage, it is tempting to surmise the appearance, in Spitsbergen at least, of its parent plant in early Viséan times. Lycopods are probably also represented by the numerous species of *Densosporites* which occur throughout the Spitsbergen Culm. Chaloner (1958a) attributed a heterosporous cone, containing *Densosporites*-type microspores, to the herbaceous lycopod *Selaginellites*, but Bharadwaj (1959) recommended the inclusion of this cone in the genus *Botlirostrobus*. The spores described herein as *Densosporites spitsbergensis* are closely similar to those recovered by Bharadwaj (1959) from the Spitsbergen Lower Carboniferous fructification *Poroostrobus zeilleri* (described originally by Nathorst 1914). Bharadwaj considered that *P. zeilleri* 'shows lepidodendroid as well as sigillarioid characters'. Other probable Lycopsidean derivatives are the genera *Endosporites* (see Chaloner 1953a, 1958b) and *Cirratriradites* (see Chaloner 1954; Hoskins and Abbott 1956). These genera are represented respectively in the Lower Carboniferous of Spitsbergen by *Eudosporites micromanifestus*, and by *Cirratriradites elegans* and *C. solaris*. It should be noted, however, that the two species of *Cirratriradites* bear little resemblance to the *C. annulatus*-type microspores recovered from *Selaginellites suissei* and from *S. crassicinctus* by Chaloner (1954) and Hoskins and Abbott (1956) respectively.

From available literature, no definite pronouncement can be made concerning the origin of the numerous other microspore genera represented in the Spitsbergen Culm. Especial caution is necessary in assessing the botanical relationships of simple, relatively unsculptured generic groups such as *Calamospora*, *Punctatisporites*, and *Leiotriletes*. Forms of this general type are known to derive from numerous plant groups including, for example, Bryophyta, Psilophytales, Equisetales, and Filicales. Fern-like plants probably contributed the bulk of azonate, often prominently sculptured, trilete spores such as *Cyclogranisporites*, *Acanthotriletes*, *Anapiculatisporites*, *Verrucosisporites*, *Convolutispora*, and *Reticulatisporites* (cf. Potonié and Kremp 1956b; W. and R. Remy 1957). There appears to be no evidence regarding the affinity of cingulate forms such as *Murospora*, *Stenozonotriletes*, *Anulatisporites*, *Labiadensites*, *Knoxisporites*, *Lophozonotriletes*, &c., but some of these may well be of lycopsid origin. The genus *Florinites*, which is well known from the Upper Carboniferous as derived from cordaite and conifer vegetation, is conspicuously absent in the Spitsbergen Culm. Indeed, *Monosaccites* comprises an essentially minor element of the microfloras; such genera as *Remysporites* and *Velosporites* may perhaps be of pteridosperm origin. The presence in minor amounts of *Chaetosphaerites* and *Tetraporina* suggests strictly subordinate fungal and algal contributions respectively.

Some consideration has already been given to differences in microspore composition of various lithological types (see text-fig. 12), all of which contain the Aurita Assemblage. In the coal (E363) and the highly carbonaceous shale (R38), *Densosporites* spp. and *Murospora aurita* are respectively the dominating forms in microfloras which show a marked paucity in generic and specific representation. These species are relatively heavy, cingulate forms and were probably not very readily dispersed by wind or water. Thus their extreme abundance in coaly sediments may suggest that the parent plants were components of the coal swamp vegetation. *Lycospora uber* is a relatively trivial constituent of both E363 and R38. In contrast, the shales (G1098, G1466) and the sand-

stone (G1102) all contain diverse, essentially similar microfloras (having high specific and generic representation) which are probably fairly representative of the overall contemporary flora. In all three samples, *Lycospora uber* is the most abundant type, but accompanied by significant amounts of *Densosporites spp.* and *Murospora aurita*. *L. uber* is a small, relatively light spore which was probably dispersed widely from its parent arborescent lepidodendrid, and was perhaps eclipsed in the coal microflora by a dominance of heavier, less dispersable forms (as *Densosporites spp.* and *Murospora aurita*).

CONCLUSIONS

The Lower Carboniferous sediments of Spitsbergen contain diverse and some exceptionally well-preserved microfloras. The vertical distribution of the microspore species, as observed in the Billefjorden Sandstones sections at Birger Johnsonfjellet, Triungen, and Citadellet, provides an effective means of stratigraphical correlation both within and outside Spitsbergen. Indeed, the present study lends considerable support to the view expressed by Ishchenko (1956, p. 135) to the effect that terrestrial sequences of Lower Carboniferous age may be subdivided precisely on the exclusive basis of their microspore content.

There is some evidence that a third microfloral assemblage may be delineable. This would incorporate the youngest microfloral elements (e.g. *Retialetes radforthii*) which indicate an Upper Viséan or lowest Namurian age. A subdivision of the Aurita Assemblage would thus be entailed, but precise delimitation is not possible from samples available at present.

External correlation is afforded by the strikingly close similarity between the microfloras described herein and those reported previously from the Lower Carboniferous of Russia, and from portions of the Mississippian of Canada. In terms of the standard European stages, the age of the Billefjorden Sandstones is shown to range from Tournaisian to at least Viséan and perhaps lower Namurian; this endorses and strengthens the preliminary view of Hughes and Playford (1961). In terms of North American (Mississippian) nomenclature, the series ranges in age from Kinderhook to lower or middle Chester.

The fact that basal Culm samples, from often not widely separated localities, are of different ages suggests that the initiation of Culm sedimentation was not everywhere contemporaneous. Such variation in the age of local base levels is not unusual in a continental sequence which developed over an irregular landscape.

The disconformity at the top of the Billefjorden Sandstones at both Triungen and Birger Johnsonfjellet indicates that Culm sedimentation may have continued well into the Namurian. As noted previously the highest collected Culm sediments from the south side of Ebbadalen (samples B609, F531, &c.) indicate an Upper Viséan or lowermost Namurian age. However, this coaly horizon is succeeded by a further 220 feet of Culm which passes by vertical transition into the Lower Gypsiferous Series (see McWhae 1953, fig. 6, stratigraphical column H). These upper Culm beds may well be Namurian A in age; the age of the Lower Gypsiferous Series is not definitely known, but is thought to be Upper Namurian or Bashkirian (Forbes *et al.* 1958, p. 470 and table 2).

APPENDIX A. DATA ON SAMPLES STUDIED

Samples are listed and described macroscopically under headings of the localities from which they were collected. Actual collector is referred to by initials: M. B. Bayly, D. E. T. Bidgood, M. H. P. Bott, C. L. Forbes, J. L. Fortescue, P. F. Friend, D. G. Gee, D. J. Gobbett, W. B. Harland, J. R. H. McWhae, B. Moore, G. Playford, O. P. Singleton, M. S. Thornton, C. B. Wilson, J. M. Wordie. The initials are followed by the preparation numbers of each sample—those prefixed with 'M' were prepared by Mrs. Margaret Mortimer; 'P' indicates preparation by the writer.

Birger Johnsonfjellet

- G1086 sandstone, pale grey, hard, medium-grained, micaceous, with plant fragments; D. J. G.; P169.
 G1087 sandstone, dark grey, hard, medium-grained, carbonaceous, micaceous; D. J. G.; P161, P170.
 G1088 shale, black, silty, carbonaceous, micaceous, with plant fragments; D. J. G.; P162, P171.
 G1089 siltstone, black, carbonaceous, micaceous, with plant fragments; D. J. G.; P163.
 G1090 siltstone, reddish-brown to black, very hard, ferruginous, carbonaceous; D. J. G.; P177.
 G1091 shale, black, highly carbonaceous, with plant fragments; D. J. G.; P139, P143.
 G1092 shale, black, highly carbonaceous, with plant fragments; D. J. G.; P158.
 G1093 shale, black, highly carbonaceous, with plant fragments; D. J. G.; P159.
 G1095 shale, dark grey, silty, carbonaceous, micaceous, with plant fragments; D. J. G.; P164.
 G1096 sandstone, pale grey, hard, medium-grained; D. J. G.; P178.
 G1098 shale, black, carbonaceous; D. J. G.; P167.
 G1099 shale, black, carbonaceous; D. J. G.; P160.
 G1101 shale, black, highly carbonaceous, with plant fragments; D. J. G.; P168.
 G1102 sandstone, dark grey, fine-grained, silty, carbonaceous, micaceous; D. J. G.; P180, P188.

Trängen

- G1473 shale, dark grey, carbonaceous; D. J. G.; P147.
 G1472 siltstone, black, carbonaceous, micaceous; D. J. G.; P148.
 G1471 sandstone, pale grey, hard, fine-grained, with carbonaceous, silty lenses; D. J. G.; P179.
 G1470 shale, black, carbonaceous, with plant fragments; D. J. G.; P149.
 G1469 shale, black, highly carbonaceous, with plant fragments; D. J. G.; P152.
 G1468 shale, black, highly carbonaceous; D. J. G.; P151.
 G1467 shale, black, highly carbonaceous; D. J. G.; P154, P157.
 G1466 shale, black, carbonaceous, micaceous, with coaly lenses; D. J. G.; P145.
 G1465 shale, black, clayey, highly carbonaceous; D. J. G.; P153.
 G1461 shale, black, carbonaceous; D. J. G.; P155.

Citadellet

- B685 sandstone, grey, fine-grained, massive, carbonaceous, micaceous, with plant fragments; B. M.; M811, M928, M949, P003.
 B687 sandstone, grey, fine-grained, silty, carbonaceous, micaceous, with plant fragments; B. M.; P226.
 G1445 sandstone, grey-black, fine-grained, silty, carbonaceous, micaceous; D. J. G.; P172.
 G1446 shale, black, carbonaceous, micaceous; D. J. G.; P173.
 G1448 shale, grey-black, carbonaceous, micaceous, very fissile; D. J. G.; P174.
 G1450 shale, black, carbonaceous, very fissile; D. J. G.; P175.
 G1451 shale, black, carbonaceous, very fissile; D. J. G.; P176.
 G1452 sandstone, dark brown, fine-grained, massive, carbonaceous, ferruginous; D. J. G.; P206.
 G1453 shale, grey-black, carbonaceous, very fissile; D. J. G.; P181.

Ebbadalen (north side)

- B706 sandstone, grey, fine-grained, silty, carbonaceous, micaceous, with 'Knorria'; B. M.; P012.
 W860 shale, black, carbonaceous, micaceous; C. B. W.; P017.

Ebbadalen (south side)

- B604 bright coal; B. M.; P018.
 B609 siltstone, grey, carbonaceous, micaceous, with *Cardiopteridium ?spetsbergense* Nathorst; B. M.; M803.
 F531 shale, black, highly carbonaceous, with *Lepidodendron rhodeanum* Sternberg; P. F. F.; M788, P225.
 F774 siltstone, black, carbonaceous, micaceous, with plant fragments; P. F. F.; P021.
 G332 shale, black, carbonaceous, with plant fragments; D. J. G.; P024.
 G334 shale, black, highly carbonaceous, with plant fragments; D. J. G.; P076.
 G366 shale, black, carbonaceous, with *Lepidophloios scoticus* Kidston; D. J. G.; P077.
 G382 siltstone, black, carbonaceous, micaceous, with *Cardiopteridium ?spetsbergense* Nathorst; D. J. G.; P029.

Wordiekammen (north side)

- S59a dull coal; O. P. S.; M883, P150.

Adolfbukta (north shore)

- W217 shale, black, highly carbonaceous, with plant fragments; J. M. W.; P034.

De Geerfjellet

- G636 shale, black, carbonaceous, with plant fragments; D. J. G.; P026, P186.
 T269 shale, black, highly carbonaceous, some layers consisting almost entirely of megaspores; M. S. T.; P141.

Ragnarbreen

- R38 shale, black, highly carbonaceous, with plant fragments; J. R. H. McW.; M821, P182.

Anservika

- R5 sandstone, grey, fine-grained, hard, micaceous, slightly carbonaceous; J. R. H. McW.; P011.
 F20 dull coal; C. L. F.; M822, P083.
 D120 sandstone, dark grey, fine-grained, hard, carbonaceous, micaceous, with plant fragments; D. E. T. B.; P033.
 G1283 siltstone, dark grey, carbonaceous, micaceous, with plant fragments; D. J. G.; P236.
 G1280 sandstone, grey-black, fine-grained, carbonaceous, micaceous, with plant fragments; D. J. G.; P156.
 G1278 siltstone, grey, sandy, carbonaceous, micaceous, with plant fragments; D. J. G.; P235.
 G1276 sandstone, grey-black, fine-grained, silty, carbonaceous, micaceous; D. J. G.; P234.

Carronelva

- G1080 siltstone, grey-black, sandy, carbonaceous, micaceous, weathered, with plant fragments; D. J. G.; P207.

Gerritelva

- 353 bright coal; W. B. H.; P015.
 390 shale, grey-black, carbonaceous, micaceous, with *Lepidophloios* sp. and *Cardiopteridium ?spetsbergense* Nathorst; W. B. H.; P064.
 391 shale, grey-black, carbonaceous, micaceous, with *Cardiopteridium ?spetsbergense* Nathorst; W. B. H.; M810, P004.

Margaretbreen

- G1339 shale, black, carbonaceous, with plant fragments; D. J. G.; P184.
 G1344 shale, dark grey, carbonaceous, micaceous, with plant fragments; D. J. G.; P203.

Svenbreen

- E363 dull coal; D. G. G.; P140.

Odellfjellet

- B680 shale, black, carbonaceous, micaceous, with *Cyclostigma* sp.; B. M.; M809, P224.
 B624 siltstone, grey, carbonaceous, micaceous, with plant fragments; B. M.; M806, P002.
 H267 shale, black, highly carbonaceous, with *Stigmara*; W. B. H.; M797, P086.

Ålandvatnet

- B616 sandstone, pale grey, fine-grained, massive, with plant fragments; B. M.; M807, P089.
 B619 sandstone, grey, fine-grained, massive, with plant fragments; B. M.; P081.

Lemströmfjellet

- B443 sandstone, pale grey, medium-grained, massive, with irregular intercalations of carbonaceous, fine-grained sandstone and siltstone; M. H. P. B.; P053.

Blårevbreen

- M365 shale, black, silty, carbonaceous, micaceous, with plant fragments; M. B. B.; P202.
 Q55 shale, black, carbonaceous; J. L. F.; P146, P165.
 Q56 shale, black, carbonaceous, with plant fragments; J. L. F.; P166.

Nordkapp, Bjørnøya

- P702 shale, black, carbonaceous, weathered, with plant fragments; G. P.; P127.
 P725 shale, grey-black, carbonaceous, with *Lepidodendron spetsbergense* Nathorst, 'Knorria', and *Carpolithus* sp.; G. P.; P134.

APPENDIX B. NOTE ON SPECIMENS ILLUSTRATED BY HUGHES
 AND PLAYFORD (1961)

Sedgwick Museum Specimen numbers (L.880–L.938) have been allocated to type and other figured specimens of the preliminary study by Hughes and Playford (1961).

CONTENTS OF PARTS ONE AND TWO

	<i>page</i>
Introduction	550
Acknowledgements	551
References	552
Stratigraphy	556
Previous investigations of Lower Carboniferous microfloras	563
Preparation and examination of samples	569
Systematic descriptions of dispersed spores	571
<i>Anulatisporites labiatus</i> —Part I ends	618
Part II begins— <i>Anulatisporites orbiculatus</i>	619
Microfloral assemblages and stratigraphical applications	660
Delineation of microfloral assemblages	660
Age of the microfloral assemblages	665
Correlation within Svalbard	668
Botanical relationships	672
Conclusions	675
Appendix A. Data on samples studied	676
Appendix B. Note on specimens illustrated by Hughes and Playford (1961)	678

GEOFFREY PLAYFORD
 Department of Geology and Mineralogy,
 University of Queensland,
 St. Lucia, Brisbane,
 Australia

SECTIONS OF SOME SPORES FROM THE LOWER CARBONIFEROUS OF SPITSBERGEN

by MARY E. DETTMANN and G. PLAYFORD

ABSTRACT. Sections of four Lower Carboniferous dispersed-spore species, *Labiadensites fimbriatus* (Waltz) Hacquebard and Barss, *Cristatisporites echinatus* Playford, *Camptozonotriletes velatus* (Waltz) Playford, and *Spinozonotriletes uncatius* Hacquebard, are discussed and illustrated.

IN a recent paper, Hughes, Dettmann, and Playford (1962) discussed and illustrated sections of selected Carboniferous spore species and demonstrated the usefulness of sections in the morphological interpretation of spores with equatorial wall thickenings. The present paper incorporates sections of four of the microspore species which Playford (1962—this volume) described from the Lower Carboniferous succession of Spitsbergen. Two of these species are cingulate, one is zonate, and one, provisionally assigned to *Incertae Sedis* by Playford, shows wall features similar to those of mesospore types.

All the sections illustrated in Pl. 96 were cut at 3μ intervals transverse to the equatorial plane; the sectioning technique is described in Hughes, Dettmann, and Playford (1962). For each illustrated specimen, the preparation and slide number, followed by the reference co-ordinates of Leitz Laborlux microscope no. 1, and registered numbers (prefixed L) of the Sedgwick Museum, are stated. Precise locality and stratigraphical details are given in Playford (1962).

Acknowledgements. Grateful acknowledgement is made by M. E. D. to the International Federation of University Women for the award of the Ida Smedley Maclean Fellowship; and by G. P. to the Australian Commonwealth Scientific and Industrial Research Organization for the award of an Overseas Postgraduate Studentship.

SYSTEMATIC SECTION

Anteturma SPORITES H. Potonié 1893

Turma ZONALES (Bennie and Kidston) R. Potonié 1956

Subturma ZONOTRILETES Waltz 1935

Infraturma CINGULATI Potonié and Klaus 1954

Genus LABIADENSITES Hacquebard and Barss 1957

Labiadensites fimbriatus (Waltz) Hacquebard and Barss 1957

Plate 96, figs. 1, 2

Discussion. Sections clearly show the differentiated cingulum, which consists of a relatively wide, thick, non-tapering inner portion and a narrow, 'frilled' outer portion. Inner and outer portions connected only at the proximal and distal surfaces of the cingulum. Exine one-layered; forms the broad, flat, laesurate lips.

Genus CRISTATISPORITES Potonié and Kremp 1954

Cristatisporites echinatus Playford 1962

Plate 96, figs. 3-5

Discussion. The exoexine, which envelops the thin homogeneous intexine, forms the wedge-shaped cingulum, the laesurate lips, and the distal spinose sculptural elements. The sections also show an inner differentiated zone of the exoexine, but this may be due to corrosion.

Infraturma ZONATI Potonié and Kremp 1954

Genus CAMPTOZONOTRILETES Staplin 1960

Camptozonotriletes velatus (Waltz) Playford 1962

Plate 96, figs. 10-12

Discussion. The zona of this species is relatively thin, and near the equator it appears to enclose a cavity. Exine two-layered; exoexine forms zona and surrounds the thinner intexine (Pl. 96, fig. 12).

INCERTAE SEDIS

Genus SPINOZONOTRILETES Hacquebard 1957

Spinozonotriletes uncatus Hacquebard 1957

Plate 96, figs. 6-9

Discussion. Sections show that the exoexine, which is composed of granules, loosely envelops the homogeneous intexine. Exoexine shows spinose sculpture and forms the elevated lips of the laesurae.

Conflicting interpretations of the wall stratification of this species have been presented by previous authors. Hacquebard (1957) designates the outer sculptured layer as a perispore, whereas Potonié (1960) suggests that the thin inner layer is a mesospore. Some

EXPLANATION OF PLATE 96

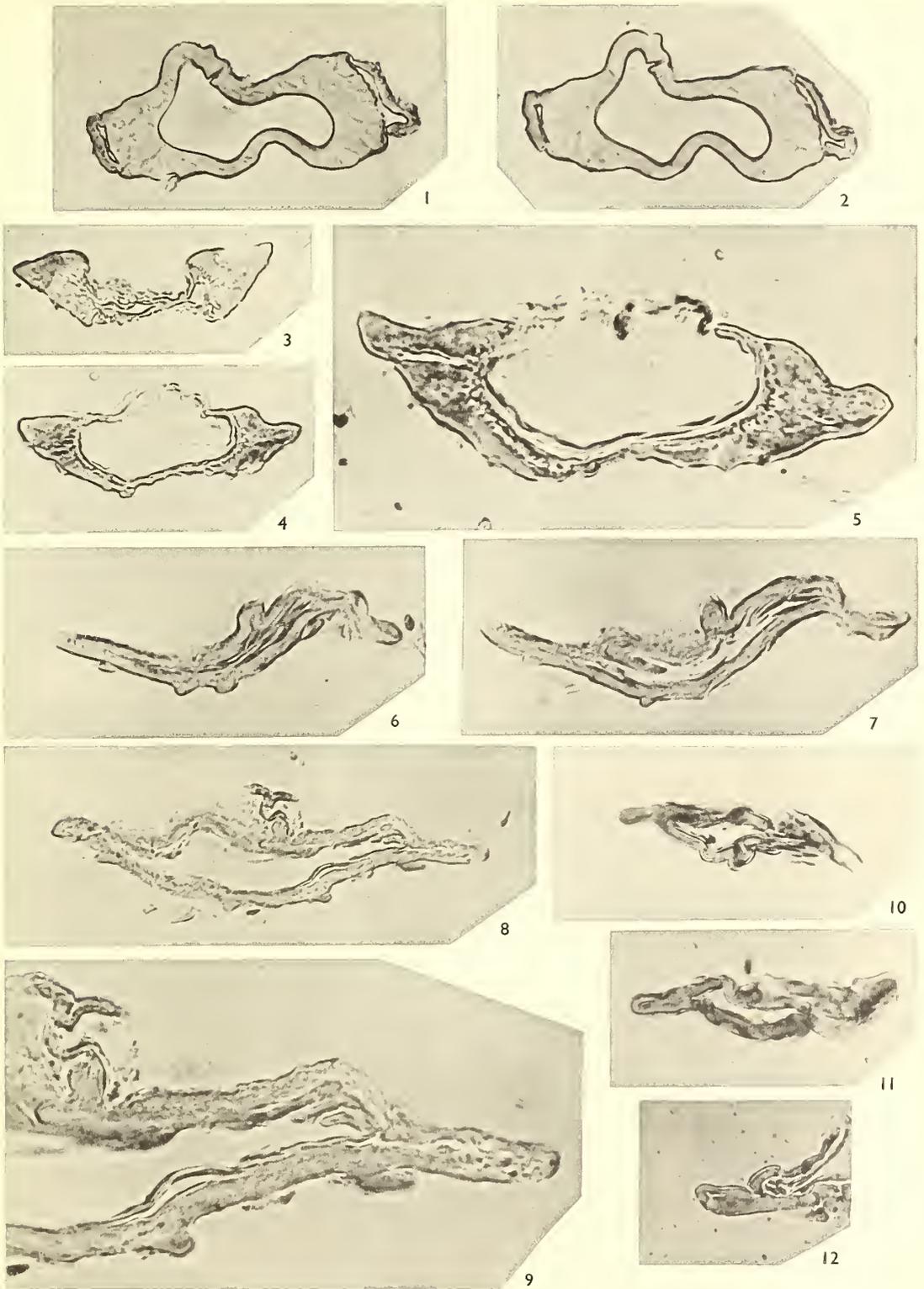
All figures $\times 500$ unless otherwise specified; from unretouched negatives.

Figs. 1, 2. *Labidensites fimbriatus* (Waltz) Hacquebard and Barss 1957. Sections of specimen with one-layered exine showing differentiated cingulum. Preparation P148/S45b/3-4. 1, 32.9 125.1 (L.1270h); 2, 27.0 123.0 (L.1270i).

Figs. 3-5. *Cristatisporites echinatus* Playford 1962. Sections of specimens with two-layered exine consisting of an inner homogeneous intexine and an outer differentiated exoexine which forms the wedge-shaped cingulum and distal spinae. 3, Preparation P148/S46b/2, 26.8 115.1 (L.1271e); 4, Preparation P148/S46c/2, 61.4 122.7 (L.1272d); 5, $\times 1,000$, Preparation P148/S46c/2, 47.3 122.2 (L.1272g).

Figs. 6-9. *Spinozonotriletes uncatus* Hacquebard 1957. Sections showing exine consisting of an inner, homogeneous intexine and an outer, sculptured exoexine which is composed of granules and forms the elevated lips of the laesurae. Preparation P148/S44a. 6, 44.9 113.0 (L.1273c); 7, 54.8 115.3 (L.1273f); 8, 9, Polar section 59.1 118.2 (L.1273g), 9, $\times 1,000$.

Figs. 10-12. *Camptozonotriletes velatus* (Waltz) Playford 1962. Sections of specimen showing zona and distal muri. Preparation P164/S39a. 10, 52.7 120.2 (L.1274f); 11, 29.7 121.3 (L.1274c); 12, $\times 1,000$, showing two-layered exine, the outer layer (exoexine) forms 'cavate' zona. 48.7 120.1 (L.1274e).



DETTMANN and PLAYFORD, Sections of microspores

evidence for the latter interpretation is provided by the Spitsbergen specimens. The spores figured by Playford (1962, pl. 94, figs. 4-6) and the sections, illustrated herein, clearly show that the inner wall layer is loosely enveloped, particularly in the equatorial region, by the outer wall layer. Such a wall feature is characteristic of described mesospore forms, for example *Duosporites congoensis* Høeg, Bose, and Manum 1955 and *Grandispora spinosa* Hoffmeister, Staplin, and Malloy 1955 (see Potonié 1958).

Furthermore, as discussed by Playford (1962, p. 657), the thick, sculptured outer wall layer, which forms the conspicuously elevated laesurate lips, shows little morphological or structural resemblance to either the bladder of typical Palaeozoic monosaccate spores or the, usually filmy, perispore of perinate spores.

REFERENCES

- HACQUEBARD, P. A. 1957. Plant spores in coal from the Horton group (Mississippian) of Nova Scotia. *Micropaleontology*, **3**, 301-24.
- HUGHES, N. F., DETTMANN, M. E., and PLAYFORD, G. 1962. Sections of some Carboniferous dispersed spores. *Palaeontology*, **5**, 2, 247-52.
- PLAYFORD, G. 1962. Lower Carboniferous microfloras of Spitsbergen. *Ibid.* **5**, 550-678.
- POTONIÉ, R. 1958. Synopsis der Gattungen der Sporae dispersae. II. Teil: Sporites (Nachträge), Saccites, Aletes, Praecolpates, Polypliates, Monocolpates. *Beih. Geol. Jb.* **31**, 1-114.
- 1960. Synopsis der Gattungen der Sporae dispersae. III. Teil: Nachträge Sporites, Fortsetzung Pollenites. Mit Generalregister zu Teil I-III. *Ibid.* **39**, 1-189.

MARY E. DETTMANN
Department of Geology,
Sedgwick Museum,
Cambridge

GEOFFREY PLAYFORD
Department of Geology and Mineralogy,
University of Queensland,
St. Lucia, Brisbane, Australia

THE EOSPIRIFERIDAE

by A. J. BOUCOT

ABSTRACT. The impunctate, spire-bearing family Eospiriferidae contains the subfamilies Eospiriferinae and Cyrtiinae. The Eospiriferinae appear in the Upper Llandovery and persist until the Eifelian; whereas the Cyrtiinae appear in the Upper Llandovery and persist with certainty until the close of the Ludlow, but there is a single specimen from beds of Emsian age in Czechoslovakia. The family is characterized by the possession of radial filar ornamentation externally combined with a spiriferoid form. Internally, the brachial valve is characterized by having long crural plates on either side of a linear, unstriated diductor attachment area. The interior of the pedicle valve is relatively generalized.

The eospiriferids disappear from the Western Hemisphere at the end of the Gedinnian, but continue on into the Eifelian in part of the Old World. In the Old World, the eospiriferids are absent from the Rhenish facies of the Devonian, as well as the Devonian of South Africa and Antarctica.

The genus *Plicocyrtia* is proposed for laterally plicate cyrtiinids, and the genera *Havlicekia*, *Macroplewa*, and *Nikiforovaena* for eospiriferinids with external forms differing substantially from previously described members of the subfamily. The genera *Najadospirifer* and *Pinguispirifer* are rejected from the Eospiriferidae on the basis of differing internal structures and external fine ornamentation.

The evolution of plicated eospiriferids from unplicated forms is discussed.

IN the course of a study of Silurian and early Devonian spiriferids, it became apparent to the writer that the eospiriferids were morphologically so far removed from any of the subfamilies of the Spiriferidae (King 1846) that they should be assigned to a separate family, the Eospiriferidae. The eospiriferids, world-wide in distribution (text-fig. 1), are of value in subdividing the Silurian. They appear, near the end of Llandoveryan time, fully developed on both sides of the North Atlantic. No closely related precursors of the eospiriferids have been reported from strata of Lower or Middle Llandoveryan age, but strata of those ages will doubtless eventually produce closely related genera and species. The disappearance of the family was relatively slow in Bohemia, the Carnic Alps, northern France, North Africa, the region of the Bosphorus, central Asia, the Appalachians, and New Zealand, with members of the family in some areas persisting into the Middle Devonian (text-figs. 2, 3), but was relatively rapid in the Malvinokaffric facies of South America and South Africa (text-fig. 1) and in the Rhenish facies of Germany ('*Spirifer*' *solitarius* Krantz possesses neither the internal nor external characteristics of an eospiriferid), Belgium, southern England, Poland, and Nova Scotia, where representatives of the family may be found in the late Silurian but not in the early Devonian. From the first appearance of the family in late Llandoveryan time two lineages, here assigned to the subfamilies Eospiriferinae Schuchert and LeVene 1929 (emended) and the Cyrtiinae Fredericks 1924, are distinct and well developed.

The writer acknowledges with pleasure the criticisms of Dr. J. E. Hede, Lund University; Dr. Valdar Jaanusson, Uppsala University; Dr. Jean Berdan and Dr. Charles Merriam, U.S. Geological Survey; and Dr. T. W. Amsden, Oklahoma Geological Survey, each of whom read the manuscript. Photographs of *Nikiforovaena ferganensis* were provided by Dr. O. Nikiforova, Leningrad, and specimens of *Janius insignis* by Dr. Hede. Ing. Jose Carrillo Bravo, Petroleos Mexicanos, Tampico, Tamaulipas, provided the collections from which the Ciudad Victoria eospiriferids were extracted. Dr. M. A. Rzonitskaya, Leningrad, made a number of useful comments regarding Soviet stratigraphy and eospiriferids. Prof. D. Nalivkin, Leningrad, arranged for the writer to study the material in the Tscherny-

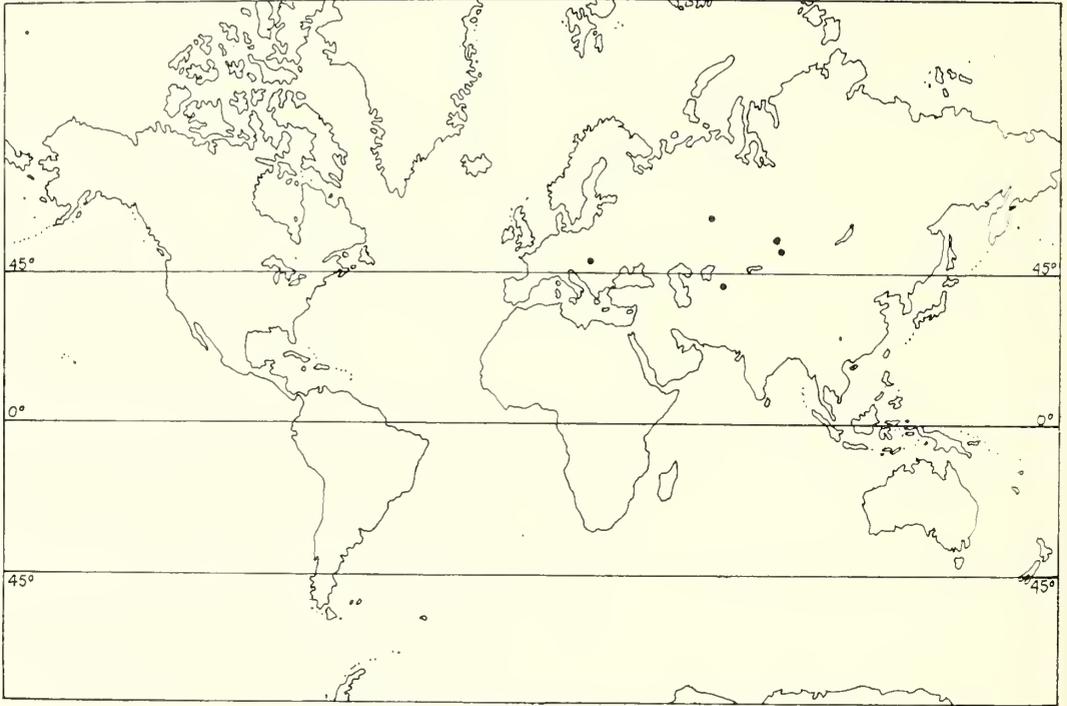


TEXT-FIG. 1. Known distribution of eospiriferids in strata of Llandoveryan to Gedinnian age.



TEXT-FIG. 2. Known distribution of eospiriferids in strata of Siegenian to Emsian age.

chev Geological Museum. Dr. V. Havlíček, Prague, discussed the manuscript with the writer and pointed out the peculiar ornamentation of '*Eospirifer*' *secans* and '*E.*' *turjensis*. Dozent Dr. F. Prantl, Prague, made available for the study the rich collections in the National Museum. Mr. Winfried Haas, Bonn, gave the writer an opportunity to collect *Eospirifer* and *Cyrtia* from strata he is studying in the Istanbul region. Dr. Brian Norford, Geological Survey of Canada, Ottawa, provided information on the occurrence of *Cyrtia* in the Silurian of British Columbia. Much of the research for this paper was supported by a National Science Foundation grant to the Massachusetts Institute of Technology (DSR contract 298).



TEXT-FIG. 3. Known distribution of eospiriferids in strata of Eifelian age.

SYSTEMATIC DESCRIPTIONS

Superfamily SPIRIFERACEA King 1846

Family EOSPIRIFERIDAE Schuchert and LeVene 1929 (nom. transl. Boucot, herein, et *Eospiriferinae* Schuchert and LeVene 1929)

Diagnosis. Impunctate spiriferids with fine ornamentation consisting of fila which bifurcate anteriorly and which originate anteriorly by implantation. The fila do not have spinose anterior terminae and are crossed by concentric growth-lines which may or may not be nodose. The delthyrium is either completely or partially closed by discrete deltidial plates which in large specimens become medially conjunct, enclose a foramen, and in many specimens are then overlain by an outer layer which simulates a pseudodeltidium. In the brachial valve long crural plates support the discrete hinge plates. Discrete chilidial plates may be present and in large specimens may be medially conjunct. The area of diductor attachment is unstriated. The ribbon-like crura and primary lamella form an

obtuse angle where they join above the short jugal process. In the pedicle valve long dental lamellae are present.

Comparison. The Eospiriferidae may be distinguished from the contemporaneous Delthyrinae and Kozłowskiellinae by the presence of long crural plates in the brachial valve, and by the absence of a striated diductor attachment area in the brachial valve and of external striations terminating anteriorly over the edge of each growth lamella as a fringe of minute spines. The Cyrtinopsidae possess crenulated growth lamellae that are unstriated radially.

Distribution. World-wide in strata of Upper Llandoveryan to Eifelian age.

Subfamilies. Eospiriferinae Schuchert and LeVene 1929 (emended) and Cyrtiinae Fredericks 1924.

Subfamily EOSPIRIFERINAE Schuchert and LeVene 1929 (emended)

Diagnosis. Members of the Eospiriferidae having a convex, but not pyramidal, pedicle valve and a triangular, but not narrowly elongate, delthyrium. The deltidial plates are usually narrow, border the delthyrial cavity, and are inserted normal to the interarea. In some specimens the deltidial plates may coalesce to form a pseudodeltidium.

Genera:

Eospirifer Schuchert 1913, in Zittel-Eastman, *Textbook of Paleontology*, **1**, 2nd ed., p. 411.

Striispirifer Cooper and Muir-Wood 1951, *J. Washington Acad. Sci.* **41**, 6, p. 195 (= *Schuchertia* Fredericks 1926).

Janius Havlíček 1957b, p. 247.

Havlicekia gen. nov.

Macroleura gen. nov.

Nikiforovaena gen. nov.

Genera rejected:

Najadospirifer Havlíček 1957b, p. 246. Restudy of topotype material shows that the type species of this genus possesses short crural plates and a striated area for diductor attachment in the brachial valve; the fine ornamentation consists of coarse spinules distributed along growth lamellae in a fashion similar to that of the reticularids.

Pinguispirifer Havlíček 1957b, pp. 246–7. Restudy of topotype material shows that the type species of this genus does not possess low, eospiriferid-type crural plates or a smooth, narrow notothyrial chamber for diductor attachment in the brachial valve. The musculature of the pedicle valve is unlike that of the Eospiriferidae. The finely striate ornamentation is not well enough preserved on the specimens studied to suggest the familial affinity of this genus.

Distribution. World-wide in strata of Upper Llandoveryan to Eifelian age.

Genus EOSPIRIFER Schuchert 1913

Plate 97, figs. 1–15

Type species. *Spirifer lineatus* J. de C. Sowerby 1825, *Mineral Conchology*, **5**, p. 151, pl. 493, figs. 1–2.

Diagnosis. Eospiriferinids having unplicated flanks, fold, and sulcus, as well as an elongate hinge line one-half to almost equal the maximum width.

Comparison. *Eospirifer* lacks the lateral plications present in *Striispirifer*, *Macropoleura*, and *Nikiforovaena*, and the anteriorly bifurcating plications on the flanks present in *Janius*. *Havlicekia* has an acuminate form, extremely high fold in the brachial valve, and striispiriferid-type plications in the early growth stages.

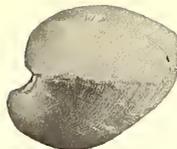
Pedicle exterior. Pedicle valve strongly convex, subcircular to laterally ellipsoidal in outline. Lateral margins rounded in forms where the greatest width is anterior of the posterior margin, relatively straight in forms where the greatest width is at the posterior margin. Anterior margin uniplicate. Interarea straight, posteriorly concave, and striated by growth-lines that parallel the hinge-line. Inclination of interarea catacline (for terminology of interarea inclination see Schuchert and Cooper 1932, p. 20), but the actual angle is distinctive for each species. The delthyrium encloses an angle of about 60 degrees. Beak straight to strongly incurved. The deltidial structures in small specimens consist of discrete plates bordering the margins of the delthyrium. With increase in size the deltidial plates may coalesce medially to enclose a pedicle foramen, and in larger specimens an outer layer of shell material completely covers the conjunct deltidial plates and foramen, simulating a pseudodeltidium (Beecher and Clarke 1889, pl. 6, figs. 9, 11). When large, the deltidial structures are striated by growth-lines paralleling the hinge-line. Sulcus well developed, gently rounded to subrectangular in cross-section. In some variants the peri-

EXPLANATION OF PLATE 97

- Figs. 1-6. *Eospirifer radiatus* (Sowerby, 1825). Mulde marl; Djupviks fiskläge, Eksta, Gotland. U.S.N.M. No. 84363. 1, Anterior view ($\times 1$). Note the relatively broad, low fold and sulcus. 2, Side view ($\times 1$). Note the incurved interarea of the pedicle valve. 3, Posterior view ($\times 1$). 4, Posterior view ($\times 2$). Note the narrow deltidial plates bordering the delthyrium and inclined normal to the interarea. 5, Brachial view ($\times 1$). Note the finely striate radial ornamentation and the lack of lateral plications. 6, Pedicle view ($\times 1$).
- Fig. 7. *Eospirifer* cf. *radiatus* (Sowerby, 1825). Chesuncook limestone. U.S.G.S. locality No. 3249-SD, islet about 3 miles south-east from mouth of Quaker Brook, Chesuncook Lake, Piscataquis County, Maine. U.S.N.M. No. 125257. Impression of interior of pedicle valve ($\times 1$). Note the relatively long dental lamellae.
- Figs. 8-10. *Eospirifer radiatus* (Sowerby, 1825). Chicago formation; Chicago, Illinois. 8, Posterior view of internal impression ($\times 1$). Note the long, slender, crural plates and the unstriated area of diductor attachment. U.S.N.M. No. 125255B. 9, Impression of interior of pedicle valve ($\times 1$). Note the relatively long dental lamellae. U.S.N.M. No. 125255A. 10, Impression of interior of pedicle valve ($\times 1$). Note the long dental lamellae and the variability present between the muscle impressions of this specimen and that illustrated in figs. 7 and 8. U.S.N.M. No. 125255B.
- Fig. 11. *Eospirifer radiatus* (Sowerby, 1825). Racine dolomite; Bridgeport, near Chicago, Illinois. Posterior view of impression of interior ($\times 3$). Note the relatively long crural plates and the unstriated area of diductor attachment. U.S.N.M. No. 8409.
- Fig. 12. *Eospirifer radiatus* (Sowerby, 1825). Racine dolomite; Racine, Wisconsin. Anterior view of cardinalia and dental lamellae ($\times 3$). Note the laterally flaring hinge plates supported by long crural plates which enclose the narrow, unstriated area of diductor attachment. U.S.N.M. No. 9762.
- Fig. 13. *Eospirifer radiatus* (Sowerby, 1825). Waldron shale; Waldron, Indiana. Calcined preparation ($\times 2$) showing short jugal process (outlined in India ink below) directed towards interior of pedicle valve at the junction of the primary lamella of the spire and the crura. Note the change in direction of curvature where the primary lamella and the crura fuse. M.C.Z. No. 9425B.
- Figs. 14, 15. *Eospirifer radiatus* (Sowerby, 1825). Racine dolomite; Wisconsin. 14, Dolomitized interior showing spire, jugal process, and crura ($\times 2$). Note the short jugal process and the obtuse angle included by the crura and the primary lamella. M.C.Z. No. 9426. 15, Dolomitized interior showing spire, jugal process, and crura ($\times 2$). Note the short jugal process. M.C.Z. No. 9426.



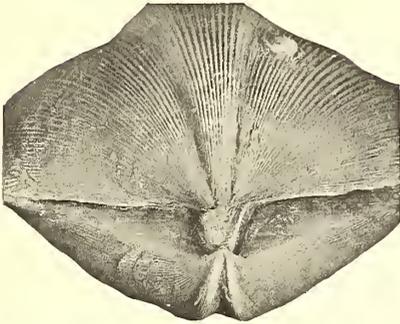
1



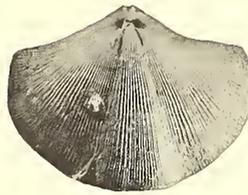
2



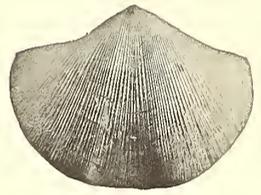
3



4



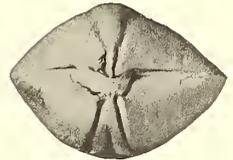
5



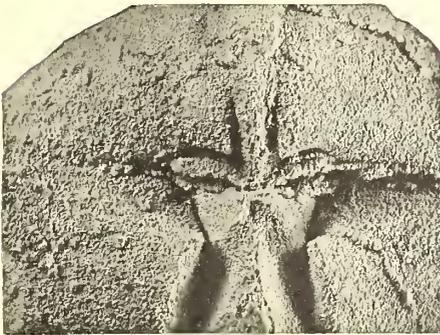
6



7



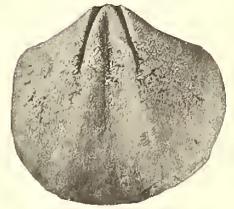
8



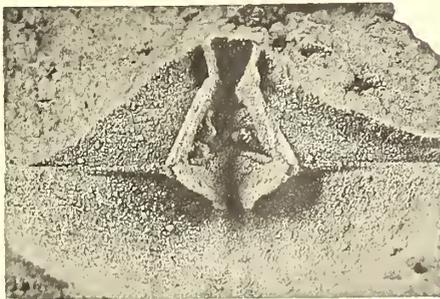
11



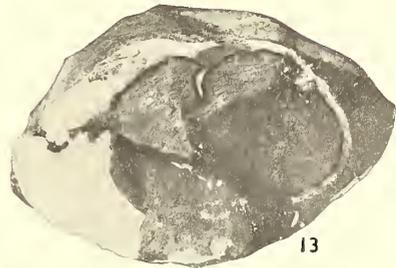
9



10



12



13



14



15

phery and anterior margin tend to become plicated in larger specimens, but normally no lateral plications or plications in the sulcus are present. Fine ornamentation consists of radial fila intersected, in well-preserved specimens, by concentric growth-lines. The intersections tend to be nodose. Strong growth-lines uncommon, but if present are few in number.

Brachial exterior. Valve gently convex, subrounded to laterally elongate in outline. A low fold with a gently rounded to subrectangular cross-section is present. Interarea orthocone to gently apsacone, very short in comparison with that of the pedicle valve.

Pedicle interior. Delthyrium bordered by two strong dental plates that extend about one-third the length of the shell and support stubby hinge teeth. Almost no secondary material is deposited around the plates except for a small amount in the apex of the valve and the extremities of the umbonal cavities. The dental lamellae diverge from the midline at an angle of about 20 to 30 degrees. The muscle field, very poorly impressed except for a low myophragm, extends about one-third of the distance to the anterior margin. Myophragm laterally bounded by anteriorly expanding diductor impressions which are longitudinally striate and posteriorly enclose the small, elliptical adductor impressions. Anterior and lateral periphery of valve smooth.

Brachial interior. The cardinalia consist of discrete hinge-plates supported medially by long crural plates. Area of diductor attachment smooth. A low myophragm about one-third the length of the valve bisects the feebly impressed muscle field. Anterior and lateral margins smooth. The dental sockets are closed postero-laterally and flare antero-laterally. The ribbon-like crura make an oblique angle with the primary lamellae. A short jugal process is directed toward the pedicle valve near the junction of the crura and the primary lamellae. St. Joseph (1935, pp. 322-3; pl. xv, fig. 10, text-fig. 3) reports a band connecting the jugal processes medially, but the writer found no evidence of one.

Species:

- Eospirifer consobrinus* Poulsen 1943, pp. 52-54, pl. 6, fig. 104.
Spirifer contortus Barrande 1879, pl. 107, fig. ii.
Spirifer davousti de Verneuil 1850, *Bull. Soc. Geol. France*, 2nd ser., 7, p. 781 (probably the same as *togatoides*).
Spirifer devonicans Barrande 1879, pl. 4, fig. 19.
Eospirifer eastoni Gill 1949, pp. 98-99, pl. 3, figs. 20, 21, 23.
Eospirifer fusus Borisyak 1955, p. 72, pl. 12, fig. 10.
Spirifer grandis Hedstrom 1923, pp. 10-11, pl. 2, figs. 5-9.
Spirifer (Eospirifer) ignobilis Khodalevitch 1939, p. 109 (English), p. 66 (Russian), pl. 27, fig. 3.
Spirifer insidiosus Barrande 1879, pl. 72, fig. iii.
Spirifer lineatus J. de C. Sowerby 1825, *Mineral Conchology*, 5, p. 151, pl. 493, figs. 1-2.
Spirifer marklini de Verneuil 1848, *Bull. Soc. Geol. France*, 2nd ser., 5, p. 344.
Eospirifer paralentius Gill 1950, pp. 247-8, pl. 1, figs. 1-6.
Spirifer plicatellus var. *globosus* Salter 1848, *Mem. Geol. Surv.* 11, i, p. 382.
Eospirifer praeseicans Havlíček 1959, pp. 52-53, pl. 9, figs. 1-4, 6.
Spirifer (Eospirifer) pseudoindifferens Nalivkin 1930, pp. 111-12, pl. viii, fig. 7.
Eospirifer quinqueplicatus Poulsen 1934, pp. 18-19, pl. 2, figs. 17-19.
Spirifer radiatus-obsoletus Foerste 1909b, p. 14, pl. 2, fig. 10.
Eospirifer subradiatus Wang 1956, pp. 577-8, pl. vii, c, figs. 1-2.
Spirifer subsinuatus A. Romer 1855, *Beitr.* 3, p. 3, pl. 2, fig. 5.

- Spirifer tenuistriatus* Shaler 1869, *Bull. Mus. Comp. Zool.* **1**, 4, p. 70.
Spirifer togatoides Paeckelmann 1925, pp. 128–9, pl. 6, fig. 1a–e.
Spirifer togatus Barrande 1848, *Haid. Naturw. Abh.* **ii**, pp. 167–8, pl. 15, fig. 2.
Eospirifer tuvaensis Chernychev 1937, pp. 79–80, pl. v, figs. 18–21.

Distribution. The distribution lists have been prepared to give complete geographic and stratigraphic coverage of the world; however, space does not permit including every reference from the literature for any given area. The following abbreviations are used: Sil. (Silurian), Dev. (Devonian), Lland. (Llandovery), Wen. (Wenlock), Lud. (Ludlow), Skal. (Skalian), Ged. (Gedinnian), Sieg. (Siegenian), Ems. (Emsian), Cobl. (Coblentzian), Eif. (Eifelian).

In North America, widely distributed in strata of Upper Llandoveryan to Ludlovian age:

- Northern Newfoundland: *E. radiatus*, Pike Arm fm., U. Lland. (C₆) to Wen. (Shrock and Twenhofel 1938, p. 262).
 Northern Greenland: *E. radiatus*, *E. consobrinus*, *E. quinqueplicatus*, U. Lland. (C₃ or younger) (Poulsen 1934, pp. 18–19; 1943, pp. 52–54).
 South-western Ontario: *Eospirifer* sp., De Cew fm., Wen. (Bolton 1957, p. 141). *E. radiatus*, 'Irondequoit' fm., Rochester fm., Ancaster chert of Goat Island member of Lockport fm., Wen.; Wiarthon member of Amabel fm., Guelph fm., Lud. (ibid., tables 7, 8, 10, 11, 12).
 Gaspé: *E. radiatus*, La Vieille fm., Wen., and West Point fm., Lud. (Northrop 1939, p. 190).
 Anticosti Island: *E. radiatus*, Jupiter fm., U. Lland. (C₃ to C₆), and Chicotte fm., Wen. (Twenhofel 1928, p. 219).
 Coastal New Brunswick: *Eospirifer* sp., Long Reach fm. and Mascarene series, U. Lland. (C₆) to Wen. (identified by writer).
 Coastal Maine: *E. radiatus*, Eastport region, U. Lland., and Ames Knob fm., U. Lland. (C₅) to Wen. (Beecher and Dodge 1892, p. 417).
 Northern Maine: *E. cf. radiatus*, Limestone Hill (Somerset Co.) and Chesuncook ls. (Piscataquis Co.), Wen. (identified by writer). *E. radiatus*, Aroostook Co., Wen. (Twenhofel 1941, p. 172; list probably also includes collections from a Lud. horizon).
 Yukon: *E. radiatus*, unnamed beds, U. Lland. (C₃ or younger) to Lud. (Kindle in Cairnes 1914, p. 73).
 New Hampshire: *E. cf. radiatus*, upper quartzite of Clough fm., U. Lland. (C₄ to C₆) (Boucot and Thompson 1958, pp. 362–3).
 Massachusetts: *E. cf. radiatus*, quartzite of Bernardston fm., U. Lland. (C₃ or younger) to Lud. (Boucot, MacDonald, Milton, and Thompson 1958, pp. 860–1).
 New York: *E. radiatus*, U. Lland. (Irondequoit ls. [C₅ to C₆], Williamson sh., [C₅ to C₆], Wolcott ls. [C₃ or younger], Reynales ls. [C₃ or younger]), to Wen. (Rochester sh., Herkimer ss.) (Gillette 1947, p. 20). Unknown in Lud. strata in New York.
 Pennsylvania: *E. radiatus*, Clinton sh., U. Lland. (C₃ or younger) to Wen. (Lesley 1890, p. 1028).
 Maryland: *E. radiatus*, Rose Hill fm., U. Lland. (C₃ or younger), to Rochester fm., Wen. (Prouty and Swartz 1923, pp. 452–3).
 Indiana: *E. radiatus*, Waldron sh., Wen. (Hall and Clarke 1893, pl. 21, figs. 11–13, 26); Osgood fm., U. Lland. (C₆) (Tillman 1961); Louisville ls., Wen. (Nettleroth 1889), pl. 29, figs. 13–16).
 Wisconsin: *E. radiatus*, Racine dolomite, Wen. (Hall and Clarke 1893, pl. 21, figs. 14–18).
 Oklahoma: *Eospirifer* sp., Clarita member of Chimneyhill fm., U. Lland. (C₄) to Wen. (Amsden 1957, p. 23).
 Arkansas: *Eospirifer* sp., St. Clair fm., U. Lland. (C₃ or younger) to Lud. (Amsden 1957, p. 23; Thomas 1926, p. 390–3).
 Kentucky: *E. radiatus*, West Union bed, U. Lland. (C₃ or younger) (Foerste 1909b, pp. 14–15).
 Ohio: *E. radiatus*, Massie Clay, Wen. (Foerste 1935, p. 153).
 Tennessee: *E. foggi*, Lobelville fm., Wen.; 'Lego ls.', U. Lland. (C₃ or younger) to Wen. (Foerste 1935, pp. 172, 178, 197).
 State of Tamaulipas, Mexico: *Eospirifer* sp., vicinity of Ciudad Victoria (J. Carrillo, collections Ca 1689B, Ca 1684), U. Lland. (C₃ or younger) to Lud.

In Europe widely distributed in strata of Upper Llandoveryan to Emsian age:

- Norway: *E. markliui*, Oslo region, L. Lland. (6c) (Kiaer 1908, p. 589). If it could be confirmed, this would be the earliest known eospiriferid occurrence, but after examining three specimens that presumably formed most of Kiaer's material, this earliest reported occurrence appears dubious. One specimen, labelled '*Spirifer sp.*' (Pal. Mus. Oslo No. 52361), is the pedicle valve of a *Stricklandia*. The second, labelled '*Spirifer marklini*' (Pal. Mus. Oslo, uncatalogued), is indeed *Eospirifer marklini*, but an old note with the specimen suggests that it came from Gotland rather than from Oslo. The third, labelled '*Spirifer marklini*' (Pal. Mus. Oslo, uncatalogued), is also *Eospirifer marklini*, but again the locality is in serious doubt. Dr. Gunnar Henningsmoen, curator of the Palaeontological Museum in Oslo, writes (1961) regarding the two specimens of *E. markliui*: 'As to the two other specimens, it is correct to say that their horizon is unknown, and their localities uncertain. They are thus no proof of a Lower Llandoveryan occurrence of *Eospirifer marklini*.'
- Gotland: *E. marklini*, *E. globosus*, L. Visby marl, U. Lland., to Slite group, Wen. (Hede 1921, p. 94). *E. radiatus*, U. Visby marl, U. Lland.; Hogklint ls., Slite group, Halla ls., Mulde marl, Wen. (Hede 1927a, p. 53; 1927b, p. 51; 1936, p. 41; 1940, p. 66).
- Podolia: *E. radiatus*, Kitaygorod fm., U. Lland., and Borshechov fm., L. Ged. (Nikiforova 1954, p. 135). *E. togatus*, schistes marneaux a Strophomenides, Wen., to Schiste d'Onut, Ged. (Vascautau 1931, p. 504, 532).
- Carnic Alps: *E. togatus*, Capolago, Ems. (Gortani 1915, pp. 130-2).
- Czechoslovakia: *E. togatus*, Tachlowitz, e2, Wen. or Lud.; Konieprus, f2, and Mnienian, f2, L. Ems. (Barrande 1879, pl. 5, figs. 10-16). *E. praesecans*, L. Lud. and Wen. (Havliček 1959, p. 53). *E. coutortus*, Lud. (ibid., p. 56). *E. togatus insidiosus*, Koneprusy ls., L. Ems. (ibid., p. 43). *E. devonicaus*, Kopanina beds, Lud. (ibid., p. 57).
- Harz Mts.: *E. togatus*, Kalk des Joachimskopfes, Ems. (Kayser 1878, p. 161). *E. togatus* var. *subsiuuata*, Kalk des Schneckenberges und Badeholzes bei Magdesprung, Ems. (ibid., p. 162).
- Great Britain: *E. radiatus*, widely distributed in U. Lland. to early Lud.
- Urals: *E. iguobilis*, U. Marginalis beds, Ged. (Khodalevitch 1939, p. 109). *E. cf. radiatus*, Striatus beds, Lud. (ibid., pp. 67-68).
- Brittany: *E. davousti*, calcaire d'Erbray, Ems. (Barrois 1888, p. 145).

Outside of Europe scattered occurrences in strata of Silurian to Middle Devonian age (unrecognized in South Africa and South America; its absence in South America is probably due to the almost total lack of information concerning shelly Silurian strata in that continent):

- Altai Mts.: *E. pseudotogatus* Khalfin 1948, *Pseudotogatus* horizon, concluded to be Sieg. (Khalfin 1948, p. 220).
- Kuznetsk Basin: *E. secans*, Baskukan beds, M. Dev. (Eif. or U. Ems.) (Rzonsnitskaya 1952, p. 35).
- Burma: *E. cf. radiatus*, Namhsim ss., Sil. (Reed 1906, pp. 108-9).
- New Zealand: *E. togatus*, Baton River beds, probable Ems. (Shirley 1938, pp. 476-9).
- Asia Minor: *E. togatoides*, Pendik Schichten (Bosphorus region), Ems. (Paeckelmann 1925, pp. 128-9).
- North Africa: *E. togatus*, Gisement du Kilometre 30 (Algeria), Sieg. (LeMaitre 1952, pp. 117-18). *E. cf. togatus*, French Morocco, L. Dev. (Termier 1936, p. 1144). *E. radiatus*, Morocco, Sil. (Gigout 1951, p. 45).
- Turkestan: *E. togatus*, Marginalis beds, Lud. (Nikiforova 1937b, p. 49). *E. davousti* and *E. pseudoidifferens*, highest Eif. (Nalivkin 1930, pp. 110-11).
- Kazakhstan: *E. radiatus* and *E. fusus*, U. Lland. (Borisyak 1955b, pp. 70-72).
- China: *E. subradiatus*, Sil. (Wang 1956, pp. 577-8).
- Australia: *E. eastoni*, beds at Sandy's Creek (Victoria), early Dev. (Gill 1949, pp. 98-99).
- Tasmania: *E. paralentius*, Bell Shale, Early Dev. (Gill 1950, pp. 247-8).
- Turkey: *Eospirifer*, Chamosite horizon near Cumakoy (NW. of Aquiran) in Istanbul region, U. Lland.
- Tuva: *E. tuvaensis*, Sil. (Chernychev 1937, pp. 79-80; pl. v; figs. 18-21).
- T'ien-Shan: *Eospirifer sp.*, locality 14 of Arpishmebulag Series, Sil. and early Dev. (identified from photographs kindly provided by Prof. G. Regnell, Lund).

Genus *MACROPLEURA* gen. nov.

Plate 98, figs. 1-8; plate 99, figs. 1-9; plate 100, figs. 1-5

Type species. Delthyris macropleurus Conrad 1840, *4th Ann. Rpt. New York Geol. Surv.*, p. 207.

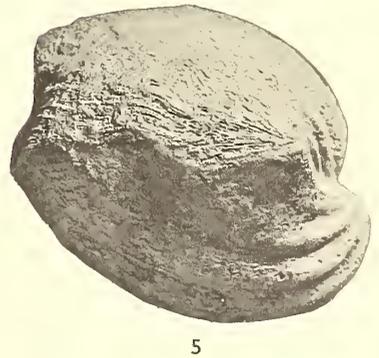
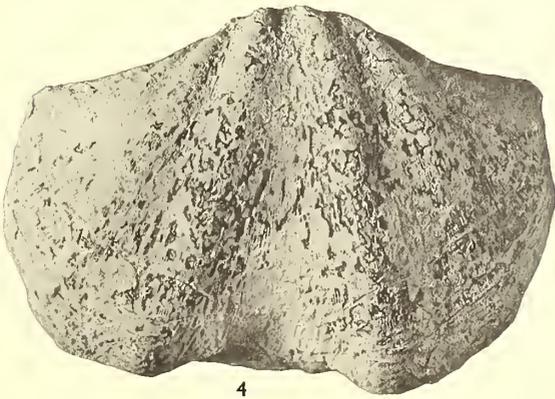
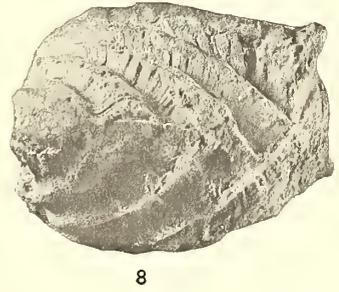
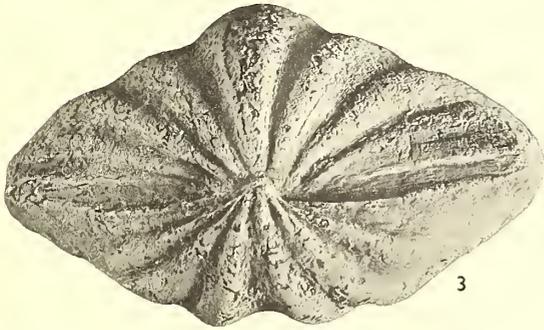
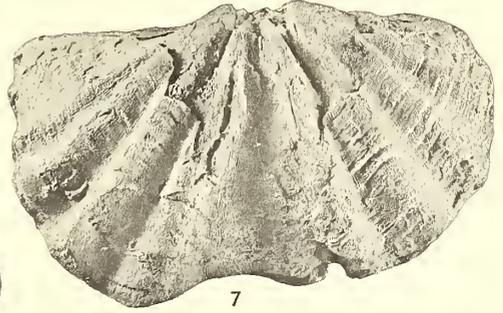
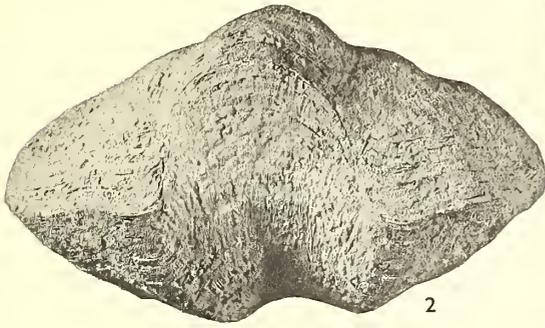
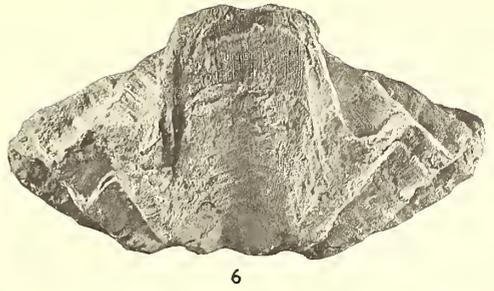
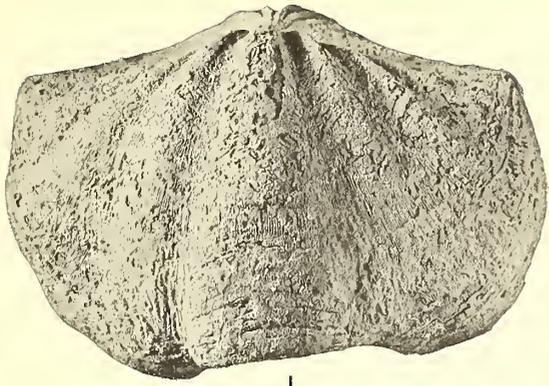
Diagnosis. Transversely elongate to elliptical eospiriferinids possessing a broad, flat fold and a limited number (usually three to six) of lateral plications on each flank, separated by broad, rounded interspaces.

Comparison. *Macropleura* differs from *Striispirifer* and *Nikiforovaena* in that the latter two, although having a relatively broad fold, also have a large number of lateral plications which are not separated from each other by broad interspaces. *Eospirifer* has flanks that are either smooth or faintly plicated anteriorly, never approaching the folded state attained by *Macropleura*. *Macropleura* lacks the anteriorly bifurcating plications which characterize *Janius*. *Havlicekia* has smooth flanks in large specimens, in contrast to the plicate condition of *Macropleura*.

Exterior. Shells subequally biconvex (the brachial valve having a slightly greater degree of convexity), transversely elongate, and elliptical in outline. Maximum width extends from the straight hinge-line to about the midlength. Lateral margin relatively straight in posterior part, evenly curved in anterior part. Anterior margin evenly curved laterally, but straight medially. The brachial valve bears a broad fold with circular to rectangular cross-section. The fold rises from the descending anterior portion of the valve at an angle of about 20 degrees and first becomes prominent near the umbo. The pedicle valve has a corresponding sulcus. Lateral to the fold are three to four rounded costae on each flank, separated by broad, rounded interspaces of about the same width as the costae. Interarea of pedicle valve catacline to steeply apsacline, very long, concave posteriorly. Interarea of brachial valve orthocline, very short. Lateral margins of interarea striated by ornamentation identical with that on the body of the valve. Beak of pedicle valve suberect. Deltidial plates are usually not preserved, and the delthyrium, which encloses an angle of about 60 degrees, is left open. However, in well-preserved specimens a pair of narrow deltidial plates, normal to the interarea, line the sides of the delthyrium and are either apically conjunct or almost so. No specimens have been observed in which the delthyrium was completely covered. The observed specimens correspond to stages 1 and 2 of Beecher and Clarke (1889, p. 79, fig. 4), and no specimens have been observed that

EXPLANATION OF PLATE 98

- Figs. 1-5. *Macropleura macropleura* (Conrad, 1840). New Scotland formation; Helderbergs, New York, M.C.Z. No. 9259. 1, Brachial view ($\times 1$). Note the fine striations. 2, Anterior view ($\times 1$). Note the broad, rounded fold and sulcus, and the weakly crenulated anterior commissure. 3, Posterior view ($\times 1$). Note the rounded lateral plications separated by broad, rounded interspaces. 4, Pedicle view ($\times 1$). Note the relatively broad sulcus and the broad interspaces between the plications. 5, Side view ($\times 1$). Note the incurved, relatively short interarea of the pedicle valve.
- Figs. 6-8. *Macropleura macropleura* (Conrad, 1840). New Scotland formation; North American Cement Quarry, Alsen, New York. U.S.N.M. No. 137738, Zimm Collection, Acc. No. 167820. 6, Anterior view ($\times 1$). Note the relatively rectangular cross-section of the fold and the crenulated anterior commissure. 7, Pedicle view ($\times 1$). Note the crenulated anterior and lateral margins. 8, Side view ($\times 1$).



approximate their stages 3, 4, and 5. The fine ornamentation consists of radiating fila which originate both by bifurcation and implantation and are crossed by concentric growth lamellae. A few of the concentric growth lamellae are very pronounced and frill-like, but the majority are mere lines whose intersections with the radial fine ornamentation may become nodose in well-preserved specimens. Anterior commissure uniplicate and strongly crenulate. Anterior portion of pedicle valve projects up as a tongue to meet the fold of the brachial valve.

Pedicle interior. Relatively small, pointed hinge teeth occur on the inner margin of the hinge line, where they are supported by plate-like dental lamellae which diverge from the midline at an angle of about 20 to 30 degrees. Dental lamellae convex medially, thickened in large specimens by the deposition of secondary material in the umbonal cavities and the delthyrial cavity. Muscle field triangular in outline, extending anteriorly about one-third of the distance to the anterior margin, bisected by low, rounded myophragm. On either side of myophragm are elongate, anteriorly expanding, longitudinally striate diductor impressions, which posteriorly surround the small, elliptical adductor impressions. In some specimens a thick pad of secondary material floors the rear of the delthyrial cavity and may have been the site of the pedicle callist. The sides of the upper portion of the delthyrial cavity are striated and bear a series of indentations that parallel the sides of the delthyrium and probably served to help seat the deltidial plates. The interior of the valve is strongly plicated by the impression of the external ornamentation.

Brachial interior. The cardinalia consist of a narrow chamber that occupies the position of the cardinal process and is laterally flanked by discrete, inclined hinge-plates tilted basomedially. The hinge plates are supported basally by long crural plates. The floor of the dental sockets is relatively flat. A low myophragm extends from the notothyrial cavity to about midlength. The adductor field is not noticeably impressed.

Species:

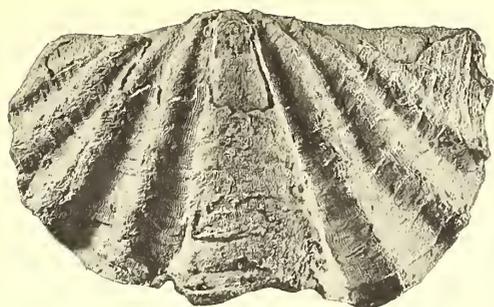
- Spirifer (Eospirifer) admirabilis* Nikiforova 1937*b pars.* p. 49, pl. 10, figs. 1, 2, 4, *non* fig. 3.
Spirifer altaicus Tschernychev 1893, pp. 25–26, pl. 4, figs. 5–6.
Eospirifer balchaaschensis Nikiforova 1937*a*, pp. 26–27, pl. ii, figs. 6–7.
Eospirifer? bascusanicus Rzonznitskaya 1952, p. 43, pl. i, fig. 12 (inspection of the holotype shows the presence of eospiriferid-type fine ornamentation).
Spirifer perlamellosus J. Hall var. *densilineata* Chapman 1908, pp. 223–4, pls. iv–v.
Spirifer eudora Hall 1861, *Ann. Rpt. Wisconsin Geol. Surv.*, pp. 25–26.
Spirifer geronticus Foerste 1909*a*, p. 92, pl. 2, fig. 30.
Spirifer gibbosus Hall 1861 *non* Barrande 1879, *Ann. Rpt. Wisconsin Geol. Surv.*, p. 25.
Delthyris macroleura Conrad 1840, *4th Ann. Rpt. New York Geol. Surv.*, p. 207.
Spirifer macroleuroides Clarke 1907, *Bull. 107, New York State Mus.*, p. 259.
Spirifer niagarensis oligoptylchus Roemer 1860, p. 68, pl. 5, fig. 8.
Spirifer pollens Barrande 1848, *Haid. Naturw. Abh.* 2, pp. 182–3, pl. 17, fig. 6.
Spirifer rollandi Barrois 1886, pp. 182–4, pl. v, fig. 1.
Spirifer sibiricus Tschernychev 1893, pp. 24–25, pl. 4, fig. 4.
Spirifer sinuosus Hedstrom 1923, pp. 12, 13, pl. 4, figs. 1–9.
Spirifera striolata Lindstrom 1861, *Ofversigt Kongl. Vetenskapsakad., Forh.*, Arg. 17 (1860), 8, p. 259, pl. 12, fig. 2.
Spirifer teleplus Barrande 1879, pl. 73.
Spirifer uralaltaicus Gruenewaldt 1854, *Mem. savants etrang.* 7, pp. 32–34, pl. 6, fig. 20*a–f*.
Spirifer vetulus Eichwald 1840, *Lethaea Rossica*, pp. 719–20, pl. 35, fig. 1.

Distribution. In North America widely distributed in strata of Wenlockian to Gedinnian age:

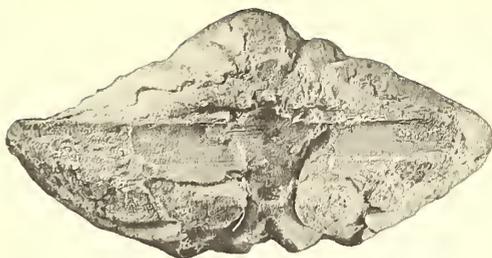
- South-east Alaska: A form resembling *Macrolepura* (erroneously compared with *J. irbitensis*), Lud. (Kirk and Amsden 1951, p. 63; pl. 10, fig. 6).
- South-western Ontario: *M. eudora*, Lockport dolomite, Wen. (Williams 1919, p. 67). *M. eudora*, Warton, Eramosa, and Colpoy Bay members of Amabel fm., Guelph fm., Lud. (Bolton 1957, p. 58, 102; tables 11, 12). *M. cf. eudora*, Fossil Hill fm., U. Lland. (C₅) to Wen. (ibid., table 9).
- Northern Maine: *M. macrolepuroides*, Chapman sandstone (Aroostook Co.), Ged. (Clarke 1909, pp. 119–20). *M. macrolepura*, Somerset Co., Ged. (Boucot, in preparation), and Aroostook Co. (Square Lake ls.), Ged. (Billings 1869, pl. 1, fig. 16).
- New York: *M. macrolepura*, New Scotland fm. (Helderbergs and Green Pond outlier), Ged.
- Maryland and West Virginia: *M. eudora*, Rose Hill fm., U. Lland. (C₃ or younger), to Rochester fm., Wen. (Prouty and Swartz 1923, pp. 453–4). *M. macrolepura*, New Scotland member, Ged. (Schuchert 1913, p. 396).
- Western Tennessee: *M. macrolepura*, Birdsong fm., Ged. (Dunbar 1919, p. 53). *M. niagarensis oligopychus*, Brownsport fm., Wen. (Roemer 1860, p. 68).
- Virginia: *M. macrolepura*, New Scotland ls., Ged. (Butts 1940, pp. 265, 278).
- New Jersey: *M. macrolepura*, Coeymans ls., Ged. (Weller 1903, pp. 288, 313).
- Ohio: *M. eudora*, West Union bed, U. Lland. (C₃ or younger) (Foerste 1909b, p. 16).
- Wisconsin: *M. eudora*, Racine dolomite, Wen. (Hall and Clarke 1893, pl. 21, figs. 19–20).
- Indiana: *M. eudora*, Waldron shale (Hall and Clarke 1893, pl. 21, figs. 21, 29); and Osgood fm., U. Lland. (C₅ to C₆) (Tillman 1961).
- Pennsylvania: *M. eudora*, 'Niagara fm.', Sil., and *M. macrolepura*, New Scotland equivalents—'Stormville shales' and 'Stormville ls.', Ged. (Lesley 1990, pp. 1010, 1016).

EXPLANATION OF PLATE 99

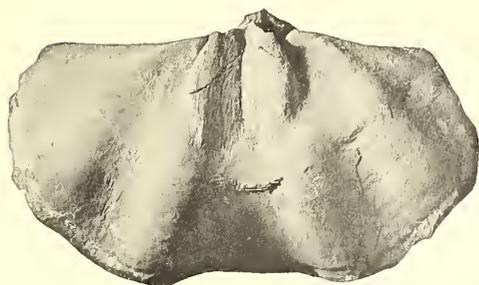
- Figs. 1, 2. *Macrolepura macrolepura* (Conrad, 1840). New Scotland formation; North American Cement Quarry, Alsen, New York. U.S.N.M. No. 137738, Zimm. Collection, Acc. No. 167820. 1, Brachial view ($\times 1$). Note the fine striations and the beaded effect due to the intersection of fine, concentric growth-lines and radial striae. 2, Posterior view ($\times 1$). Note the relatively long interarea of the pedicle valve.
- Figs. 3, 4. *Macrolepura macrolepura* (Conrad, 1840). New Scotland formation; Clarksville, Albany County, New York. M.C.Z. No. 9427. 3, Impression of interior of pedicle valve ($\times 1.5$). Note the impression of the broad, rounded lateral plications. 4, Impression of the interior (posterior view $\times 1.5$). Note the presence of narrow crural plates.
- Fig. 5. *Macrolepura macrolepura* (Conrad, 1840). Birdsong shale; just south of Camden, Tennessee. U.S.N.M. No. 137729. Interior of pedicle valve ($\times 1$). Note the stout dental lamellae, the secondary material deposited in the umbonal cavities, and the pitting of the floor of the valve in the umbonal region.
- Fig. 6. *Macrolepura eudora* (Hall, 1861). Waldron shale; Locality 521a, Quarry on south side of U.S. 70, 2 miles east of Pegram Station, Tennessee. U.S.N.M. No. 137730. Posterior view ($\times 3$). Note the narrow deltidial plates bordering the delthyrium and inserted normal to the interarea. The fine, beaded ornamentation is formed from the intersection of fine concentric growth lamellae and radial striae.
- Figs. 7, 8. *Macrolepura macrolepura* (Conrad, 1840). New Scotland formation; locality 526, U.S. 40, east bank of Licking Creek, 2½ miles west of Indian Springs, Maryland. U.S.N.M. No. 126051. 7, Interior of brachial valve ($\times 2$). Note the relatively long, slender crural plates supporting the discrete hinge-plates, and the laterally directed dental sockets. 8, Interior of brachial valve ($\times 2$). Note the unstriated area of diductor attachment.
- Fig. 9. *Macrolepura macrolepura* (Conrad, 1840). Shale of New Scotland age; Cornwall, Orange County, New York. U.S.N.M. No. 17164. Impression of interior of pedicle valve ($\times 1$). Note the massive dental lamellae.



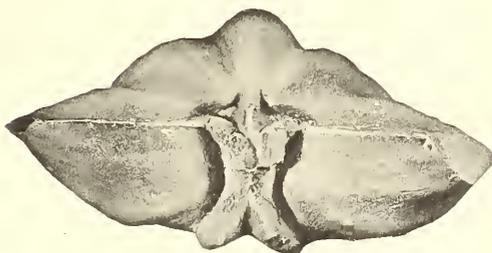
1



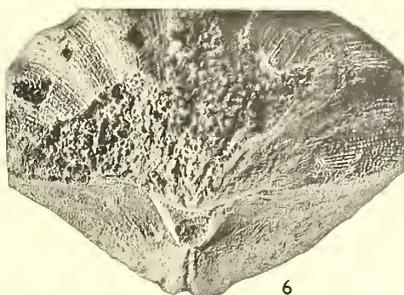
2



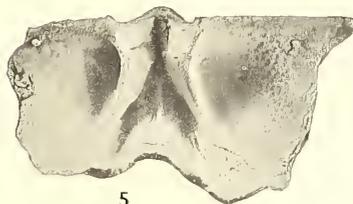
3



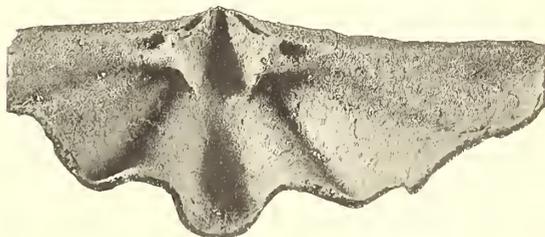
4



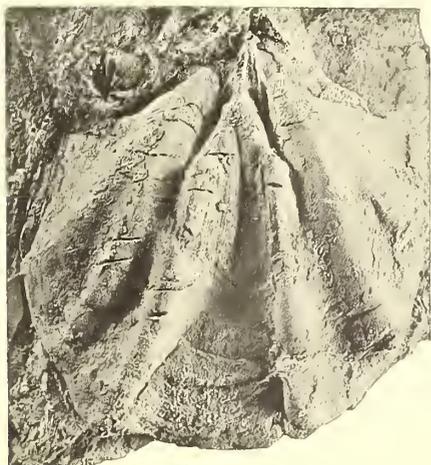
6



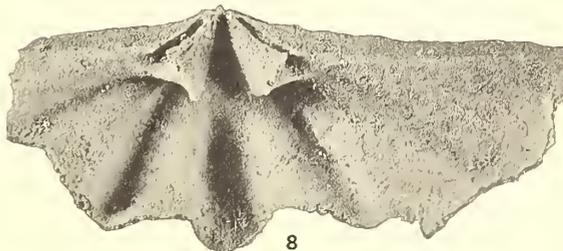
5



7



9



8

In Europe known from strata of Upper Llandoveryan to Emsian age:

- Czechoslovakia: *M. teleplus*, Collines entre Luzetz et Lodenitz (e2), Wen. (Barrande 1879, pl. 4, fig. 6). *M. pollens*, same locality, Wen. (ibid., pl. 1, fig. 16). Havlíček (1959, p. 52) cites this locality as of Lower Ludlow (Kopanina) age.
- Gotland: *M. striolata*, Eke marl and Hamra ls. Lud. or possibly Ged. (Hede 1921, p. 94). *M. simosa*, Slite group, Wen. (ibid., 1927b, p. 51; 1928, p. 63; 1933, p. 57; 1936, p. 41; 1940, p. 66).
- Urals: *M. exsul* (without anteriorly bifurcating ribs like *J. exsul* of Barrande). Striatus beds, Lud. (Khodalevitch 1939, p. 68, pl. 27, fig. 6).
- France: *M. thetidis* Le Maitre *non* Barrande, Calcaire de Chaudefonds, Ems. (LeMaitre 1934, p. 73). *M. rollandi*, same ls. (Barrois 1886, p. 182-4).

Outside of Europe and eastern North America recognized only in Asia and Australia:

- Mongolia: Chernychev (1937, p. 79, pl. v, figs. 22-23) illustrates Silurian material (*Eospirifer* aff. *radiatus*) that belongs to *Macroleura*.
- Altai Mts.: *M. sibiricus*, light grey ls. of Krjukowski Grube, and *M. altaicus*, reddish ls. of same place, Eif., together with '*Goniatites*' *lateseptatus* Beyrich (Tschernychev 1893, pp. 24-26).
- Kuznetsk Basin: *M. sibiricus*, Chumishsk beds, Eif.; *M. bascuscanicus*, Pesterevo beds, Cobl.; *M. cf. rollandi*, Salairkin beds, Eif. (Rzonsnitskaya 1952, pp. 41-43).
- Turkestan and western Balkhash Land: *M. balchaaschensis*, Marginalis beds, Ged. (Nikiforova 1937b, pp. 48-49). *M. admirabilis* Nikiforova 1937 *pars* (pl. 10, figs. 1, 2, 4, *non* 3), Manak beds, Ged.
- Kazakhstan: *E. radiatus* Borisyak *non* Sowerby, Wen. (Borisyak 1955a, pp. 54-55, pl. 8, figs. 1-6). Borisyak (1960, p. 270) emends the age to Lud.
- Kolyma River headwaters: *M. vetulus*, Taskwan River, Sil. (Nalivkin 1936, p. 23, pl. ii, fig. 6). Rzonsnitskaya (1960, oral communication) states that this locality is U. Ems. or L. Eif.
- Australia: *M. densilineata*, Sil. or L. Dev. (Chapman 1908, pp. 223-4).

Genus HAVLICEKIA gen. nov.

Plate 103, figs. 12-17

Type species. *Spirifer secans* Barrande 1848, *Haid. Naturw. Abh.* II, pp. 168-9, pl. xvi, fig. 6.

Name. The genus is named in recognition of the major contributions of Dr. Vladimir Havlíček, to knowledge of Lower Palaeozoic brachiopods.

Diagnosis. Eospiriferinids with striispiriferid-type plications in the early growth stages, smooth flanks during the later growth stages, and an acuminate form during the later growth stages, together with a very high tongue at the anterior margin of the pedicle valve which produces a very extended, uniplicate anterior margin.

Comparison. *Havlicekia* lacks, in the later growth stages, the lateral plications present in *Striispirifer*, *Macroleura*, and *Nikiforovaena*. The acuminate form and abnormally shaped, uniplicate anterior margin are unique among the eospiriferinids.

Pedicle exterior. Valve strongly convex, laterally ellipsoidal in outline, maximum width slightly anterior of posterior margin. Interarea catacline, straight, posteriorly concave. The delthyrium encloses an angle of about 60 degrees. The beak may be relatively straight or strongly incurved. The deltidial structures have not yet been distinguished, but are presumably similar to those present in other members of the subfamily. In the early growth stages (up to about 1-1½ cm. long) the shell bears striispiriferid-type lateral plications on the flanks, but these plications disappear beyond this early stage. The fine ornamentation consists of radial fila. Lateral margins rounded; anterior margin uniplicate and abnormally high in large specimens as a result of the acuminate form of the

large shells compared with the non-acuminate form of the early growth stages. The anterior portion of the valve projects up as a long tongue.

Brachial exterior. Valve gently convex in early growth stages, strongly convex (about equal to that of pedicle valve) in large specimens. Interarea orthocone to gently apsacone, very short as compared with that of pedicle valve, and strongly incurved over that of pedicle valve. In large specimens the fold is very high anteriorly with vertical sides and U-shaped cross-section. The tremendous change in form accompanying the development of an anterior tongue in the pedicle valve and the steep-sided fold in the brachial valve is well documented by Havlíček (1959, fig. 7).

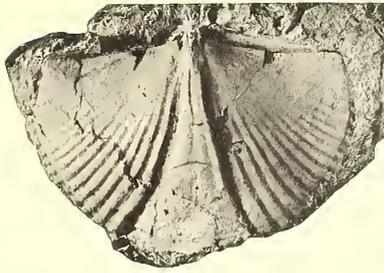
Pedicle interior. Two strong dental plates, about one-third the length of the shell, border the delthyrium and support the stubby hinge teeth. Almost no secondary material is deposited around the plates except for a small amount in the apex of the valve and the extremities of the umbonal cavities. The dental lamellae diverge from the midline at an angle of about 20 to 30 degrees. The muscle field extends about one-third of the distance to the anterior margin and is very poorly impressed except for a low myophragm. The myophragm is laterally bounded by anteriorly expanding diductor impressions which are longitudinally striate and posteriorly enclose the small, elliptical adductor impressions. Anterior and lateral periphery of valve smooth, umbonal regions crenulated by impress of external plications.

EXPLANATION OF PLATE 100

- Figs. 1-5. *Macropleura eudora* (Hall, 1861). Waldron shale; Dupont, Indiana. U.S.N.M. No. 88008. 1, Side view ($\times 1$). Note the incurved beak of the pedicle valve. 2, Pedicle view ($\times 1$). Note the broad sulcus. 3, Posterior view ($\times 1$). Note the relatively short interarea of the pedicle valve. 4, Brachial view ($\times 1$). Note the broad, rounded interspaces between the lateral plications. 5, Anterior view ($\times 1$). Note the crenulated anterior commissure.
- Fig. 6. *Striispirifer niagarensis* (Conrad, 1842). Clinton shale; Lockport, New York. U.S.N.M. No. 126048. Impression of interior of brachial valve ($\times 1$). Note the relatively long crural plates and the unstriated area of diductor attachment.
- Fig. 7. *Striispirifer niagarensis* (Conrad, 1842). Racine dolomite; Wauwatosa Wisconsin. U.S.N.M. No. 137731. Impression of interior (posterior view, $\times 2$). Note the long, slender crural plates and the unstriated area of diductor attachment.
- Fig. 8. *Striispirifer plicatella* (Linnaeus, 1767). Wenlock limestone; Dudley, England. U.S.N.M. No. 99946. Posterior view ($\times 3$). Note the narrow deltidial plates bordering the delthyrial cavity and inserted normal to the interarea.
- Figs. 9-13. *Striispirifer niagarensis* (Conrad, 1842). Clinton group; Lockport, New York. U.S.N.M. No. 3900. 9, Side view ($\times 2$). Note the slightly incurved beak of the pedicle valve. 10, Posterior view ($\times 2$). 11, Anterior view ($\times 2$). Note the rounded cross-section of the fold and sulcus, and the crenulated anterior commissure. 12, Brachial view ($\times 2$). Note the narrow interspaces between the lateral plications. 13, Pedicle view ($\times 2$). Note the broad sulcus and the narrow interspaces between the lateral plications.
- Fig. 14. *Striispirifer plicatella* (Linnaeus, 1767). Mulde marl; Djupviks fiskläge, Eksta, Gotland. M.C.Z. No. 2803. Preparation of spire ($\times 2$). Note the short jugal process, and the obtuse angle included between the crura and the primary lamella.
- Fig. 15. *Striispirifer plicatella* (Linnaeus, 1767). Strata of Silurian age; Gotland. M.C.Z. No. 2075. Preparation of spire ($\times 2$). Note the short jugal process, and the obtuse angle included between the crura and the primary lamella.



1



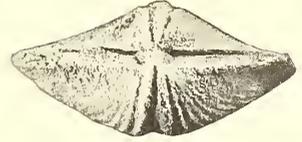
6



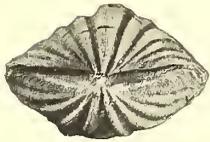
9



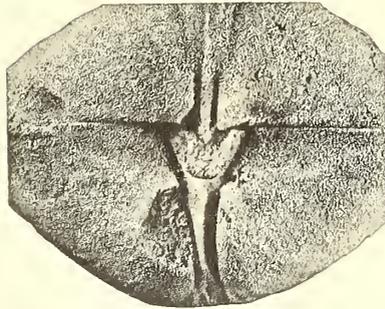
2



10



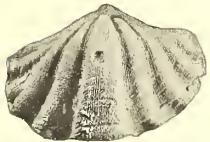
3



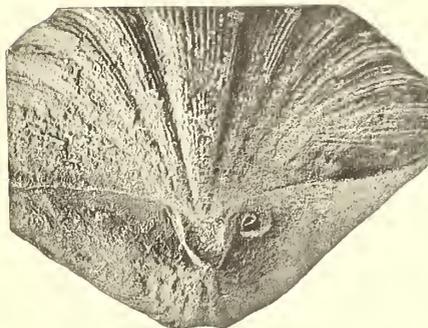
7



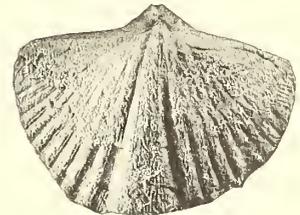
11



4



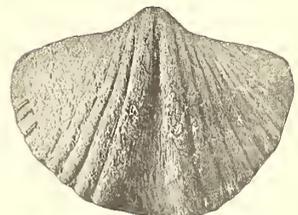
8



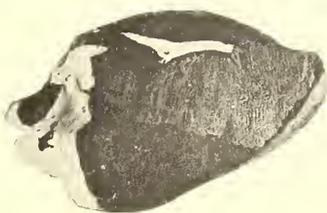
12



5



13



14



15

Brachial interior. The cardinalia consist of discrete hinge-plates supported medially by long crural plates. Dental sockets closed postero-laterally, flared antero-laterally. Area of diductor attachment smooth. A low myophragm about one-third the length of the valve bisects the feebly impressed muscle field. Anterior and lateral margins smooth, umbonal regions crenulated by impress of external plications.

Species:

Spirifer secans Barrande 1848, op. cit.

Spirifer (Eospirifer) secans var. *rarus* Khodalevitch 1951, p. 97, pl. 30, fig. 2.

Spirifer turjensis Tschernychev 1893, *Mem. Com. Geol.* 4, 3, pp. 170-1.

Distribution. Widely distributed in the Old World; but only a single specimen known in the New World:

Czechoslovakia: *H. secans*, Koneprusy ls., L. Ems. (Havlíček 1959, p. 41). *H. turjensis*, Pridoli ls., Skal. (ibid., p. 49).

Carnic Alps: *H. secans*, Capolago, Ems. (Gortani 1915, pp. 130-2).

Kuznetsk Basin: *H. secans*, Baskuskan beds, U. Ems. or Eif. (Rzonsnitskaya 1952, p. 35).

New Zealand: *H. secans*, Baton River beds, probably Ged. (Shirley 1938, pp. 476-9).

North Africa: *H. secans*, L'Erg Djemel (Algeria), Ems. (LeMaitre 1952, pp. 117-18).

Urals: *H. turjensis*, Wen. (Khodalevitch 1939, pp. 65-66). *H. secans* var. *rarus* Cobl. (ibid. 1951, p. 97). *H. turjensis*, L. Dev. (ibid. 1937, p. 67).

Germany: *H. secans*, Erbsloch graywacke L. Ems. (Assmann 1910, p. 152 pl. 8 fig. 13).

Indiana: *H. cf. secans*, Huntingdon dolomite Lud. (identified by writer in collections of Indiana University from 'N. Bluff 1/2 mi. E. of Georgetown').

Genus STRIISPIRIFER Cooper and Muir-Wood 1951

Plage 100, figs. 6-15

Type species. *Delthyris niagarensis* Conrad 1842, *J. Acad. Nat. Sci. Philadelphia*, 8, p. 261.

Diagnosis. Eospiriferinids having an unplicated fold and sulcus laterally bordered by numerous costae separated from each other by narrow, V-shaped interspaces.

Comparison. *Striispirifer* lacks the anteriorly bifurcating costae of *Janius*, the broad U-shaped interspaces of *Macroleura*, the unplicated flanks of *Eospirifer*, and the plicate fold and sulcus of *Nikiforovaena*.

Exterior. Shells impunctate, subcircular to laterally elongate, with a spiriferiform shape. The pedicle valve is about two to three times as deep as the gently convex brachial valve. Hinge-line straight, almost equal in length to the maximum length, which is situated about one-third of the distance to the anterior margin. Lateral extremities evenly rounded to alate, anterior margin evenly rounded, crenulate, and plicate. Interarea of pedicle valve apsacline and concave posteriorly, interarea of brachial valve anacline. Interarea of pedicle valve about three to four times the length of that of the brachial valve. The interareas bear growth-lines paralleling the hinge-line. The delthyrium includes an angle of about 60 degrees and may be bordered by discrete deltidial plates, medially conjunct deltidial plates which include a pedicle foramen, or a pseudodeltidium-like structure formed by the deposition of secondary material as illustrated by Hall and Clarke (1893, p. 21, fig. 4; pl. 37, fig. 1) and Beecher and Clarke (1889, pl. 6, fig. 8). Coarse ornamentation consists of radial costae separated from each other by narrow,

V-shaped interspaces. Large shells carry up to fifteen costae on each side of the fold, which is about five times as wide as the first lateral costa, low, and unplicated, with circular to subrectangular cross-section. Fine ornamentation consists of radial fila intersected by fine growth lamellae.

Pedicle interior. Dental lamellae well developed, blade-like, and unthickened by secondary material except in the apices of the umbonal and delthyrial cavities. The short, stubby hinge teeth, situated on the inner side of the hinge-line, are supported by the dental lamellae. A low myophragm bisects the muscle field, which extends laterally about one-third of the length of the valve. Periphery and most of the interior crenulated by the impress of the costae. Musculature similar to that of *Macrolepura* and *Eospirifer*.

Brachial interior. Similar to that of the other eospiriferinids except where the impress of the costae reflects the outer character of the shell. Relatively long crural plates support discrete hinge-plates. Area of diductor attachment smooth. A low myophragm bisects the muscle field. The crura make an obtuse angle with the primary lamellae. The short jugal process descends toward the pedicle valve near the junction of the crura and primary lamella.

Species:

- Spirifer foggi* Nettleroth 1889, p. 117, pl. 32, figs. 28–31.
Spirifer interlineatus Sowerby 1839, *Sil. Syst.*, pl. 12, fig. 6.
Delthyris niagarensis Conrad 1842, *J. Acad. Nat. Sci. Philadelphia*, 8, p. 261.
Anomia plicatella Linnaeus 1767, *Syst. Nat.*, 12th ed., p. 1154.
Spirifer repertus Foerste 1909b, p. 16, pl. 1, fig. 14a–b; pl. 2, fig. 5.
Eospirifer stonehousensis McLearn 1924, pp. 84–85, pl. 9, fig. 8.
Spirifer (Eospirifer) subviator Khodalevitch 1951, p. 99, pl. 29, figs. 1–2.
Spirifer tennis Barrande 1879, pl. 138, fig. ix.
Spirifer viator Barrande 1848, *Haid. Naturw. Abl.*, 2, p. 181, pl. 15, fig. 3.

Species to be investigated:

- Delthyris cyrtaena* Dalman 1828, *K. Vetensk. Handl.*, 1827, p. 120, pl. 3, fig. 3.

Distribution. In eastern North America widely distributed in strata of Upper Llandoveryan to Ludlovian age:

- Nova Scotia: *S. stonehousensis*, French River fm., Pictou Co. Maehl, 1961, (p. 52), U. Lland. (C₃ or younger). *S. stonehousensis* is also listed by McLearn (1924, p. 84) from a boulder that he believed came from the Stonehouse fm., of L. Ged. (*Podolella* and *Proschizophoria* occur in the top of the fm. near Pictou at one of Maehl's localities) and possible Lud. age, but the writer concludes that McLearn's boulder came from the French River fm.
- Gaspé: *Striispirifer* cf. *niagarensis*, St. Leon fm., early Lud. (Alcock 1935, p. 50). If the material is correctly identified, it represents the only member of the genus thus far recognized in Gaspé.
- South-western Ontario: *S. niagarensis*, 'Irondequoit' dolomite member and Rochester shale fm., Wen.; Lockport dolomite, Wen. (Williams 1919, pp. 51, 55, 67). *S. niagarensis*, 'Reynales' fm., 'Irondequoit' fm., Rochester fm., Ancaster chert of Goat Island member of Lockport fm., Lockport fm., Wen.; Warton member of Amabel fm., Wen. and Lud. (Bolton 1957, pp. 27, 31, 48, 85, 94, 109, 126, 130, 137, 139, tables 7, 8, 10, 11).
- New York: *S. niagarensis*, Irondequoit ls., U. Lland. (C₅ to C₆), to Rochester shale and Herkimer ss., Wen. (Gillette 1947, p. 20).
- Maryland: *S. niagarensis*, Rochester fm., Wen. (Prouty and Swartz 1923, p. 455).
- Ohio: *S. niagarensis* and *S. plicatellus*, Dayton ls. U. Lland. (C₅ or younger) (Foerste 1935, p. 151).

Kentucky: *S. foggi*, Niagara group, Lud. (Nettleroth 1889, pp. 117–19).

Indiana: *S. foggi*, Liston Creek reef, Lud. (Cummings 1930, p. 209). *S. niagarensis*, Osgood fm. and Laurel ls., U. Lland. (C₅ to C₆) (Tillman 1961).

Pennsylvania: *S. niagarensis*, 'Clinton fossil ore', Sil. (Lesley 1890, p. 1024).

In Europe widely distributed in strata of Silurian and Devonian age:

Podolia: *S. interlineatus*, Kitaygorod fm., U. Lland (Nikiforova 1954, p. 136).

England: *S. interlineatus*, Wenlock shale and ls., Wen., and Aymestry ls., Lud. (Davidson 1871, pl. 9, figs. 9–12).

Czechoslovakia: *S. viator*, Collines entre Luzetz et Lodenitz (e2), Dlauha Hora (e2), Wohrada (e2), Listice (e2), Rochers de Kozel (e2); Wen. or Lud. (Barrande 1879, pl. 7, figs. 4–11; pl. 73, fig. iii, 1–8; pl. 138, fig. 9). *S. temis*, Liten to Lochkov beds, Wen. to Ged. (Havlíček 1959, p. 60).

Gotland: *S. interlineatus* (Hedstrom *non* Sowerby), Slite group, Wen. (Hede 1927b, p. 51; 1933, p. 57; 1936, p. 41; 1940, p. 65). *S. cf. interlineatus* (Sowerby) Hemse group, L. Lud. (ibid. 1927a, p. 53).

Norway: *S. plicatella*, Oslo region, U. Lland. (7c) and Wen. (8a, b, c) (Kiaer 1908, p. 589).

Estonia: *S. cf. interlineatus* Hedstrom, Jaagarahu-Kalkstein, Wen. (Luha 1930, p. 9).

Urals: *Spirifer (Eospirifer) subviator*, L. Dev. to Eif. (Khodalevitch 1951, p. 99).

Genus NIKIFOROVAENA gen. nov.

Plate 103, figs. 1–6

Type species. Spirifer (Eospirifer) fergauensis Nikiforova 1937b, p. 48 (Russian text); pp. 80–81 (English text); pl. 10, figs. 5a–d, 6a–b.

Name. The genus is named in recognition of Dr. Olga Nikiforova's major contributions to knowledge of Lower Palaeozoic brachiopods.

Diagnosis. Transversely elongate to elliptical eospiriferids with flanks ornamented by gently rounded costae separated by U-shaped interspaces, and with one or more prominent median grooves on the fold and corresponding plication or plications in the sulcus.

Comparison. *Nikiforovaena* has the lateral costae of *Macroleura*, with the addition of a groove or grooves on the fold and corresponding plication or plications in the sulcus. No other eospiriferid has this type of lateral costae combined with a grooved fold and a plicated sulcus.

Exterior. Shells elliptical in outline, laterally elongate, unequally biconvex, the pedicle valve being about one and a half times as deep as the brachial valve. Hinge-line straight, equal to maximum width. Lateral and anterior margins evenly rounded. Anterior commissure uniplicate and crenulate. Interarea striated by growth-lines paralleling hinge-line. Interarea of pedicle valve apsacline, posteriorly concave, about three to four times as long as that of brachial valve. Interarea of brachial valve anacline. Coarse ornamentation consists of costae with rounded cross-sections, separated by U-shaped interspaces on the flanks, a deep median groove or grooves on the fold, and a sharp median plication or plications in the sulcus. The tongue of the sulcus is serrated terminally by the junction of the median plication and the groove. Each flank bears about four to eight plications. Fine ornamentation consists of radial striae crossed by fine concentric growth-lines to give a reticulate effect. Delthyrium open, includes an angle of about 60 degrees. Narrow delthyrial plates may be present.

Pedicle interior. The interior of the pedicle valve has two prominent dental lamellae.

Brachial interior. No information available.

Species:

Spirifer (Eospirifer) admirabilis Nikiforova 1937b, p. 49 (Russian text), pl. 10, fig. 3, *non* figs. 1, 2, 4.

Spiriter bowningensis Mitchell 1921, pp. 545–6, pl. 21, figs. 21–22.

Spirifer (Eospirifer) ferganensis Nikiforova 1937b, p. 48 (Russian text); pp. 80–81 (English text); pl. 10, figs. 5a–d, 6a–b.

Spirifer lynxoides Nalivkin 1926, *Sketch of Turkestan Geology*, p. 34 (first figured by Nikiforova 1937b, p. 80, pl. 10, figs. 7a–c, 8–11).

Spirifer (Eospirifer) tingi Grabau 1926, pp. 37–43, pl. 2, figs. 16–21.

Distribution:

Australia: *N. bowningensis*, Lower and Middle Trilobite beds, Wen. or Lud. (Mitchell 1921, p. 546).

Japan: *N. tingi*, Stage G₂ of the Gion-Yama Series (Kuma-Kii), Wen. or Lud. (Hamada 1961, p. 29).

China: *N. tingi*, Miaokao group (eastern Yunnan), Lud. (Grabau 1926, pp. 18–19).

Turkestan: *N. ferganensis* and *N. lynxoides*, Marginalis and Isfara beds, Lud. (Nikiforova 1937b, p. 48, 50, 80). *N. admirabilis*, Ged. (*ibid.*, p. 49, pl. 10, fig. 3, *non* figs. 1, 2, 4).

Genus JANIUS Havlíček 1957

Plate 101, figs. 1–13; plate 103, figs. 7–11; plate 104, figs. 9–14

Type species. *Spirifer nobilis* Barrande 1848, *Haid. Naturw. Abh.* 2, p. 32, pl. 18, fig. 2.

Diagnosis. Eospiriferids with anteriorly bifurcating costae. The fold and sulcus may or may not be costate.

Comparison. *Janius* can be distinguished from all other members of the Eospiriferinae because it has anteriorly bifurcating costae on the flanks.

Exterior. Shells transversely elongate, elliptical in outline, unequally biconvex, with brachial valve gently convex and pedicle valve subpyramidal. The brachial valve bears a fold which is subrectangular in cross-section; the pedicle valve has a corresponding sulcus. Hinge-line straight, almost as wide as the maximum width, which is located near the midlength. Interarea of pedicle valve steeply apsacline, concave posteriorly, about five to seven times longer than that of brachial valve. Interarea of brachial valve gently apsacline. Lateral margins of interarea striate, but remainder smooth except for growth-lines which parallel the hinge-line. Lateral margins and lateral portion of anterior margin evenly rounded, but median portion of the anterior margin almost straight. Anterior commissure uniplicate and crenulate. Deltidial cavity bordered by narrow deltidial plates which are apically conjunct and resemble those figured by Beecher and Clarke (1889, p. 79, fig. 4, no. 3). Coarse ornamentation consists of three to five costae on each flank. In some species two costae are present on the fold and one or two in the sulcus. The costae on the flanks bifurcate anteriorly. Costae rounded in cross-section, separated by U-shaped interspaces of about same width and curvature as costae. Fine ornamentation consists of radial fila and fine concentric growth-lines. The fila increase both by implantation and bifurcation. The junctions of the concentric and radial fine ornamentations are nodose in well-preserved specimens. A few prominent concentric growth-lines are present.

Pedicle interior. Relatively small hinge teeth at medial ends of the hinge-line are supported by long dental lamellae. Dental lamellae convex medially, include an angle of about 30 degrees. On the specimens studied, the muscle field is poorly impressed; it consists of diductor impressions which expand anteriorly, are separated by a low median myophragm, and posteriorly include a small pair of elongate, feebly impressed adductor impressions. Interior crenulated by impress of external ornamentation.

Brachial interior. The cardinalia consist of a small chamber (occupying the position of the cardinal process) laterally bounded by long crural plates which support the discrete hinge-plates. The hinge-plates floor the dental sockets. A low myophragm bisects the area of muscle attachment, which is very feebly impressed and appears to consist of a pair of elongate adductor impressions extending to a position just short of the mid-length. Interior strongly impressed by external coarse ornamentation. The ribbon-like crura make an oblique angle with the primary lamellae. No jugal processes were found in the three specimens of *J. schmidti* studied.

Geologic range. Highest Wenlockian (zones of *Cyrtograptus radians* and *Monograptus testis* in Bohemia) to Eifelian.

Species:

Spirifer exsul Barrande 1848, *Haid. Naturw. Abl.* 2, p. 184, pl. 15, fig. 5.

Spirifer incoustans Hall 1862, *Rpt. Wisconsin Geol. Surv.*, p. 26, 1, 1, 1867, p. 436, pl. 69, fig. 6.

Spirifer insignis Hedstrom 1923, pp. 13–15, pl. 5, figs. 1–24.

Spirifer nobilis Barrande 1848, *Haid. Naturw. Abl.* 2, pp. 184–5, pl. 18, fig. 2.

Spirifer nobilis var. *fortiuscula* Barrande 1879, pl. 7, fig. 12.

Spirifer nobilis var. *irbitensis* Tschernychev 1893, *Mém. Com. Géol.* 4, 3, pp. 55–56, pl. 8 figs. 1–5.

Spirifer racinensis McChesney 1861, *New Paleozoic Fossils*, p. 84; plates, 1865, pl. 8, figs. 3–3b.

Spirifer reluctant Barrande 1879, pl. 74, fig. ii (1–4).

Spirifer rostellum Hall and Whitfield 1872, pp. 182–3.

Spirifer schmidti Lindstrom 1861, *Ofver. Vetenskapsakad.*, Arg. 17 (1860), 8, pp. 358–9, p. 12, fig. 1.

Spirifer schmidti var. *pyramidalis* Wenjukow 1899, *Mater. Geol. Russ., St. Petersburg*, 19, pp. 137–8, pl. 2, fig. 11.

Eospirifer vetuloides Nalivkin 1960, pp. 382–3, pl. 89, figs. 1–2.

Spirifer (Eospirifer) weberi Nalivkin 1930, pp. 112–13, pl. x, figs. 25–26.

Distribution. In eastern North America widely distributed in strata of highest Wenlockian and Lower Ludlovian age:

Gaspé: *Eospirifer* cf. *eudora* (resembles *J. racinensis* [McChesney]), Gascons fm. L. Lud. (Northrop 1939, p. 191; Pl. 101, fig. 10).

New Brunswick: *Janius* cf. *nobilis* in association with *Conchidium* cf. *knighti*, Gambol Brook, Bathurst–Newcastle map-area (identification of *J.* cf. *nobilis* by the writer, of *C.* cf. *knighti* by Dr. L. M. Cumming) (Pl. 103, figs. 20–22).

Northern Maine: *Janius* sp., collections made by Dr. R. B. Neuman, U.S. Geol. Surv., on White Horse Lake, Shin Pond quadrangle, Penobscot County, L. Lud. (identifications by the writer; Pl. 103, figs. 23–24).

Illinois: *J. nobilis*, Chicago fm., Wen. and early Lud. (Hall and Clarke 1893, pl. 29, fig. 16).

Wisconsin: *J. nobilis*, Racine dolomite, Wen. (Hall and Clarke 1893, pl. 37, figs. 2–3).

Indiana: *J. nobilis*, Liston Creek reef, Lud. (Cummings 1930, p. 209). *J. rostellum* Louisville ls., Lud. (Hall and Whitfield 1872; 1875, pl. 9, figs. 11–13) (Nettleroth 1889, pl. 27, figs. 17–19; pl. 29, fig. 25).

Alaska: *J. nobilis*, unnamed beds, U. Lland. (C₃ or younger) to Lud. (Kindle 1908, p. 325).

In Europe widely distributed in strata of highest Wenlockian to Ludlovian and possibly Lower Gedinnian age:

Gotland: *J. schmidti*, Hemse group, L. Lud., and Eke group, Lud. or possibly slightly younger (Hede 1921, p. 94). (For a discussion of the age of the Eke group see Boucot 1960, p. 290.) *J. insignis*, Hemse group and Eke group, Lud. (Hedstrom 1923, p. 13).

Podolia: *J. schmidti*, Malinovetski fm., Lud. (Nikiforova 1954, pp. 136–8; Vascautanu 1932, p. 509). *J. pyramidalis*, Malinovetski fm., Lud. (Nikiforova 1954, pp. 138–9), and Skal. (Vascautanu 1932, p. 463).

Novaya Zemlya: *J. irbitensis*, Kostin Shar, Lud. (Alferov 1937, p. 10). *J. vetuloides*, U. Eif. (Nalivkin 1960, p. 383).

England: *J. cf. nobilis*, L. Lud. (this paper, Pl. 101, fig. 10). *Janius* Wenlock ls., Wen. (this paper, Pl. 101, fig. 9).

Czechoslovakia: *J. nobilis*, Collines entre Luzetz et Lodenitz (e2), Wen. or Lud. (Barrande 1879, pl. 7, figs. 13–15). *J. exsul* Barrande, Kopanina beds, Lud. (Havlicek 1959, pl. k2, figs. 1–5). *J. reluctans*, Listice (e2), Wen. or Lud. (Barrande 1879, pl. 74, fig. ii, 1a, 4; Havlicek 1959, p. 62, concludes that *J. reluctans* is the young of *J. exsul*). *J. exsul*, Lodenitz (e2) and Collines entre Luzetz et Bubowitz (e2), Wen. or Lud. (ibid., pl. 1, figs. 1, 2; pl. 76, fig. 2).

EXPLANATION OF PLATE 101

Figs. 1–6. *Janius schmidti* (Lindstrom, 1861). Probably from the Eke Group; Gotland (probably from Lau backar, Lau parish, Ronehamn map sheet). U.S.N.M. No. 126057. 1, Pedicle view ($\times 1$). Note the plications in the sulcus and the bifurcating lateral plications. 2, Brachial view ($\times 1$). Note the presence of anteriorly bifurcating lateral plications and bifurcating plications on the fold. 3, Side view ($\times 1$). Note the relatively long interarea of the pedicle valve. 4, Anterior view ($\times 1$). Note the crenulated anterior commissure. 5, Posterior view ($\times 1$). Note the narrow deltidial plates bordering the delthyrial cavity and inserted normal to the interarea. 6, Exterior of pedicle valve ($\times 3$). Note the beaded fine ornamentation formed by the intersection of the concentric growth lamellae and the radial striae.

Figs. 7, 8. *Janius cf. schmidti* (Lindstrom, 1861). Racine dolomite; Racine, Wisconsin. U.S.N.M. No. 126053. 7, Posterior view of impression of interior ($\times 1$). Note the relatively long crural plates and the unstriated area of diductor attachment. 8, Brachial view of impression of interior ($\times 1$). Note the presence of anteriorly bifurcating lateral plications and bifurcating plications on the fold.

Fig. 9. *Janius cf. nobilis* (Barrande, 1848). Wenlock limestone; old quarry at Iron Bridge, in Benthall Wood, Grid Ref. 665/034, map sheet 118 (Shrewsbury). Boucot loc. 56GB170, U.S.N.M. No. 137739. Pedicle view ($\times 1$). Note the unplicated sulcus and the anteriorly bifurcating lateral plications.

Fig. 10. *Janius cf. nobilis* (Barrande, 1848). Lower Ludlow; Old quarry, 250 yards WNW. of milestone (1 mile to Hundred House) and 1 mile S. 39° E. of Church, Abberley, Worcs., G.B. Geological Survey Collection No. Gr.–249. Rubber replica ($\times 1$) of brachial valve exterior. Note the unplicated fold and the presence of anteriorly bifurcating lateral plications.

Fig. 11. *Janius cf. nobilis* (Barrande, 1848). Upper Gascons formation; Black Cape, Quebec. Peabody Museum, Yale Univ. No. 2850/6. Brachial view ($\times 1\frac{1}{2}$). Note the anteriorly bifurcating medial plication.

Figs. 12, 13. *Janius schmidti* (Lindstrom, 1861). Eke Group; Lau backar, Lau parish, Ronehamn map sheet, Gotland. 12, Preparation of spire ($\times 2$). Note the absence of a jugal process, and the obtuse angle included by the crura and primary lamella. U.S.N.M. No. 137732. 13, Impression of interior (posterior view, $\times 3$). Note the relatively long crural plates and the unstriated area of diductor attachment. U.S.N.M. No. 137733.



1



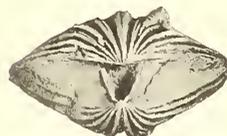
2



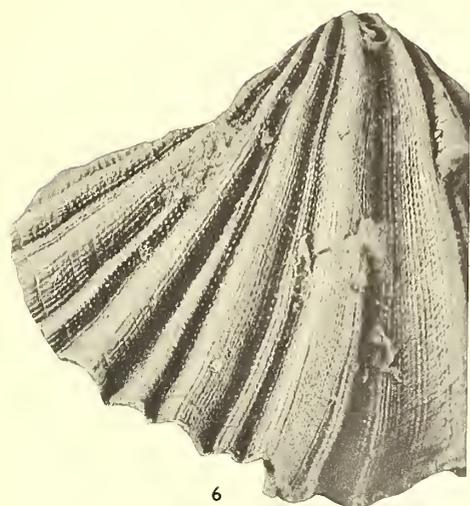
3



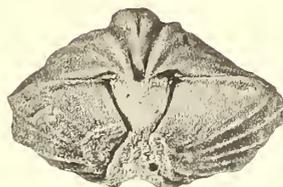
4



5



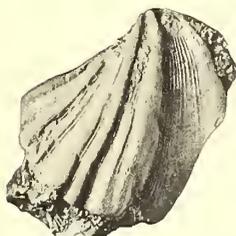
6



7



8



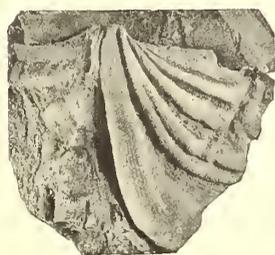
9



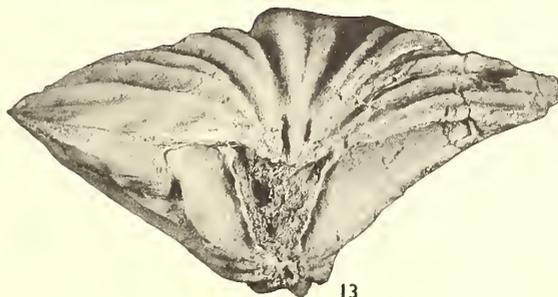
10



12



11



13

Urals: *J. irbitensis*, Striatus beds, L. Lud., and Marginalis beds, U. Lud. (Khodalevitch 1939, pp. 64–65); L. Dev. (ibid. 1937, p. 67).

Estonia: *J. schmidti*, Lud. (Schmidt 1881, p. 49).

Outside of Europe and eastern North America recognized only in central Asia:

Turkestan: *J. irbitensis*, Marginalis beds and possibly Isfara beds, bed. and Lud. ? (Nikiforova 1937, p. 50). *J. irbitensis*, Eif. (Nalivkin 1930, pp. 108–9), together with *J. weberi* (ibid., pp. 112–13) and *J. vetulus* (ibid., p. 107).

Kuznetsk Basin: *J. ex. gr. nobilis*, Salairkin beds, Eif. (Rzonsnitskaya 1952, p. 39).

Subfamily CYRTIINAE Fredericks 1924

Diagnosis. The subfamily Cyrtiinae is redefined to include those members of the Eospiriferidae having a pyramidal pedicle valve, a catacline to steeply procline pedicle interarea, and an elongate delthyrium occupied by a complex deltidium. The brachial valve has chilidial plates or a chilidium.

Genera:

Cyrtia Dalman 1828, *K. Vetenskapsakad. Handl. f. 1827*, pp. 92, 93, 97.

Plicocyrtia Boucot gen. nov.

Geological range. Upper Llandoveryan to Eifelian.

Geographical range. Europe, eastern North America, Tasmania, and possibly Turkestan if *C.?* aff. *petasus* (Nikiforova 1937, p. 51) belongs to *Plicocyrtia*.

Genus CYRTIA Dalman 1828

Plate 102, figs. 1–5, 12–17; Plate 104, figs. 4–8

Type species. *Anomites exporrectus* Wahlenberg 1821, *Nova Acta Reg. Soc. Sci. Uppsaliensis*, 8, p. 64, no. 3.

Diagnosis. *Cyrtia* is characterized by unplicated flanks and an unplicated fold and sulcus.

Comparison. *Cyrtia* may be distinguished from *Plicocyrtia* by the absence of plicated flanks.

Pedicle exterior. Valve pyramidal, in outline subcircular to laterally elongate or even alate. Interarea incurved gently, catacline to steeply apsacline, unstriated but bearing the trace of growth lamellae paralleling the hinge-line. Hinge-line straight and the place of maximum width. Delthyrium narrow, occupied by a complex series of plates. In small specimens these plates appear to be a pair of narrow discrete deltidial plates. With increase in shell size the plates join medially in the apical half of the delthyrium. With further increase in size another plate fills the entire base of the delthyrium except for a small foramen. In large specimens a deposit of secondary material may be laid down over the entire structure, obscuring the foramen and giving the impression of a pseudo-deltidium. Fine ornamentation consists of fine radial fila which in well-preserved specimens are seen to be crossed by concentric growth lamellae. The junction of the concentric and radial ornamentation may be nodose. Anterior commissure uniplicate. Median sulcus prominent, gently rounded to subrectangular in cross-section.

Brachial exterior. Valve gently convex, posteriorly overhangs the pedicle valve. Interarea orthocline to apsacline. Discrete chilidial plates present on small specimens, but on large specimens may be medially conjunct. Fold gently rounded to subrectangular in cross-section. Fine ornamentation similar to that of pedicle valve. Shell impunctate.

Pedicle interior. Dental lamellae long, surmounted by stubby hinge teeth. Muscle field almost free of secondary deposits, as are the umbonal cavities. A low myophragm discernible in some specimens. Sulcus impressed upon the interior; peripheral regions smooth.

Brachial interior. Crural plates long, support discrete chilidial plates. Area of diductor attachment unstriated. Muscle field not noticeably impressed, although a low myophragm is discernible in some specimens. Periphery smooth. The dental sockets narrow posteriorly and flare rapidly antero-laterally. The crura make an obtuse angle with the primary lamellae. The short jugal processes descend toward the pedicle valve near the intersection of the crura and primary lamellae.

Species:

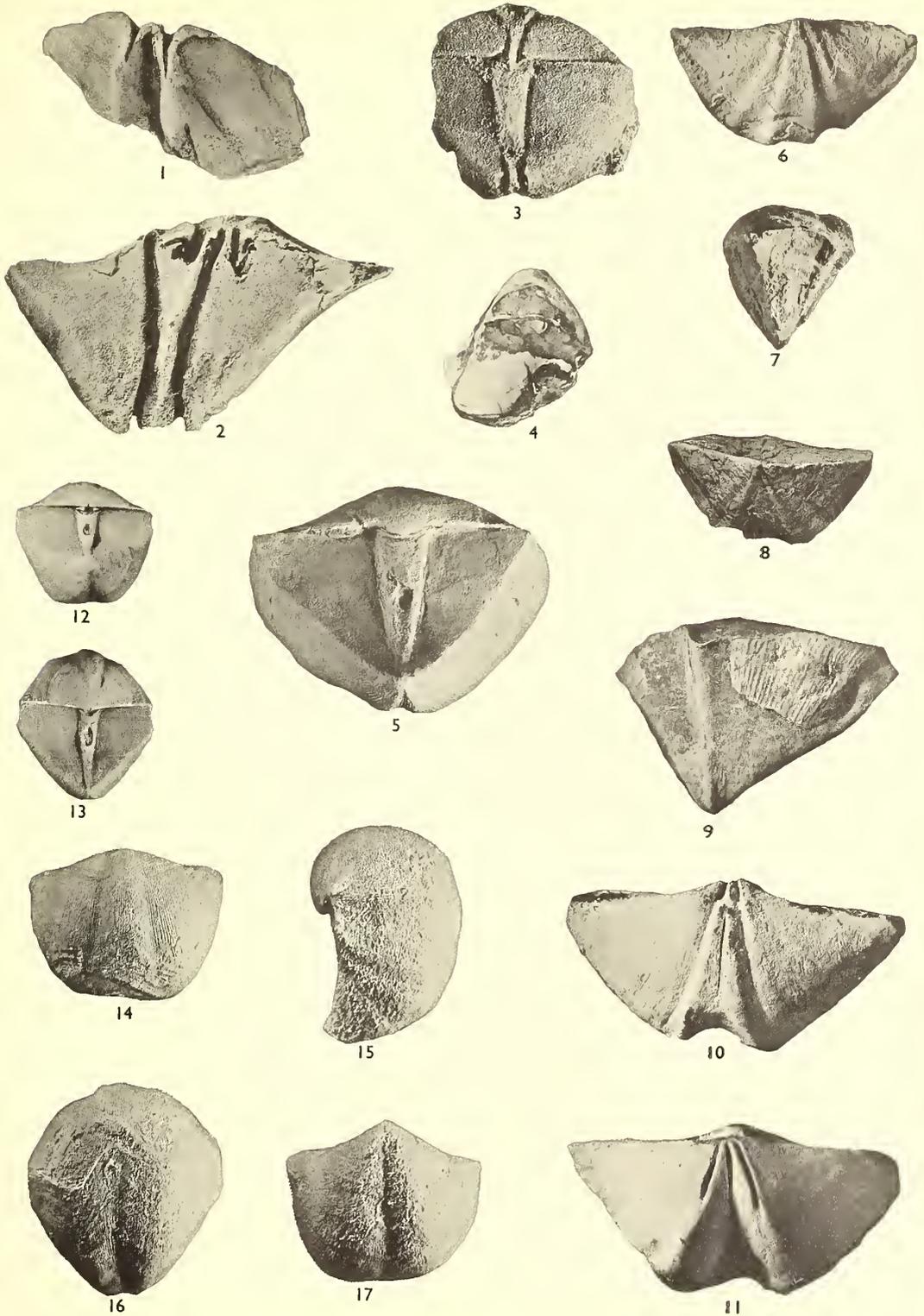
Spirifer approximans Barrande 1879, pl. 4, fig. 5.

Cyrtia cliftonensis Foerste 1903, *J. Geol.* **11**, p. 709; 1909a, p. 91, pl. 2, fig. 32.

Anomites exporrectus Wahlenberg 1821, *Nova Acta Reg. Soc. Sci. Uppsaliensis*, **8**, p. 64, no. 3.

EXPLANATION OF PLATE 102

- Figs. 1, 2. *Cyrtia sp.* Bilobites zone; Locality 4-24, Duck Harbor, Edmunds Township, Washington County, Maine. U.S.N.M. No. 126083. 1, Impression of interior of pedicle valve ($\times 3$). Note the relatively long dental lamellae. 2, Impression of interior (posterior view, $\times 4$). Note the relatively long dental lamellae and the impression of the inner face of the deltidial plate.
- Fig. 3. *Cyrtia sp.* Cedarville dolomite; Mills quarry, south-west of Springfield, Ohio. U.S.N.M. No. 87495. Impression of interior (posterior view, $\times 2$). Note the relatively long crural plates and the unstriated area of diductor attachment.
- Fig. 4. *Cyrtia exporrecta* (Wahlenberg, 1821). Upper Visby marl; Shore at Gnisvärds fiskläge, Tofta parish, Klintehamn map sheet, Gotland (Boucot locality No. 56G47). U.S.N.M. No. 137734. Preparation of spire ($\times 2$). Note the short jugal process and the obtuse angle included between the crura and the primary lamella.
- Fig. 5. *Cyrtia trapezoidalis* Hisinger, 1828. Wenlock limestone; Dudley, England. U.S.N.M. No. 99909. Posterior view ($\times 2$). Note the narrow chilidium bordering the upper margin of the deltidial plate.
- Figs. 6-11. *Plicocyrtia petasus* (Barrande, 1848). Liten beds; Lodenice, Czechoslovakia. 6, Brachial valve ($\times 1$). Note the lateral plications. M.C.Z. No. 9428A. 7, Side view ($\times 1$). Note the lateral plication adjacent to the sulcus and the relatively elongate, slightly curved interarea of the pedicle valve. M.C.Z. No. 9428A. 8, Pedicle valve ($\times 1$). Note the lateral plications bordering the sulcus. M.C.Z. No. 9428A. 9, Exterior ($\times 3$). Note the radially striate fine ornamentation remaining on the unexfoliated portion of the shell. M.C.Z. No. 9428c. 10, Impression of interior of brachial valve ($\times 2$). Note the elongate crural plates and the unstriated area of diductor attachment. M.C.Z. No. 9428B. 11, Impression of interior of pedicle valve ($\times 2$). Note the relatively long dental lamellae and the myophragm medially dividing the muscle field. M.C.Z. No. 9428B.
- Figs. 12-17. *Cyrtia exporrecta* (Wahlenberg, 1821). Probably from the Upper Visby marl; Visby, Gotland. U.S.N.M. No. 53505. 12, Exterior (posterior view, $\times 2$). Note the discrete chilidial plates. 13, Exterior (posterior view, $\times 2$). Note the elongate deltidium. 14, Brachial view ($\times 3$). Note the low, rounded fold, smooth flanks, and fine radial striae. 15, Side view ($\times 3$). Note the elongate, slightly curved interarea. 16, Anterior view ($\times 3$). Note the uniplicate anterior commissure. 17, Pedicle view ($\times 3$). Note the broad sulcus and the smooth flanks.



BOUCOT, Eospiriferidae

- Cyrtia exporrecta ludlowensis* Boucek 1940, p. 13, pl. ii, fig. 2.
Cyrtia exporrecta maior Boucek 1940, p. 14, pl. ii, fig. 3.
Cyrtia exporrecta postera Boucek 1940, p. 15, pl. i, fig. 6.
Cyrtia exporrecta spiriferoides Boucek 1940, p. 15, pl. ii, fig. 4.
Cyrtia extensa Bolton 1957, p. 71, pl. 12, figs. 3–6.
Cyrtia humilis Boucek 1940, p. 10, pl. 1, fig. 1b.
Cyrtia meta Hall 1867, *20th Rpt. New York State Cab. Nat. Hist.*, p. 372, pl. 13, figs. 12–13.
Cyrtia myrtia Billings 1862, *Paleozoic Fossils*, 1, p. 165, fig. 149.
Cyrtia radians Hall and Clarke 1893, *Paleontology of New York*, 8, pt. 2, pp. 42, 362, pl. 13, figs. 12–13.
Cyrtia tasmaniensis Gill 1948, pp. 60–61, pl. 8, figs. 23–26.
Cyrtia trapezoidalis Hisinger 1828, Pridrag till Sveriges geognosie, *Anteckningar i fysik och geognosie*, 4, p. 220, pl. 6, fig. 1a, b, c.
Cyrtia trapezoidalis var. *arrectus* Hall and Whitfield 1872, p. 183.

Distribution. In eastern North America widely distributed in strata of Upper Llandoveryan to Ludlovian age:

- Anticosti Island: *C. myrtia*, Chicotte fm., Wen. (Twenhofel 1928, p. 219).
 Gaspé: *C. sp. nov.* aff. *C. exporrecta*, St. Leon fm., early Lud. (Alcock 1935, p. 50). *C. cf. exporrecta*, near Matapedia, Sil. (noted by writer in a collection made by Dr. Jacques Beland, Quebec Dept. of Mines).
 New Brunswick: *C. cf. exporrecta*, Mascarene series at Back Bay near St. George, U. Lland. (C₆) to Wen.
 Maine: *Cyrtia*, Shin Pond quadrangle (loc. no. BB4 of R. B. Neuman), U. Lland. (C₆) to Wen. (identified by writer), and Eastport region (Pl. 102, figs. 1–2).
 New York: *C. myrtia* and *C. meta*, Irondequoit ls. and Williamson sh., U. Lland. (C₅ to C₆) (Gillette 1947, p. 20).
 Kentucky: *C. arrecta*, strata of Louisville age (Wen.) (Hall and Clarke 1893, p. 28, figs. 2–3).
 Ohio: *Cyrtia sp.*, Cedarville dolomite, Wen. (pl. 6, fig. 3).
 Arkansas: *C. exporrecta*, St. Clair ls., U. Lland. (C₃ or younger) to Lud. (Thomas 1926, pp. 394–5).
 Wisconsin: *C. radians*, Racine dolomite, Wen. (Hall and Clarke 1893, p. 39, fig. 33).
 Indiana: *C. myrtia*, Liston Creek reef, Lud. (Cumings 1930, p. 209). *C. trapezoidalis*, Osgood fm., U. Lland. (C₅ to C₆) (Tillman 1961).
 Ontario: *C. meta*, Lockport dolomite, Wen. (Williams 1919, p. 67). *C. extensa*, Warton member of Amabel fm., Wen. and Lud. (Bolton 1957, p. 71; pl. 12, figs. 3–6; table 11).
 British Columbia: *Cyrtia sp.*, basal 150 ft. of Sandpile group near junction of Dall and Turnagain rivers (Geol. Surv. of Canada specimens no. 15795, 15796 from coll. No. 35174), U. Lland. (C₃–C₅).

In Europe widely distributed in strata of Upper Llandoveryan to Emsian and possibly Eifelian age, but rare elsewhere:

- Norway: *C. exporrecta*, Oslo region, U. Lland. (7c) and Wen. (8a) (Kiaer 1908, p. 589).
 Gotland: *C. exporrecta*, U. and L. Visby marl. U. Lland.; Tofta ls. and Slite group, Wen. (Hede 1921, p. 94). *C. trapezoidalis*, Mulde marl and Klinteberg ls., Wen. and L. Lud. (ibid.).
 Podolia: *C. exporrecta*, Kitaygorod fm. to Malinovetski fm., U. Lland. to Lud. (Nikiforova 1954, pp. 148–50).
 Poland: *Cyrtia*, Holy Cross Mts., Lud. (Tomszykowa 1959, p. 67).
 Urals: *C. trapezoidalis*, Striatius beds, Lud. (Khodalevitch 1937, pp. 69–70).
 Novaya Zemlya: *C. trapezoidalis*, Lud. (Yermolaev 1937, p. 105).
 Great Britain: *C. trapezoidalis* and *C. exporrecta*, U. Lland. to Lud. (observed by writer).
 Czechoslovakia: *C. trapezoidalis*, Collines entre Luzetz et Lodenitz (e2), Tachlowitz (e2), and Dlauha Hora (e2), Wen. or Lud. (Barrande 1879, pl. 8, figs. 10–15). *C. approximans*, Ems. or Eif. (Havlíček 1959, pp. 73–75). *C. exporrecta exporrecta*, e2; *C. exporrecta postera*, e3; *C. humilis*, e1;

C. exporrecta ludlowensis e1; *C. exporrecta maior*, e2; *C. exporrecta exporrecta spiriferoides*, e2 (Boucek 1940, plate explanation).

Tasmania: *C. tasmaniensis*, Eldon group, Sil., as evidenced by the presence of *Encrinurus* (Gill 1948, pp. 60–61). The *Protoleptostrophia* cited by Gill 1948, pp. 64–65 from the fauna may well belong to *Leptostrophia*, but no information on the brachial interior is available for positive identification.

Turkey: *Cyrtia*, Chamosite horizon near Cumakoy (NW. of Aquiran) in the Istanbul region, U. Lland.

T'ien-Shan: *Cyrtia* sp. from locality 13 of Arpishmebulag Series, Sil. (identified from photographs provided through the courtesy of Prof. G. Regnell, Lund).

Genus PLICOCYRTIA gen. nov.

Plate 102, figs. 6–11; plate 104, figs. 1–3

Type species. *Cyrtia petasus* Barrande 1848, *Haid. Naturw. Abh.* 2, p. 183, pl. 17, fig. 1; 1879, pl. 7, figs. 7–9.

EXPLANATION OF PLATE 103

Figs. 1–6. *Nikiforovaena ferganensis* (Nikiforova, 1937). Isfara beds; outcrop 1885, northern slope of the Alai Range, Fergana. Cat. No. 1841/5037 (Holotype). 1, Anterior view ($\times 1$). Note the grooved fold and corresponding rib in the sulcus. 2, Pedicle view ($\times 1$). 3, Brachial view ($\times 1$). 4, Posterior view ($\times 1$). 5, Side view ($\times 1$). 6, Fine ornamentation ($\times 5$). Note the eospiriferid-type striae.

Figs. 7–9. *Janius* sp. Strata of Ludlovian age; Junction of road and Gambol Brook (loose blocks almost in situ), Field No. CE-16, Stratum No. 30801, Tetagouche Lakes area, New Brunswick, Canada. L. M. Cumming, collector, 1957. 7, Impression of interior of pedicle valve ($\times 2$). Note the plication in the sulcus. G.S.C. No. 15152. 8, Impression of portion of exterior ($\times 2$). Note the eospiriferid-type striations. G.S.C. No. 15153. 9, Impression of interior of pedicle valve ($\times 2$). Note the anteriorly bifurcating lateral plications and the plication in the sulcus. G.S.C. No. 15154.

Figs. 10, 11. *Janius* sp. Strata of Ludlovian age; Small island near southern end of Whitehorse Lake, Shin Pond quadrangle, Maine. U.S.N.M. No. 137737. 10, Impression of exterior ($\times 3$). Note the eospiriferid-type striations and the anteriorly branching lateral plications. 11, Impression of pedicle valve interior ($\times 3$).

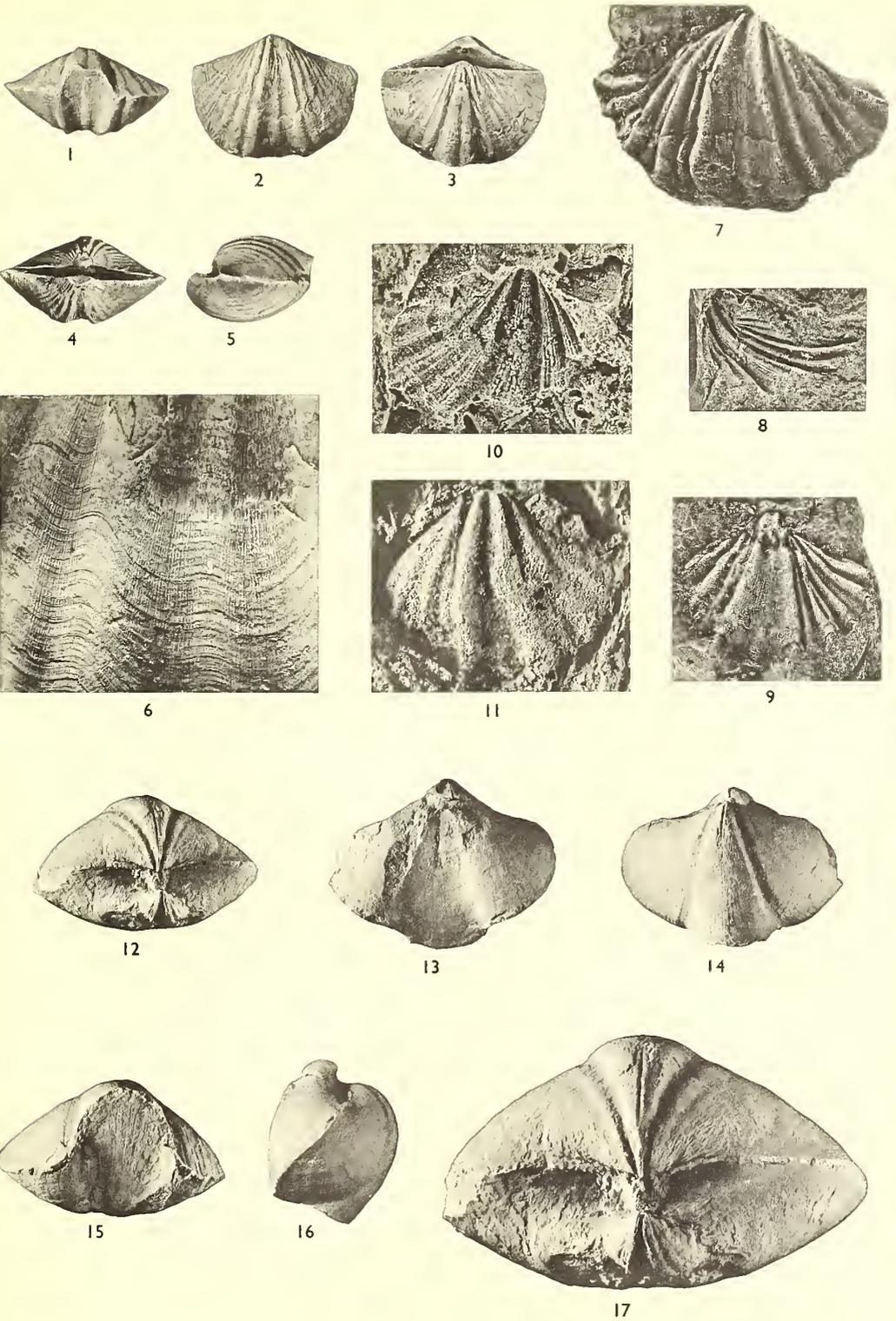
Figs. 12–17. *Havlicekia* sp. Lower portion of Lochkov limestone. Svaty Jan pod Skalou, small valley under the hill 'Mramor', south-west of the village. Right side of the Kacak stream, Czechoslovakia. Boucot locality No. B-60-32. 12, Posterior view ($\times 1$). 13, Pedicle view ($\times 1$). 14, Brachial view ($\times 1$). 15, Anterior view ($\times 1$). 16, Side view ($\times 1$). 17, Posterior view ($\times 2$). Note the long crural plates and the unstriated area for diductor attachment. U.S.N.M. No. 137738.

EXPLANATION OF PLATE 104

Figs. 1–3. *Plicocyrtia petasus* (Barrande, 1848). Liten beds; Lodenice, Czechoslovakia. M.C.Z. No. 9248A. 1, Posterior view ($\times 1$). Note the deltidial cover. 2, Anterior view 3, ($\times 1$). Anterior view ($\times 1$). Note the short dental lamella.

Figs. 4–8. *Cyrtia exporrecta* (Wahlenberg, 1821). Upper Visby marl; Gotland. Pal. Inst. Uppsala, Wahlenbergs samling Nr. G. 199. These figures are of the lectotype, which is here designated from the three cotypes. 4, Brachial view ($\times 3$). 5, Pedicle view ($\times 3$). 6, Posterior view ($\times 3$). 7, Anterior view ($\times 3$). 8, Side view ($\times 3$).

Figs. 9–14. *Janius insignis* (Hedstrom, 1923). Eke Group; Lau backar, 1.3 km. north-east of Church of Lau, parish of Lau, Gotland. Collected and identified by Dr. J. E. Hede. 9, Side view ($\times 3$). U.S.N.M. No. 137735. 10, Pedicle view ($\times 3$). Note the plication in the sulcus. U.S.N.M. No. 137735. 11, Brachial view ($\times 3$). Note the grooved fold. U.S.N.M. No. 137735. 12, Anterior view ($\times 3$). U.S.N.M. No. 137735. 13, Posterior view ($\times 3$). Note the ribbon-like deltidial plates. U.S.N.M. No. 137735. 14, Posterior view of internal impression ($\times 3$). Note the long crural plates. U.S.N.M. No. 137736.

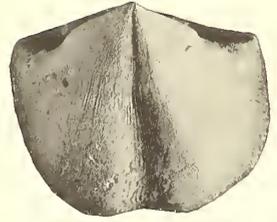




1



4



5



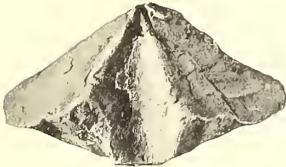
2



6



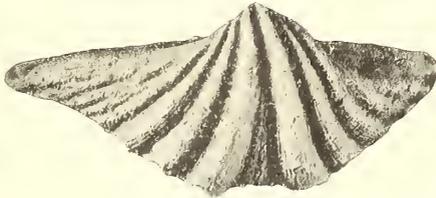
7



3



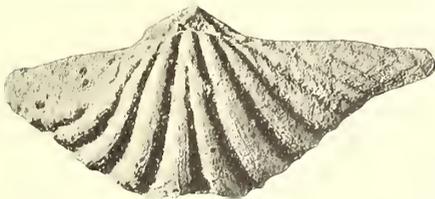
9



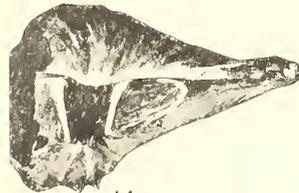
10



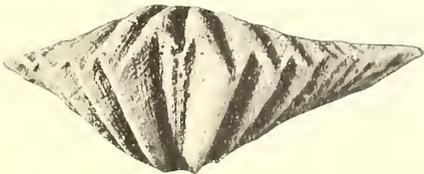
8



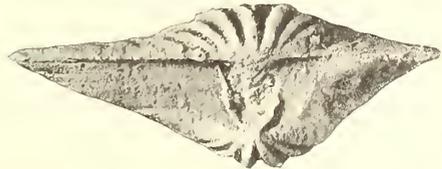
11



14



12



13

Diagnosis. Cyrtiinids bearing lateral plications on either side of the fold and sulcus.

Comparison. *Plicocyrtia* differs from *Cyrtia* only in having lateral plications on either side of the fold and sulcus.

Pedicle exterior. Valve pyramidal, laterally elongate tending to become alate. Interarea unstriated, gently incurved, catacline to steeply apsacline. Hinge-line straight, equal to maximum width. Delthyrium narrow, elongate, filled by a convex deltidial plate. The detailed structure and mode of origin of the deltidial plate is not known. Fine ornamentation consists of fine radial fila. Anterior commissure uniplicate and crenulate. Sulcus prominent, rounded in cross-section, bordered laterally by one to three lateral plications having low, rounded cross-sections and separated by broad, U-shaped inter-spaces. Flanks smooth.

Brachial exterior. Valve gently convex, laterally elongate tending toward alation; posteriorly it overhangs the pedicle valve. Shell impunctate. Interarea orthocline to apsacline. The presence or absence of chilidial plates was not determined. Fold rounded in cross-section, bordered laterally by one to three plications lateral to which the flanks are smooth. Fine ornamentation same as that of pedicle valve.

Pedicle interior. Hinge teeth stubby, supported basally by the long, thin dental lamellae. Muscle field and umbonal cavities almost free of secondary deposits. A well-developed myophragm medially divides the muscle field and extends anteriorly to about the mid-length. The external ornamentation is impressed upon the interior.

Brachial interior. The cardinalia consist of slender crural plates which laterally border the unstriated area of diductor attachment and basally support the discrete hinge-plates. A low myophragm bisects the feebly impressed muscle field and extends anteriorly past the midlength.

Species:

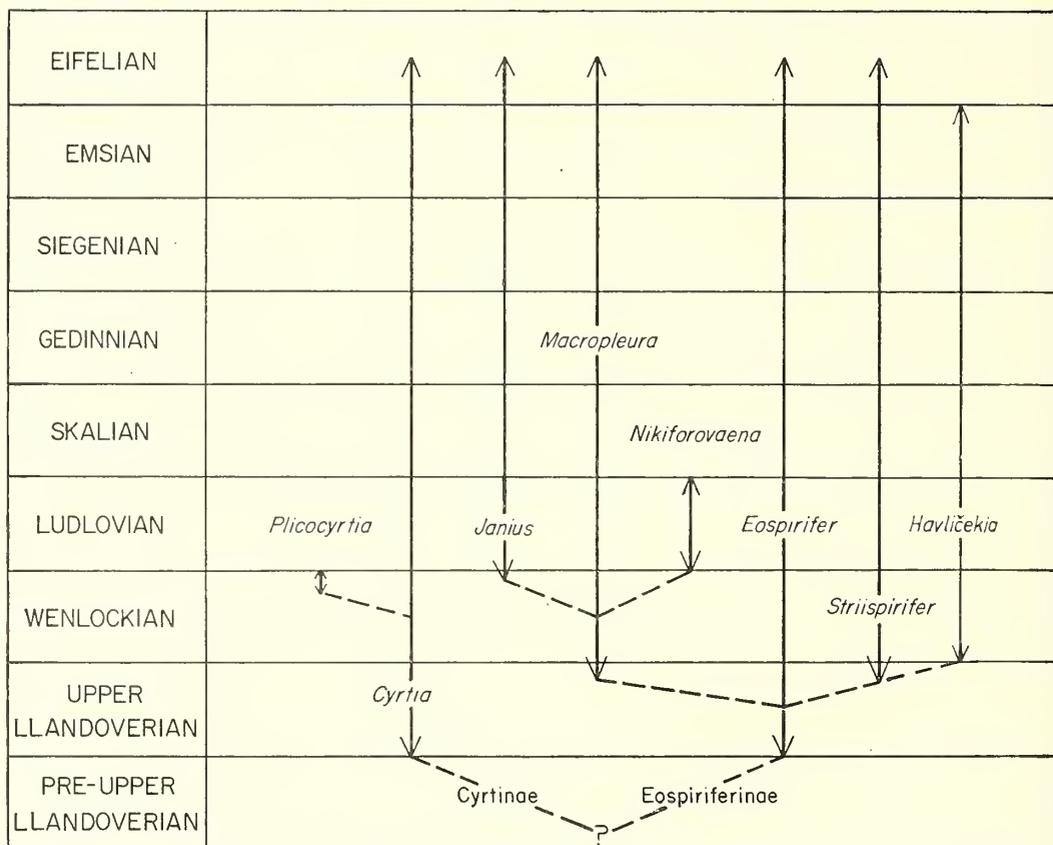
Cyrtia petasus Barrande 1848, *Haid. Naturw. Abh.* **2**, p. 183, pl. 17, fig. 1.

Distribution. Known from the Upper Liten beds (uppermost Wenlockian) of Czechoslovakia, and possibly from strata of Ludlow age in Turkestan if *C.?* aff. *petasus* (Nikiforova 1937, p. 51) belongs to the genus.

EVOLUTION OF THE EOSPIRIFERIDAE

The oldest known genera of the family Eospiriferidae (text-fig. 4), *Eospirifer* and *Cyrtia*, appear in strata of early Upper Llandovery age on both sides of the North Atlantic. The similar cardinalia, spires, interiors of pedicle valves, and fine ornamentation of both genera clearly suggest that they have a common ancestor somewhere in pre-Upper Llandoveryan time. Both genera belong to the brachiopod fauna which first appears in the North Atlantic region during Upper Llandoveryan time from an unknown area. Among known Ordovician or pre-Upper Llandoveryan brachiopods there are no closely related genera and, in fact, no genera that could reasonably be included in the same family. The Cyrtiinae, as exemplified by *Cyrtia*, appear to have been a relatively stable stock which, for unknown reasons, did not give rise to such diverse plicated forms

as those in the *Eospiriferinae*. The genus *Eospirifer*, for example, by the development of different types of plications on flanks and sulcus proliferated a number of genera. The gradual transition between specimens with smooth flanks (*Eospirifer*) and those with undulating plications separated by U-shaped interspaces of the *Macropleura* type, or those with V-shaped interspaces of the *Striispirifer* type, strongly suggests that



TEXT-FIG. 4. Relations of the Eospiriferidae.

Eospirifer was ancestral to both of the latter genera. It is probable that the long-lived stock of smooth-flanked eospiriferids repeatedly gave rise to forms with plicated flanks, but this cannot be demonstrated on the basis of available collections and information.

Some relevant information comes from the genus *Havlicekia*. Havlíček (1959, pp. 52–53) has concluded, on morphological grounds, that the Ludlovian species *E. praesecans* from the Kopanina beds is ancestral to the Lower Devonian form *H. secans*, as large specimens of both have the peculiarly large, steep-sided fold with U-shaped cross-section. It is more probable that *E. praesecans* is ancestral to *E. togatus togatus*, which, as described by Havlíček (ibid., pp. 42–43), is very similar to *E. praesecans*, and that *H. turjensis*, which occurs in the Pridoli beds (overlying the Kopanina beds) and also in the Urals in strata reported to be of Wenlockian age (Khodalevitch 1939, pp. 65–66), is ancestral to *H. secans*.

The Kopanina beds also contain *Striispirifer viator*, which has a steep-sided fold similar to that of *Havlicekia* and *E. praesecans*. This suggests that at least one species of *Striispirifer* was derived from a smooth eospiriferid similar to *E. praesecans* in pre-Kopanina time (presumably during the late Llandovery), and that *Havlicekia* was derived from a similar source at about the same time. From a consideration of fold cross-sections, it seems likely that species of *Striispirifer* similar to *S. niagarensis* were derived from an *Eospirifer* similar to *E. radiatus*, which suggests that *Striispirifer* is polyphyletic.

Macroleura is transitional to the later-appearing genus *Janius*, the early growth stages of which have *Macroleura*-type ornamentation. On morphological grounds, the U-shaped interspaces between the rounded plications of *Nikiforovaeva* ally it closely with *Macroleura*, and it is concluded that the former was derived from the latter by the development of a plicated fold and sulcus.

The coarse ornamentation of *Plicocyrtia* suggests its origin from the unplicated genus *Cyrtia*.

From a phylogenetic point of view, the Eospiriferidae show a repeated tendency to develop forms with lateral plications in the adult (large specimen), whereas the early growth stages are usually reminiscent of an ancestral type (e.g. smooth, unplicated umbonal beak region in such genera as *Macroleura*, *Striispirifer*, and *Plicocyrtia*). *Havlicekia* suggests that the genetic processes responsible for the development of lateral plications in adults could also operate in the reverse manner, to produce lateral plications in the umbonal region in the young and smooth flanks in the adult.

'*Eospirifer*' *iorensis* Nikiforova 1937, from strata of Ludlow age in Turkestan, is undoubtedly an eospiriferid, as evidenced by its fine ornamentation. The presence of a deep groove in its fold, associated with a corresponding rib in the sulcus, separates it generically from all other members of the Eospiriferidae, but the writer does not propose a new genus to receive this unique species because its internal morphology is not clear.

Havlíček (1959, p. 231) noted that both '*Eospirifer*' *olgae* Borisyak 1955 and '*Eospirifer*' *kassini* Borisyak 1955 may belong to a group in which the brachial valve bears a sulcus containing a median plication. Inspection of Borisyak's figured specimens shows that they are too fragmentary for certainty on this point, although their fine ornamentation indicates they are undoubtedly eospiriferid.

STRATIGRAPHIC VALUE OF THE EOSPIRIFERIDAE

Members of the Cyrtiinae are known in beds of Upper Llandoveryan to possible Eifelian age, and members of the Eospiriferinae from beds of Upper Llandoveryan to Eifelian age. Representatives of both groups occurring in pre-Upper Llandoveryan beds will probably eventually be found. *Eospirifer* itself ranges from the Upper Llandoveryan to the Eifelian. In the North Atlantic region, *Macroleura* appears in uppermost Llandoveryan time; it continues through Gedinnian time and possibly into the lowest Siegenian interval, although elsewhere it persisted into Eifelian time. *Striispirifer* appears in uppermost Llandoveryan time and continues through to Eifelian time. *Janius* appears in uppermost Wenlockian time and continues into the Eifelian. The species of *Janius* without plicae on the fold or sulcus appear earlier (in late Wenlockian time) than those forms with such plicae (Ludlow), making it possible to distinguish between beds of

latest Wenlockian to Ludlovian age on this basis. *Nikiforovaena* is known in strata of Ludlovian age. *Havlicekia* is known from strata of Wenlockian to Eifelian age.

In North America, eospiriferids are not known after the Gedinnian (New Scotland formation and its equivalents). In the Old World, eospiriferids normally occur as high as the Emsian, except in the Rhenish facies of northern Europe where they are unknown in either the Siegenian or Emsian, and in Central Asia and Czechoslovakia, where they also occur in the Eifelian. The available distribution data suggests that the family became progressively restricted geographically after the Gedinnian until, by the end of Eifelian time, they became extinct.

REFERENCES

- ALCOCK, F. J. 1935. Geology of the Chaleur Bay region. *Mem. Canada Geol. Surv.* **183**, 1-146.
- ALFEROV, B. A. 1937. Geological description of the south-western coast of Novaya Zemlya. *Internat. Geol. Cong., XVII, The Novaya Zemlya Excursion*, 5-31.
- AMSDEN, T. W. 1957. Stratigraphy of the Hunton Group. *Oklahoma Geol. Surv. Circ.* **44**, 1-57.
- 1960. Stratigraphy and paleontology of the Hunton Group in the Arbuckle Mountain region. Pt. VI, Hunton stratigraphy. *Bull. Oklahoma Geol. Surv.* **84**, 1-311.
- ASSMANN, P. 1910. Die Fauna der Erbsloch-Grauwacke bei Densberg im Kellerwald. *Jahrb. Preuss. Geol. Land. f. 1910*, Bd. XXXI, **1**, 1, 136-72.
- BARRANDE, J. 1879. *Système silurien du centre de la Bohême*, 5.
- BARRAIS, C. 1886. Mémoire sur le Calcaire Devonien de Chaudfontaine (Maine-et-Loire). *Ann. Soc. Géol. Nord.* 170-205.
- 1889. Faune du Calcaire d'Erbray. *Mém. Soc. Géol. Nord.* **3**, 1-348.
- BEECHER, C. E., and CLARKE, J. M. 1889. The development of some Silurian Brachiopoda. *Mem. New York State Mus.* **1**, 1-95.
- and DODGE, W. W. 1892. On the occurrence of Upper Silurian strata near Penobscot Bay, Me. *Amer. J. Sci.* **3**, 43, 412-18.
- BILLINGS, E. 1869. Description of some new species of fossils with remarks on others already known from the Silurian and Devonian rocks of Maine. *Proc. Portland (Maine) Soc. Nat. Hist.* **1**, 104-26.
- BOLTON, T. E. 1957. Silurian stratigraphy and palaeontology of the Niagara escarpment in Ontario. *Mem. Canada Geol. Surv.* **289**, 1-145, pl. 1-13.
- BORISYAK, M. A. 1955a. Material on the stratigraphy and fauna of the Ordovician and Silurian sediments of Central Kazakhstan, No. 1, Silurian (Wenlockian) brachiopods from Karaganda oblast. *All-Union Sci. Inv. Geol. Inst. (VSEGEI)*, n.s., *Paleont. and Stratigr.* **3**, 1-92.
- 1955b. Material on the stratigraphy and fauna of the Ordovician and Silurian sediments of Central Kazakhstan, No. 2, Stratigraphy and brachiopods of the Silurian of the region of the Chinghiz Mountains. *Ibid.* **5**, 1-108.
- 1960. Conference on the unification of the stratigraphic scheme of the pre-Paleozoic and Paleozoic of Eastern Kazakhstan. T. 1, pre-K, K, O, S. *Acad. Sci. Kazakhstan, Alma-Ata*, 1-298.
- BOUCEK, B. 1940. Über die Variabilität der Brachiopoden *Dayia navicula* (Sow.) und *Cyrtia exporrecta* (Wahl.). *Mitt. Tschech. Akad. Wiss.* **50**, 1-17.
- BOUCOT, A. J. 1960. Lower Gedinnian brachiopods of Belgium. *Mém. Inst. Géol. Louvain*, **21**, 283-324.
- 1961. The Lower Paleozoic rocks of west-central Maine. *Bull. U.S. Geol. Surv.* **1111**.
- *et al.* 1958. Metamorphosed Middle Paleozoic fossils from central Massachusetts, eastern Vermont, and western New Hampshire. *Bull. Geol. Soc. Amer.* **69**, 855-870.
- and THOMPSON, J. B., JR. 1958. Late Lower Silurian fossils from sillimanite zone near Claremont, N.H. *Science*, **128**, 3320, 362-3.
- BUTTS, CHARLES. 1940. Geology of the Appalachian Valley in Virginia. *Bull. Virginia Geol. Surv.* **52**, 1-568.
- CAIRNES, D. D. 1914. The Yukon-Alaska International Boundary, between Porcupine and Yukon Rivers. *Mem. Geol. Surv. Canada*, **67**.

- CHAPMAN, F. in JUTSON 1908. The Silurian rocks of the Whittlesea District. *Proc. Roy. Soc. Victoria*, **21** (N.S.), 1, 211–25.
- CHERNYCHEV, B. B. 1937. The Silurian brachiopods of Mongolia and Tuva. *Trudy Mongolian Comm.* **29**, *Izdatelstvo Akad. Sci. USSR*, 1–94.
- CLARKE, J. M. 1909. Early Devonian history of New York and eastern North America. *Mem. New York State Mus.* **9**, pt. 2, 1–250.
- CUMINGS, E. R. 1930. Silurian studies. *Proc. Indiana Acad. Sci.* **39**, 183–211.
- DAVIDSON, T. 1871. The Silurian brachiopods: A monograph of the British fossil Brachiopoda, pt. 7, **4**, 249–397.
- DUNBAR, C. O. 1919. Stratigraphy and correlation of the Devonian of western Tennessee. *Bull. Tennessee State Geol. Surv.* **21**, 1–127.
- FOERSTE, A. F. 1909a. Fossils from the Silurian formation of Tennessee, Indiana, and Kentucky. *Bull. Denison Univ. Sci. Lab.* **14**, 61–116.
- 1909b. Silurian fossils from the Kokomo, West Union, and Alger horizons of Indiana, Ohio, and Kentucky. *J. Cincinnati Soc. Nat. Hist.* **21**, 1–141.
- 1935. Correlation of Silurian formations in south-western Ohio, south-eastern Indiana, Kentucky and western Tennessee. *Bull. Denison Univ. Sci. Lab.* **30**, 119–205.
- GIGOUT, M. 1951. Études géologiques sur la Meseta Marocaine Occidentale. *Trav. Inst. Sci. Cherifien, Rabat*, **3**, t. 1, 1–507.
- GILL, E. G. 1948. Eldon group fossils. *Rec. Queen Victoria Mus., Launceston, Tasmania*, **2**, 57–74.
- 1949. Devonian fossils from Sandy's Creek, Gippsland, Victoria. *Mem. Nat. Mus. Victoria*, **16**, 91–115.
- 1950. Palaeontology and palaeoecology of the Eldon group. *Papers and Proc. Roy. Soc. Tasmania*, 231–58.
- GILLETTE, TRACY. 1947. The Clinton of western and central New York. *Bull. New York State Mus.* **341**, 1–197.
- GORTANI, M. 1915. Fossili Eodevonici della base del Capolago (Seekopfsockel). *Palaeontographica Italica*, **21**, 117–88.
- GRABAU, A. 1926. Silurian faunas of eastern Yunnan. *Pal. Sinica, China Geol. Surv.* **3**, Ser. B, fasc. 2, 1–86.
- HALL, JAMES and CLARKE, J. M. 1893. An introduction to the study of the genera of Palaeozoic Brachiopoda, Pt. II. *New York Geol. Surv.* 1–394.
- and WHITFIELD, R. P. 1872. *24th Ann. Rpt. New York State Mus. Nat. Hist.* for 1871.
- — 1875. *25th Ann. Rpt. New York State Mus. Nat. Hist.* for 1876.
- HAMADA, T. 1961. The middle Palaeozoic group of Japan and its bearing on her geological history. *Jour. Faculty Science Univ. Tokyo*, sec. II, XIII, pt. 1, 1–79.
- HAVLÍČEK, VLADIMIR. 1957a. Further new genera of the family Spiriferidae in the Silurian and Devonian of Bohemia. *Vestník UUG*, roc. **32**, 436–40.
- 1957b. On new genera of Spiriferidae of Bohemia (Brachiopoda). *Vestník UUG*, roc. **32**, 245–8.
- 1959. The Spiriferidae of the Silurian and Devonian of Bohemia. *Rozpravy UUG*, svazek **25**, Prague.
- HEDE, J. E. 1921. Gottlands silurstratigrafi. *Sver. geol. Undersök.*, ser. C, **305**, 1–100.
- 1927a. Berggrunden (Silursystemet) in MUNTHE, HENR., HEDE, J. E., and VON POST, LENNART. Beskrivning till kartbladet Hemse. *Ibid.*, ser. Aa, **164**, 1–155.
- 1927b. Berggrunden (Silursystemet) in MUNTHE, HENR., HEDE, J. E., and LUNDQVIST, G. Beskrivning till kartbladet Klintehamm. *Ibid.*, ser. Aa, **160**, 1–109.
- 1928. Berggrunden (Silursystemet) in MUNTHE, HENR., HEDE, J. E., and LUNDQVIST, G. Beskrivning till kartbladet Slite. *Ibid.*, ser. Aa, **169**, 1–130.
- 1933. Berggrunden (Silursystemet) in MUNTHE, HENR., HEDE, J. E., and LUNDQVIST, G. Beskrivning till kartbladet Kappelshamn. *Ibid.*, ser. Aa, **171**, 1–129.
- 1936. Berggrunden in MUNTHE, HENR., HEDE, J. E., and LUNDQVIST, G. Beskrivning till kartbladet Faro. *Ibid.*, ser. Aa, **180**, 1–82.
- 1940. Berggrunden in LUNDQVIST, G., HEDE, J. E., SUNDIUS, N. Beskrivning till kartbladen Visby och Lummelunda. *Ibid.*, ser. Aa, **183**, 1–167.
- HEDSTROM, H. 1923. Contributions to the fossil fauna of Gotland. *Ibid.*, *Undersök.* ser. C, **316**, 1–24.

- KAYSER, EMANUEL. 1878. Die Fauna der ältesten Devon-Ablagerungen des Harzes. *Abh. Geol. Specialkarte Preuss. Geol. Landesanst.*, Bd. 2, h. 4, 1-295, 36 pl. (in separate Atlas).
- KHALFIN, L. L. 1948. Fauna and stratigraphy of the Devonian beds of the High Altai. *Trans. Tomsk Polytechnic Inst.* 65, 1, 1-464.
- KHODALEVITCH, A. N. 1937. The Lower Devonian of the Ivdel Region (eastern slope of the Urals). *Mat. Central Geol. and Prospecting Inst., Paleont. and Stratigr.*, Mag. 3, 64-70.
- 1939. Upper Silurian Brachiopoda of the eastern slope of the Urals. *Trans. Ural Geol. Serv.* 1-135.
- 1951. Lower Devonian and Eifelian brachiopods of the Ivdel'sk and Serov'sk regions of Sverdlovsk Oblast. *Works of Sverdlovsk Mining Inst.* 18, 1-169.
- KIAER, J. 1908. Das Obersilur im Kristianiagebiete. *Vidensk.-Selsk. Skr., I. Math. Natrv. Kl.* 106, Bd. 2, 1-595.
- KINDLE, E. M. 1908. Geologic reconnaissance of the Porcupine Valley, Alaska. *Bull. Geol. Soc. America*, 19, 315-38.
- KIRK, E., and AMSDEN, T. W. 1952. Upper Silurian Brachiopoda from south-eastern Alaska. *U.S. Geol. Surv. Prof. Paper*, 233C, 53-66.
- LE MAITRE, D. 1934. Études sur la faune des Calcaires Devoniens du Bassin d'Ancenis. *Mém. Soc. Géol. Nord.* 12, 1-267.
- 1952. La faune du Devonien inférieur et moyen de la Saoura et des abords de l'Erg el Djemel (Sud-Oranais). *Mat. pour Carte Geol. de l'Algérie*, 1st ser., Paléont. 12, 1-170.
- LESLEY, J. P. 1890. A dictionary of the fossils of Pennsylvania. *Pennsylvania Geol. Surv.*, Rpt. pt. 4, 3, 915-1283.
- LUHA, A. 1930. Über Ergebnisse stratigraphischer Untersuchungen im Gebiete der Saaremaa-(Osel)-Schichten in Eesti (Unteroseel und Eurypterusschichten). *Acta et Comm. Univ. Tartu*, A18; *Publ. Geol. Inst. Univ. Tartu*, 22, 1-18.
- MCLEARN, F. H. 1924. Palaeontology of the Silurian rocks of Arisaig, Nova Scotia. *Canada Geol. Surv. Mem.* 137, 1-180.
- MAEHL, R. H. 1961. The Older Palaeozoic of Pictou County, Nova Scotia. *Nova Scotia Dept. of Mines, Mem.* 4, 1-112.
- MITCHELL, J. 1921. Some new brachiopods from the Middle Palaeozoic Rocks of New South Wales. *Proc. Linn. Soc. New South Wales*, 45, 543-51.
- NALIVKIN, D. 1930. Brachiopods from the Upper and Middle Devonian of the Turkestan. *Mem. Com. Geol.*, n.s., 180, 1-221.
- 1936. The Middle Paleozoic faunas of the head parts of the Kolyma and Kandyga rivers in The Paleozoic faunas of the Kolyma. *Contr. to Knowledge of Okhotsk-Kolyana Land*, ser. 1, fasc. 4, *State Trust Dalstroy*, 1-28.
- 1960. New species of Devonian Atrypidae and Spiriferidae of the Arctic. *New species of fossil plants and invertebrates of the USSR*, pt. 1, 380-96, *All-Union Sci. Res. Geol. Inst. (VSEGEI)*, Moscow.
- NETTLEROTH, H. 1889. Kentucky fossil shells: a monograph of the fossil shells of the Silurian and Devonian rocks of Kentucky. *Kentucky Geol. Surv.* 1-245.
- NIKIFOROVA, O. I. 1937a. Upper Silurian fauna of the western Balkhash Land. *Contr. to Knowledge of western Balkhash Land, Central Geol. and Prospecting Inst., Moscow*, 11-36.
- 1937b. Brachiopods of the Upper Silurian of the central Asian part of the USSR, Pt. 1. *Mon. of Paleontology of USSR*, 35, 1-94.
- 1954. Stratigraphy and brachiopods of the Silurian series of Podolia. *Trav. United Res. Geol. Inst.* 1-218.
- NORTHROP, S. A. 1939. Paleontology and stratigraphy of the Silurian rocks of the Port Daniel-Black Cape Region, Gaspé. *Geol. Soc. Amer. Spec. Paper*, 21, 1-302.
- PAECKELMANN, W. 1925. Beiträge zur Kenntnis des Devons am Bosporus, insbesondere im Bithynien. *Abh. Preuss. Geol. Landesanst.*, n.f., 98, 1-152.
- POULSEN, C. 1934. The Silurian faunas of North Greenland, I. *Medd. om Grøn.* 72, 1, 1-46.
- 1943. The Silurian faunas of North Greenland, II. *Ibid.* 3, 1-59.
- PROUTY, W. F., and SWARTZ, C. K. 1923. Sections of the Rose Hill and McKenzie formations. *Maryland Geol. Surv., Sil.* 53-104.

- REED, F. R. C. 1906. The Lower Palaeozoic fossils of the northern Shan States, Burma. *India Geol. Surv. Mem., Pal. Indica*, n.s., 2, Mem. 3, 1-154.
- REGNELL, G., and HEDE, J. E. 1960. The lower Paleozoic of Scania, the Silurian of Gotland. *Internat. Geol. Congr., 21st Sess., Norden*, 1-87.
- ROEMER, F. 1860. *Die silurische fauna des westlichen Tennessee*. Breslau, 1-100.
- RZONSNITSKAYA, M. A. 1952. Spiriferidae of the Devonian series of the margins of the Kuznetsk Basin. *Trav. United Acad. and Res. Geol. Inst.* 1-232.
- ST. JOSEPH, J. K. S. 1935. A description of *Eospirifer radiatus* (J. de C. Sowerby). *Geol. Mag.* 72, 316-27.
- SCHMIDT, F. 1881. Revision der ostbaltischen Silurischen Trilobiten. *Mém. Acad. Imp. Sci. St.-Petersburg*, 7th ser., 30, abt. 1, 1-237.
- SCHUCHERT, CHARLES. 1913. Systematic paleontology of the Lower Devonian deposits of Maryland, Brachiopoda. *Maryland Geol. Surv., Lower Dev.*, 290-449.
- and COOPER, G. A. 1932. Genera of the suborders Orthoidea and Pentameroidea. *Mem. Peabody Mus. Nat. Hist., New Haven*. 4, 1, 1-270.
- SHIRLEY, J. 1938. The fauna of the Baton River beds (Devonian), New Zealand. *Quart. J. Geol. Soc. London*, 94, 459-506.
- SHROCK, R. R., and TWENHOFEL, W. H. 1939. Silurian fossils from northern Newfoundland. *J. Paleont.* 13, 3, 241-66.
- TERMIER, H. 1936. Études géologiques sur le Maroc Central et le Moyen Atlas Septentrional. *Serv. de Mines et Carte Géol.* 3, Notes et Mém., no. 33, Paléont. 1-1566.
- THOMAS, N. L. 1926. Brachiopods from the St. Clair limestone, Arkansas. *Denison Univ. J. Sci. Lab. Bull.* 21, 385-401.
- TILLMAN, C. G. 1961. Stratigraphy and brachiopod fauna of the Osgood formation, Laurel limestone, and Waldron shale of south-eastern Indiana. *Ph.D. thesis, Harvard Univ.*
- TOMCZYKOWA, E. 1959. Preliminary study of the Middle and Upper Ludlow stratigraphy in the Swiety Krzyz Mts. *Przegląd Geologiczny*, 7, 2 (71), 65-73.
- TSCHERNYCHEV, TH. 1893. Materialien zur Kenntniss der devonischen Fauna des Altaï. *Verh. Russ.-K. Min. Gesell.*, ser. 2, 30, 1-40.
- TWENHOFEL, W. H. 1928. Geology of Anticosti Island. *Canada Geol. Surv. Mem.* 154, 1-481.
- 1941. The Silurian of Aroostook County, northern Maine. *J. Paleont.* 15, 166-74.
- VASCAUTANU, TH. 1932. Formatiunile Siluriene din malul Romanesc al Nistrului. *Ann. Inst. Geol. Romaniei*, 15, 425-663.
- WANG, Y. 1956. New species of brachiopods (II). *Scientia Sinica*, 5, 3, 577-601.
- WELLER, S. 1903. The Paleozoic faunas. *New Jersey Geol. Surv., Paleont.* 3, 1-462.
- WILLIAMS, M. Y. 1919. The Silurian geology and faunas of Ontario Peninsula and Manitoulin and adjacent islands. *Canada Geol. Surv. Mem.* 111, 1-195.
- YERMOLAEV, M. M. 1937. Stratigraphy of palaeozoic deposits on Novaya Zemlya. *17th Internat. Geol. Cong., Novaya Zemlya Excursion*, Pt. 1st general, 91-134.

A. J. BOUCOT
 Division of Geological Sciences,
 California Institute of Technology,
 Pasadena, California, U.S.A.

POLYMORPHINIDAE FROM THE UPPER CRETACEOUS OF ENGLAND

by TOM BARNARD

ABSTRACT. Various Cretaceous species of Polymorphinidae have irregular fistulose end-chambers. Similar forms occur from the Jurassic to Recent. The Upper Cretaceous fistulose forms are considered to be abortive offshoots from either the chief smooth species or from the rarer ornamented forms. Their taxonomic significance and occurrence is discussed.

MEMBERS of the family Polymorphinidae are closely related to the Lagenidae (or Nodosariidae), possessing similar wall-structures, chamber-shapes and apertures, and differing only in the arrangement of the chambers. In the Lagenidae the chambers are usually arranged in a uniserial order, with the main axis being either straight, curved, or even planispiral, whereas in the Polymorphinidae the chambers are arranged in a spire about a vertical axis, but placed at angles about this axis.

Their morphological development and suggested evolution was dealt with by Cushman and Ozawa (1930) in a monograph of Recent and Tertiary forms. A classification was put forward based on the arrangement of the chambers in a large number of specimens, widely distributed both in space and time.

It would appear that the smooth, primitive forms, *Globulina* and *Guttulina*, have not only a long geological history, but also a wide distribution in various rocks. Some genera, particularly those occurring in Tertiary rocks and Recent oceans, are restricted in their distribution, becoming highly selective and specialized. Many of these species are greatly restricted in both vertical and horizontal range. Smooth forms appear to have long ranges, whereas ornamented genera do not range widely. This may be an illusion primarily due to the difficulty in differentiating between the smooth genera and species. It is clear that overlap occurs in many early 'species' of *Guttulina* and *Eoguttulina*, and specific determination is difficult.

It appears from the study by Cushman and Ozawa (1930) that although the family Polymorphinidae made its first appearance during the Trias, and the Jurassic forms representing the genus *Eoguttulina* were of an extremely simple plan, it was not until the Cretaceous that any generic diversity occurred. This view is oversimplified, for great diversity of form does occur in the Jurassic. Individual variation in the arrangement of the chambers is well seen in specimens from the Lias, Oxford Clay, and Kimeridge Clay of England. Many variants show a chamber arrangement identical to that in forms which do not appear as definite genera until late in the Cretaceous. However, whereas the Cretaceous species become well established, most of the Jurassic variants are short-lived and do not persist.

Most of the genera belonging to this family were represented before the end of the Cretaceous. Throughout the Jurassic and Cretaceous the species generally had their chambers arranged at angles around a vertical axis, and this, together with the shape of the chambers, tended to produce globular or fusiform tests. However, in Tertiary times

some forms (and occasional abnormal specimens from the Cretaceous) tended to have the chambers arranged biserially.

Although members of the Polymorphinidae occur sporadically throughout the Mesozoic rocks of England, they are generally rare except at scattered horizons where they may be extremely abundant.

The author has not observed any species with irregular or fistulose end-chambers occurring in Jurassic rocks, although they are recorded by Terquem (1864). Apparently fistulose forms do not occur until the Cretaceous. Many such forms have been recorded from the Lower and Upper Cretaceous rocks of both Europe and America, and specimens are also rare throughout Tertiary to Recent times.

Bullard (1953), in a paper on the 'Polymorphinidae of the Cretaceous (Cenomanian) Del Rio Shale' from Texas, records a number of fistulose forms and suggests that '. . . all the various modes of growth known to the family, such as free, attached, fistulose, tubulose, and racemose are represented in the Del Rio fauna. This evidence suggests that the family had reached a mature stage in its development long before the Tertiary. . . . The extensive development of the Polymorphinidae by Del Rio time reflects a rapid expansion of the family during the Washita. . . .' Tappan (1940, 1943) recorded eight species from the Duck Creek Formation (basal Washita), and ten from the Grayson Formation, whereas nineteen are recorded from the Cenomanian. This rapid increase in development also occurs throughout the Albian of southern England and is continued into the Cenomanian, although the big increase in number of species recorded from America is probably due to the setting up of many new species, which are, in fact, just variants of well-established forms. Little account of the variation has been taken in assigning specimens to species.

Bullard suggests by her naming that fistulose forms are new species and not variants of well-established, and often long-ranged, species. *Globulina fistulosa* Bullard (p. 342), although rare in the Del Rio Formation, differs from its contemporary species *Globulina lacrima* Reuss only in having a fistulose end-chamber. Also *Pyrulina cylindroides* (Roemer) appears to have a similar relationship to the fistulose *Pyrulina longa* (Tappan). From the foraminiferal occurrence charts of the Del Rio Formation it is apparent that in most cases the forms occur together in pairs, and their ranges are contemporaneous for the whole formation, except that the smooth forms have longer ranges, as might be expected.

The present author believes that fistulose forms, as well as many attached forms belonging to this family, are abortive variants of smooth, or in rare cases ornamented species, and should not be regarded as true species, for they are of sporadic occurrence and do not appear to have become firmly established. At certain horizons, however, the abnormal forms greatly increase in number, momentarily in time, and this may be due to internal or external environmental factors.

In the Albian of England as with the Washita of America, a number of fistulose forms occur, but in England the lithology is constant and does not appear to reflect any change in environment. Fistulose specimens also occur in the Cenomanian in England, and here with the rapidly changing lithologies it would be easy to invoke environmental changes to produce aberrant forms.

Throughout the Turonian and Senonian, fistulose forms occur rarely and sporadically until the *Belemnitella mucronata* zone, where a distinct shallowing of the sea took place,

as reflected by the more arenaceous nature of the Chalk. In some ways the residues from Chalk samples and the organic content resemble the Lower Cenomanian.

The continued shallowing of the *mucronata*-chalk is shown by the Maestrichtian of Holland. Here an abundance of various species of polymorphinids occurs, often with fistulose forms. In order to make the evolutionary history of the Polymorphinidae more complete, specimens have been figured from certain horizons within the Dutch sequence.

At other horizons besides the Upper Cretaceous, abnormal, fistulose, pustulose, or hispid forms occur belonging to a variety of different genera and species. It soon becomes apparent from a study of the literature and samples from numerous horizons from Lower Jurassic to Recent, that at scattered levels these abnormal forms are produced haphazardly. They are often few in number compared with the root form. They occur in the genera *Polymorphina*, *Pyrulina*, *Pyrulinoidea*, *Guttulina*, and *Globulina*. Forms ornamented with costae are extremely rare, and the majority of species are smooth or abnormally hispid, pustulose, or fistulose.

Terquem (1864), in his monograph on the Lias polymorphinids, figures two species, *Polymorphina breoni* Terquem and *P. cruciata* Terquem, and amongst the numerous figures given, a few forms occur showing hispid tests. The ornament covers all the test, and is not confined to the end-chambers only.

Amongst forms figured by Tappan (1940) from the Grayson Formation (Albian) is the species *Pyrulina longa* Tappan, an elongate form with a small but well-formed fistulose end. Tappan states (p. 114) 'aperture generally obscured by a fistulose growth which has openings at the ends of the tubes'. Apparently this species is non-hispid, non-pustulose, with well-marked sutures.

Certain Tertiary species are worthy of attention. *Globulina inaequalis* Reuss var. *spinata* Cushman and Ozawa from the Upper Oligocene bears strong spines or tubes over the whole surface, hence differing from the typical species. Terquem (1878, pl. 4, figs. 9–12) shows variation in *Globulina oviformis* Terquem, an Upper Pliocene species. Figs. 9, 10 show normal smooth forms, whereas figs. 11, 12 show numerous outgrowths which may be confined to the last chamber or distributed over the whole test. In the Tertiary of the Vienna basin d'Orbigny (1846) records *Globulina tubulosa* d'Orbigny (p. 228, pl. 13, figs. 15, 16), a smooth globular form with a stellate fistulose, but smooth outgrowth. Terquem (1878, p. 39, pl. 3, figs. 20, 21), in a monograph on the Upper Pliocene Foraminifera from Rhodes Island, shows one figure of *Polymorphina praelonga* Terquem to have a smooth fistulose outgrowth almost stellate in development.

A number of authors working on Recent forms have also recorded abnormalities. Williamson (1858, p. 72, pl. 6, fig. 150), when describing *Polymorphina lactea* (Walker) var. *fistulosa* Williamson, states '... develops numerous irregular expansion and tubular growths. Ends which frequently dichotomise are often open, but I believe this to be the result of accident, and that in their normal state they are mere cul-de-sacs.' This is contrary to the opinion of the present author, who has observed many open tubes in this group of fossils, some broken, but many well formed, and obviously serving as supplementary apertures.

Some species, for example *Polymorphina longicollis* Brady (1881, p. 64, pl. 73, figs. 18, 19), show later chambers only becoming hispid, coupled with the development of a long, single apertural neck, the latter often having a well-marked lip. Cushman (1923) shows

some specimens of *Polymorphina extensa* Cushman to have hispid ends with the apertures occurring on elongate narrow tubular necks.

Systematic descriptions of the various species from the Chalk are given below together with an account of the abnormalities in certain species. Specimens in the British Museum (Natural History) have the prefix BM.

SYSTEMATIC DESCRIPTIONS

Genus GLOBULINA d'Orbigny 1839

Genotype. *Polymorphina (Globulina) gibba* d'Orbigny.

The two genera *Apiopterina* and *Raphanulina* were proposed by Zborzewski 1834; both the figured specimens are fistulose forms. The former, with the monotypic species *Apiopterina d'Orbignyi*, appears to be a fistulose specimen of a species belonging to the genus *Pyrulina*, and the latter, *Raphanulina humboldtii*, belongs to the genus *Globulina*. However, the two genera *Apiopterina* and *Raphanulina* predate *Pyrulina* and *Globulina* respectively as pointed out by Galloway (1933), and it is possible that if the forms were accurately described (if the type specimens are still in existence), that they would replace the genera *Pyrulina* and *Globulina*.

On the grounds of common usage it is intended in the present paper to retain the genera *Pyrulina* and *Globulina*. Also, because the original descriptions take no account of the arrangement of the chambers it would be difficult to place these forms correctly.

The present author is of the opinion that the fistulose forms are abortive offshoots of more normal polymorphine species, and it is inadvisable to establish genera on this evidence.

Globulina lacrima Reuss

Text-figs. 1a, b, k, l

1845 *Polymorphina (Globulina) lacrima* Reuss, p. 40, pl. 12, fig. 6.

1891 *Polymorphina proteus* Beissel (pars), p. 59, pl. 11, figs. 1-6; pl. 13, fig. 83; pl. 12, figs. 9-16 (non 13).

1896 *Polymorphina gibba* d'Orbigny; Chapman, p. 9, pl. 2, fig. 5.

1930 *Polymorphina lacrima* Reuss; Cushman and Ozawa, p. 77, pl. 13, figs. 1, 2.

1930 *Polymorphina gibba* d'Orbigny; Hofker, p. 5, figs. 7-9.

1946 *Globulina lacrima* Reuss; Schijfsma, p. 66, pl. 7, fig. 2.

1951 *Globulina lacrima* Reuss; Visser, p. 241, pl. 4, fig. 7.

1957 *Globulina lacrima* Reuss; Hofker, p. 170, figs. 212, 213.

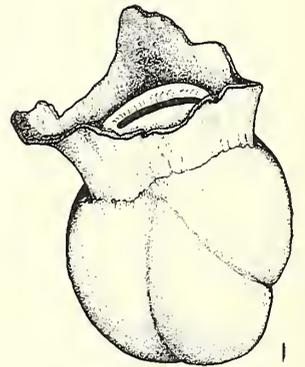
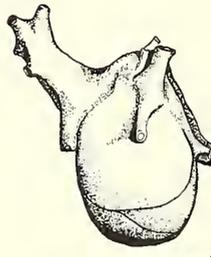
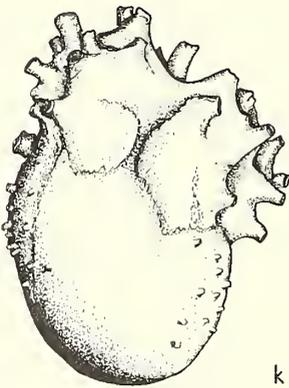
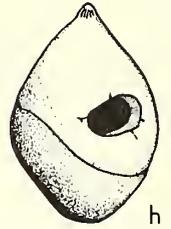
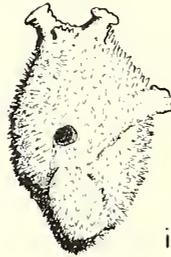
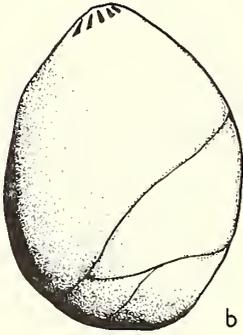
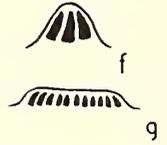
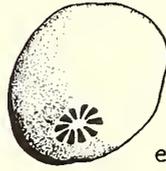
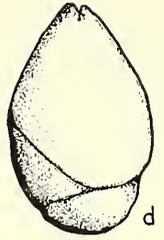
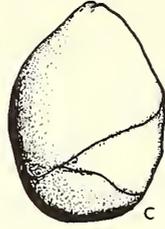
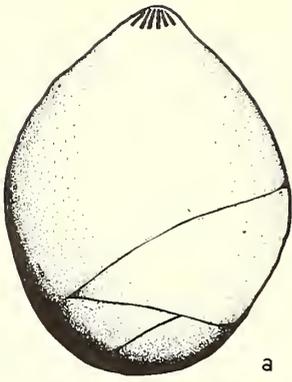
Globulina lacrima subsphaerica (Berthelin)

Text-figs. 1c-j, 3

1880 *Polymorphina subsphaerica* Berthelin, p. 58, pl. 4, fig. 18.

1957 *Globulina lacrima* Reuss var. *subsphaerica* (Berthelin); Hofker, p. 171, figs. 214, 215.

Description. The globular thick-walled smooth test shows little or no tendency to vary in shape. Smaller forms and early stages of the test show a tendency to be slightly elongated vertically. The curved sutures are flush with the surface of the test and rarely



show constrictions, so that the arrangement of the chambers is almost impossible to interpret. Occasional decorticated specimens show that there are few chambers, about five, constituting the test, and they are arranged irregularly about a vertical axis. Not only is the end-chamber large, making up one-half of the volume of the test, but it overlaps the earlier chambers.

Generally the aperture is radiate and situated on a conical protuberance, but often the aperture becomes elliptical. Numerous peculiar forms occur as offshoots from the main stock and some of these are described below.

Horizon. Zone of *Belemnitella mucronata*.

Dimensions of hypotypes:

Globulina lacrima, *a*: BM P44758. Height 1.14 mm., breadth 0.95 mm. (text-fig. 1*a*).

b: BM P44759. Height 1.06 mm., breadth 0.76 mm. (text-fig. 1*b*).

c: BM P44764. Height 1.14 mm., breadth 0.72 mm. (text-fig. 1*k*).

G. lacrima subsphaerica, *d*: BM P44760. Height 0.76 mm., breadth 0.60 mm. (text-fig. 1*c*).

e: BM P44761. Height 0.80 mm., breadth 0.53 mm. (text-fig. 1*d*).

f: BM P44762. Height 0.76 mm., breadth 0.46 mm. (text-fig. 1*i*).

g: BM P44763. Height 0.64 mm., to extension 0.84 mm., breadth 0.38 mm. (text-fig. 1*j*).

Localities. *a*, *b*, *g*: H. Attock's Pit, New Catton, Norwich, Norfolk.

d, *e*, *f*: Council's Pit, Newmarket Road, Norwich, Norfolk.

c: Earlham Limekiln, Dereham Road, Norwich, Norfolk.

The development of the Globulina lacrima Reuss group (text-fig. 2)

The writer considers that the large form *G. lacrima* Reuss, described above, is not the central root-stock of the group. A somewhat smaller, more abundant form, *G. lacrima* Reuss var. *subsphaerica* Berthelin, is considered to be the persistent and central form. This form is slightly elongated, but has the same general characters as *G. lacrima* Reuss, and ranges through the Upper Chalk. At certain horizons, as well as the abundant smaller tests, there occur specimens of *G. lacrima* Reuss, showing a tendency to become

TEXT-FIG. 1. All figs. $\times 90$, except *l* ($\times 150$).

a, *b*, *Globulina lacrima* Reuss; H. Attock's Pit, Norwich, Norfolk; *Belemnitella mucronata* Zone; normal large globular forms; *a*, BM P44758; *b*, BM P44759.

c-*j*, *Globulina lacrima* Reuss var. *subsphaerica* Berthelin; *Belemnitella mucronata* Zone. *c*, *d*, *i*, Council's Pit, Newmarket Road, Norwich, Norfolk; BM P44760, P44761, and P44762 respectively. *j*, H. Attock's Pit, Norwich, Norfolk; BM P44763.

c, *d*, common small variety;

e-*g*, showing variation of aperture;

h, broken wall to show thickness;

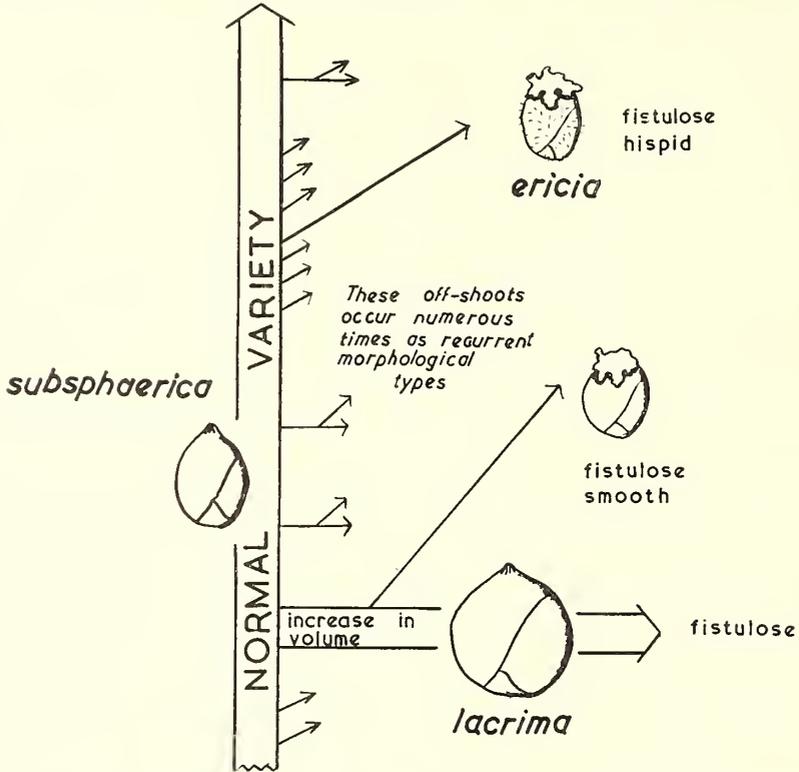
i, fistulose hispid variety;

j, smooth form with stellate fistulose chambers.

k, *Globulina lacrima* Reuss; Earlham Limekiln, Dereham Road, Norwich, Norfolk; *Belemnitella mucronata* Zone; BM P44764. Large form showing extremely complicated fistulose end-chamber with numerous apertures, also a tendency for pustules to develop along parts of the test wall.

l, *Globulina lacrima* Reuss, $\times 150$. Quarry at Curfs (near Houthem), near Maastricht, Holland; Beds *Md.*, Upper Maestrichtian; BM P44771. The specimen shows an early globular stage, followed by an irregular end-chamber. This later chamber has been broken to enable the earlier apertures to be seen. The final aperture of the globular portion shows distinct signs of resorption, changing from the normal radiate aperture to a long regular slit, following the general surface of the test.

almost spherical and to increase in size. This form rarely gives rise to fistulose forms. One of these (text-fig. 1*k*) shows the large globular test of *G. lacrima* Reuss, with an irregular pustulose ornament over the initial chambers. Later a large irregular stellate outgrowth occurs, spreading down the test. This fistulose last portion of the test has numerous tube-like prolongations, at the ends of which are circular apertures which often have small but thick lips. These tube-like extensions may be arranged irregularly



TEXT-FIG. 2. A diagrammatic representation of the variation and evolution of the *Globulina lacrima* Reuss var. *subsphaerica* Berthelin group.

over the surface, or placed along the stellate outgrowths. In both cases a wide coverage of the surface area is obtained.

Many authors have stated that these fistulose outgrowths are only the last chamber; however, specimens have been obtained where several chambers are involved and the irregular portion is not just an outgrowth from the last chamber. Also in some forms the fistulose portion stretches down almost to the initial chamber, and there are connexions through the wall of the test to earlier chambers. In these forms there is often a resorption of the internal septa or chamber walls, so that the test is almost 'unilocular', except for small but regular parts of the original walls. The regularity of these 'fragments' suggests resorption rather than subsequent alteration. The fistulose globular forms occur as sporadic offshoots from the large *Globulina lacrima* Reuss stock, and occur at disconnected levels.

Throughout the longer history of *Globulina lacrima subsphaerica*, offshoots arise with several variations. For convenience these are divided into three groups:

1. *Smooth test, with fistulose outgrowths* with:

- (a) an irregular arrangement of a few apertures;
- (b) a regular arrangement of the apertures;
- (c) a tendency for portions of the end-chambers to become tubular with bunched tubular apertures (text-fig. 3a);
- (d) sometimes a tendency for the tubular apertures to lie along the surface of the test (text-fig. 1j).

2. *Pustulose test*:

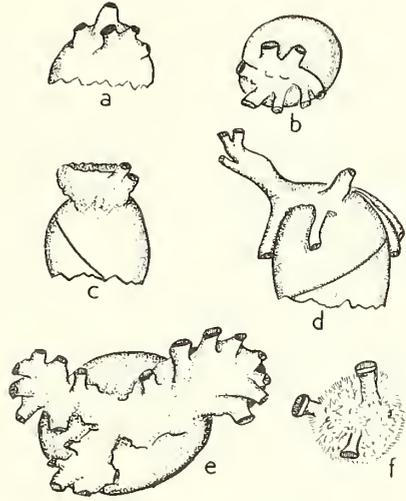
All the above types occur, but often with an irregular pustulose ornament; however, all the variants are rare.

3. *Hispid test*:

The test becomes increasingly hispid until the whole test is covered by a thick covering of small spines (text-fig. 1i). In this case the apertures are few in number, separated, and often raised well above the surface of the test and have well-developed lips.

The various arrangements and types of apertures are shown in text-fig. 3a-f. The evolution of this group of species is illustrated diagrammatically in text-fig. 2, which shows how the various morphological types fit into the pattern of development of the gens.

The dominant form or root-stock, *Globulina lacrima subsphaerica*, persists throughout the whole of the Chalk (Cenomanian to Maestrichtian). Its relative abundance varies considerably from horizon to horizon. This form gives rise repeatedly to large variants of the *G. lacrima* type, which show an increase in volume and a tendency, rarely developed, to produce fistulose, pustulose spherical forms. *G. lacrima subsphaerica* also produces smaller fistulose variants as recurrent morphological types. At scattered horizons, the smaller *G. lacrima subsphaerica* develops fistulose variants which have a hispid test ornamented by numerous short, fine spines, resembling *G. ericia* Cushman and Ozawa. A similar development has been observed by the author in specimens belonging to the gens from the Chalks of Germany, France, Holland, and Denmark.



TEXT-FIG. 3. Various apertures and fistulose outgrowths in *Globulina lacrima* Reuss var. *subsphaerica* Berthelin. a, b, Stellate arrangement of the fistulose portion. c, A small isolated outgrowth of the last chamber with only two apertures. d, The tubular apertures are either isolated and lie along the surface of the test, or are separated from it, but bunched together on a long tubular extension of the chamber. e, Stellate arrangement of numerous bunched apertural tubes. f, Hispid variety with single isolated lipped apertures.

Genus GUTTULINA d'Orbigny 1839

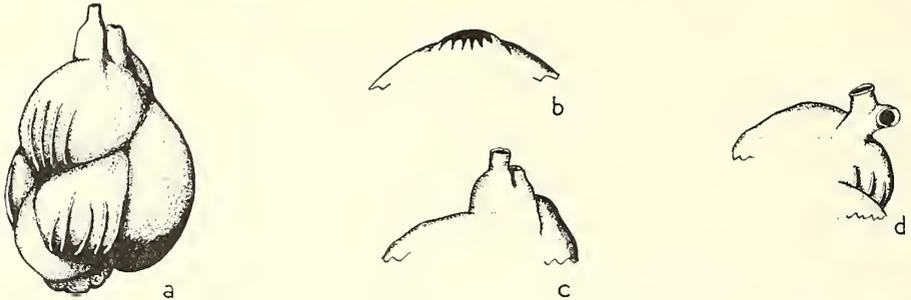
Genotype. Polymorphina (Guttulina) communis d'Orbigny.

Guttulina semicostata (Marsson)

Text-figs. 4a-d

- 1878 *Polymorphina semicostata* Marsson, p. 150, pl. 2, fig. 19a-c.
 1925 *Polymorphina semicostata* Marsson; Franke, p. 78, pl. 6, fig. 21.
 1930 *Guttulina semicostata* (Marsson); Cushman and Ozawa, p. 48, pl. 15, fig. 8.
 1948 *Guttulina spicaeformis* Roemer; Brotzen, p. 49, figs. 10, 11.
 1957 *Guttulina semicostata* (Marsson); Hofker, p. 167, fig. 206.

Description. The globular test is often slightly elongate with the broadest part more than half-way up the test. The initial end varies from broad obtuse to the more usual pointed end, a factor having a direct bearing on the ornament of the test. The chambers are rounded, inflated with well-marked, depressed sutures forming constrictions in the test.



TEXT-FIG. 4. *a*, *Guttulina semicostata* (Marsson); Earham Limekiln, Dereham Road, Norwich, Norfolk; *Belemnitella mucronata* Zone; BM P44765, $\times 90$. Fine costae developed on the lower portions of the chambers only. *b-d*, *Guttulina semicostata* (Marsson), showing variation in the aperture; *b*, radiate in the normal form; *c*, two tube-like apertures on an apertural chamberlet; *d*, bifurcating tube with circular apertures in the fistulose form, $\times 90$.

Usually the chambers do not embrace the earlier ones, and form a quinqueloculine series, as each successive chamber is added farther from the base. Often the initial end is triangular in plan view. The ornament varies considerably. In some forms the chambers are angular, with coarse, broad ribs running longitudinally along the angles, which are slightly removed from the sutures.

Occasionally a similarly shaped rib runs parallel to the main costae, so that there is an almost flattened part to the chamber between the two ribs. The flat valley may either be shallow or deep. In some specimens the ribs join at the base of the first chamber and, from the node thus formed, a small point extends. Often in these forms the ribs become less pronounced and even disappear towards the distal end. In other specimens with coarse costae, the ribs along the angles of the chambers bifurcate and sometimes a third rib is interposed. The costae on the chambers usually follow the shape of the chamber and then disappear towards the distal end of each chamber. Rarer forms with twelve fine ribs to each chamber occur, and these may belong to a different species, but one specimen was found in which the development of the ribs appears to be intermediate between the two forms above. The development of fistulose forms appears to be in its early stages in the specimens at the author's disposal, for only small 'chambers' occur on the final chamber. These influence the shape of the aperture, which is normally radiate, but becomes circular and lipped in fistulose forms and may even be multiple (text-fig. 4*b-d*).

Locality. Earlham Limekiln, Dereham Road, Norwich, Norfolk.

Horizon. Zone of *Belemnitella mucronata*.

Dimensions. Height 0.84 mm., breadth 0.46 mm.

Hypotype. BM P44765 (text-fig. 4a).

Guttulina trigonula (Reuss)

Text-fig. 5

1845 *Polymorphina trigonula* Reuss, p. 40, pl. 13, fig. 84.

1845 *Polymorphina damaecornis* Reuss, p. 40, pl. 13, fig. 85.

1891 *Polymorphina glommerata* Roemer; Beissel (pars), p. 62, pl. 12, figs. 21–29.

1951 *Guttulina trigonula* (Reuss); Visser, p. 239, pl. 4, fig. 5.

1957 *Guttulina trigonula* (Reuss); Hofker, p. 165, fig. 203.

Description. The small test consists of a few globular or slightly elongated chambers, with deep constrictions, so that each chamber is clearly seen. The initial end is rounded, and the proloculum does not have a spine attached. The test is smooth and no fistulose forms occurred in the specimens available to the author. The terminal aperture is radiate with triangular clefts opening into a central hole.

Locality. H. Attock's Pit, New Catton, Norwich, Norfolk.

Horizon. Zone of *Belemnitella mucronata*.

Dimensions. Height 0.76 mm., breadth 0.57 mm.

Hypotype. BM P44766 (text-fig. 5).

Remarks. Although Cushman and Ozawa (1930, p. 28, pl. 4, fig. 2) figure a form assigned to Reuss's species, the specimens are different and, moreover, come from the Gault Clay of Barnwell Pit near Cambridge. This is similar to the Cenomanian species described below.

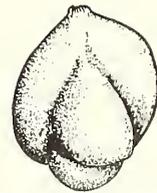
Guttulina sororia (Reuss)

Text-fig. 6a, b

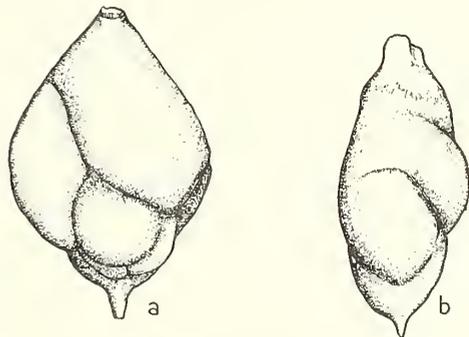
1862 *Polymorphina* (*Guttulina*) *sororia* Reuss, p. 121, pl. 2, figs. 25–29.

1896 *Polymorphina sororia* Reuss; Chapman, p. 12, pl. 2, fig. 11.

Description. The test is large, slightly compressed and elongated. The chambers, about seven in number, are easily visible because the sutures are deeply constricted. Earlier chambers tend to overlap. The initial chamber bears a characteristic strong conical spine. Usually the aperture is central, terminal and radiate, but occasionally there is a tendency for it to become multiple. This tendency shows the early stages of fistulose trend.



TEXT-FIG. 5. *Guttulina trigonula* (Reuss); H. Attock's Pit, New Catton, Norwich, Norfolk; *Belemnitella mucronata* Zone; BM P44766, $\times 90$.



TEXT-FIG. 6a, b. *Guttulina sororia* (Reuss); Sundon Lime Quarry, near Dunstable; *Schloenbachia varians* Zone, Cenomanian; showing the apiculate early chamber; BM P44767, $\times 90$.

Locality. Sundon Lime Quarry, near Dunstable.

Horizon. Zone of *Schloenbachia varians*.

Dimensions. *a*, Height 0.99 mm., breadth 0.65 mm. *b*, Height 1.03 mm., breadth 0.38 mm.

Hypotype. BM P44767 (text-fig. 6*a, b*).

Genus PYRULINOIDES Marie

Genotype. *Pyrulina acuminata* d'Orbigny, 1840.

Pyrulinoides acuminata (d'Orbigny)

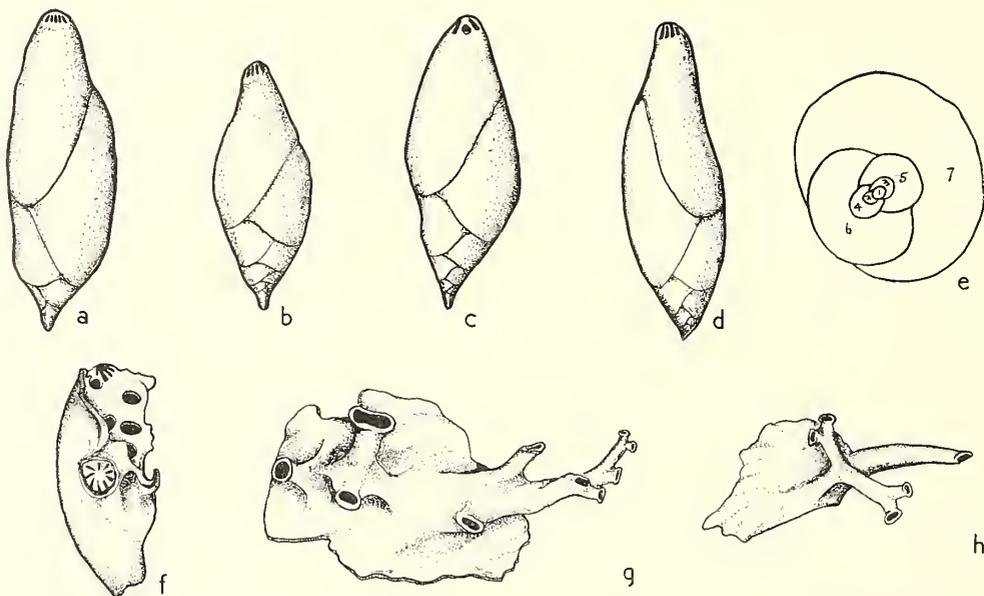
Text-figs. 7*a-h*

1840 *Pyrulina acuminata* d'Orbigny, p. 43, pl. 4, figs. 18, 19.

1941 *Pyrulinoides acuminata* (d'Orbigny); Marie, p. 170, pl. 24, figs. 243-50.

1957 *Pyrulinoides acuminata* (d'Orbigny); Hofker, p. 169, figs. 210, 211.

Description. The test is almost fusiform, long and narrow, the greatest breadth being at the centre. One side is slightly more bulbous than the other, making the test irregularly



TEXT-FIG. 7. *Pyrulinoides acuminata* (d'Orbigny). *a-d*, Council's Pit, Newmarket Road, Norwich, Norfolk; *Belemnitella mucronata* Zone; BM P44768, $\times 90$. *e*, Showing the development of the test, and chamber arrangement. *f*, Quarry at Curfs (near Houthem), near Maastricht, Holland; Beds *Md*, uppermost Maestrichtian; BM P44772, $\times 90$; broken to show part of the peculiar end-chamber, which has a small circular radiate aperture on a tube. The last chamber of the non-fistulose portion of the test shows part of the radiate aperture preserved, but over the remainder of the upper surface of the chamber a number of regular holes appear. It was originally thought that these may have been caused by an organism boring into the surface of the test. The holes, however, are confined to part only of the test, under the fistulose portion, and are not spread over the remainder of the surface. *g, h*, ?*Pyrulinoides acuminata* (d'Orbigny); Quarry at Curfs (near Houthem), near Maastricht, Holland; Beds *Md*, uppermost Maestrichtian; *g*, BM P44773, *h*, BM P44774; broken specimens to show the long extension and bifurcation of the apertural tubes and the presence of lips around the apertures, $\times 150$.

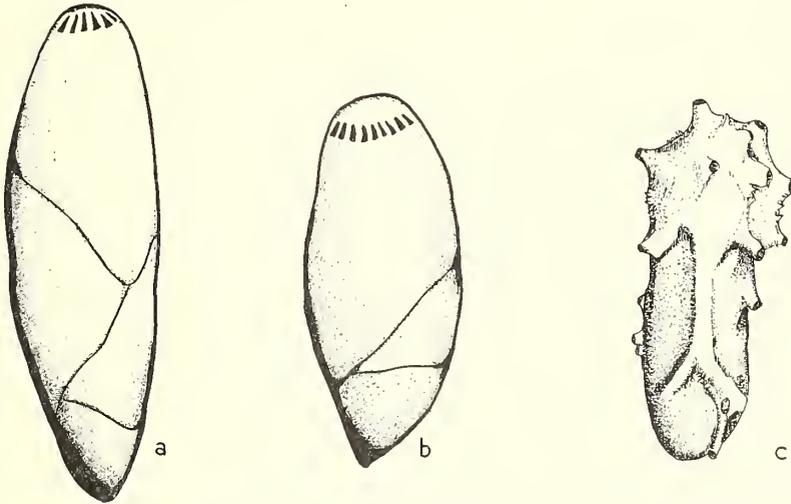
fusiform. Both the initial and apertural ends are pointed. The initial point is seen to contain several small chambers when the test is placed in aniseed oil. The end-chamber is large, elongate, and overlaps a considerable part of earlier chambers. The sutures are almost invisible, flush with the surface of the test, and show little or no constriction. The aperture is radiate, pointed, and sometimes occurs on a small prolongation of the end-chamber. No tendency towards a fistulose form was seen amongst numerous specimens.

Locality. Council's Pit, Newmarket Road, Norwich, Norfolk.

Horizon. Zone of *Belemnitella mucronata*.

Dimensions. *a*, Height 0.99 mm., breadth 0.38 mm. *b*, Height 0.91 mm., breadth 0.42 mm. *c*, Height 0.80 mm., breadth 0.38 mm. *d*, Height 0.99 mm., breadth 0.38 mm.

Hypotype. BM P44768 (text-figs. 7a-d).



TEXT-FIG. 8. *Pyrulina cylindroides* (Roemer). *a, b*, Council's Pit, Newmarket Road, Norwich, Norfolk; *Belemnitella mucronata* Zone; BM P44769, $\times 90$. *c*, Earlham Limckiln, Dereham Road, Norwich, Norfolk; *Belemnitella mucronata* Zone; BM P44770, $\times 90$; fistulose variety, with tubes extending back to the initial end of the test.

Genus PYRULINA d'Orbigny 1839

Genotype. *Polymorphina* (*Pyrulina*) *gutta* d'Orbigny.

Pyrulina cylindroides (Roemer)

Text-figs. 8a-c

- 1838 *Polymorphina cylindroides* Roemer, p. 385, pl. 3, fig. 26.
 1930 *Pyrulina cylindroides* (Roemer); Cushman and Ozawa, p. 56, pl. 14, figs. 1-5.
 1930 *Pyrulinella cylindroides* (Roemer); Hofker, p. 13, figs. 26-28.
 1951 *Sigmomorphina* sp. Visser, p. 248, pl. 3, fig. 2.
 1951 *Pyrulina cylindroides* (Roemer); Visser, p. 244, pl. 3, fig. 5.
 1957 *Pyrulina cylindroides* (Roemer); Hofker, p. 168, figs. 207-9.

Description. The elongate test is often almost fusiform or cylindrical in shape, but this depends largely upon the shape of the last chamber. The smooth test sometimes has

fistulose outgrowths on the end-chambers, and these may be either smooth, rough, or hispid. There are about five chambers with sutures either slightly constricted, or more usually flush with the surface of the test, and difficult to see except when immersed in oil. Later chambers do not overlap, but tend to be asymmetrical with one side sagging down towards the proloculum. Later sutures are almost parallel and the test becomes nearly uniserial. The terminal aperture is large and radiate, but often the radial triangular-shaped clefts composing the aperture are placed well down from the apex of the shell so that there is a solid calcite area in the centre of the aperture. The fistulose offshoots are described below.

Horizon. Zone of *Belemnitella mucronata*.

Dimensions and hypotypes:

- a, b*, BM P44769. Height: *a*, 1.56 mm.; *b*, 1.22 mm. Breadth: *a*, 0.49 mm.; *b*, 0.49 mm. (text-figs. 8*a, b*).
c, BM P44770. Height 1.22 mm., breadth 0.38 mm. (text-fig. 8*c*).

Localities. *a, b*, Council's Pit, Newmarket Road, Norwich, Norfolk.
c, Earham Limekiln, Dereham Road, Norwich, Norfolk.

Remarks. Cushman and Ozawa (1930, p. 56) show forms with a wide variation in shape, from cylindrical Upper Senonian specimens to fusiform types from the Albian. Most forms are cylindrical to fusiform, but not as pointed as in *Pyrulina acuminata* (d'Orbigny). Hofker's (1957) specimens are much more rounded at the initial end than Cushman's, and less cylindrical. However, a fairly wide variation does occur in shape, but more particularly in size.

The development of the Pyrulina cylindroides (Roemer) group

This group appears to range from the Albian to the top of the Senonian. From this long-ranged group, short-ranged forms with fistulose outgrowths arise at numerous horizons. These outgrowths seem to be less irregular than in *Globulina lacrima* (Reuss), and often show a regular connexion with earlier chambers. Forms with fistulose outgrowths often have the main part of the outgrowth with apertures concentrated on a globular end-chamber. This may be rough, or hispid with tubular apertures.

On some of these forms rib-like prolongations often extend down almost to the proloculum. These ribs have short tubular portions. When the shells possess these rib-like prolongations, the apertures along them penetrate earlier chambers. The main part of the test is smooth. Some varieties have a small, smooth, almost cylindrical early test with a blunt initial end. These have a hispid fistulose part of the test fitting on the end-chamber, and bearing tubular apertures having a stellate arrangement when viewed from the top.

Many specimens show resorption of early chambers suggesting that there is some connexion between this character and the unrestricted tubular apertures by the replacing of the constricted radiate aperture. This long-range stock shows fistulose outgrowths at numerous horizons, for example the Chalk Marl, Zone of *Schloenbachia varians*, from Dunstable (Bedfordshire); Zone of *Micraster cor-testudinarium* from Seaford Head (Sussex); and Zone of *Micraster cor-anguinum* from Northfleet (Kent).

Acknowledgements. The present work was carried out while the author was a Leverhulme Research

Fellow. Most of the material studied was part of the late Dr. A. W. Rowe's collection of Chalk Foraminifera in the British Museum of Natural History; the remainder was collected with the aid of a grant from the Central Research Fund of the University of London.

REFERENCES

- BEISSEL, I. 1891. Die Foraminiferen der Aachener Kreide. *Abh. preuss. geol. Landesanst.* **3**, 1-78, pl. 1-16.
- BERTHELIN, G. 1880. Sur les Foraminifères de l'étage Albien de Montclay (Doubs). *Mém. Soc. géol. Fr.* **5**, 1-87, pl. 1-3.
- BRADY, H. B. 1881. Notes on some of the reticularian rhizopoda of the 'Challenger' Expedition: Part 3. *Quart. J. micr. Sci.* **21**, 64, pl. 73.
- BROTZEN, F. 1936. Foraminiferen aus dem schwedischen untersten Senon von Eriksdal in Schonen. *Sver. geol. Unders. Avh.*, Ser. C, **396**, 1-206, pl. 1-8.
- 1948. The Swedish Palaeocene and its Foraminiferal Fauna. *Ibid.* **493** (*Årsb.* 42 (2)), 1-140, pl. 1-19.
- BULLARD, F. J. 1953. Polymorphinidae of the Cretaceous (Cenomanian) Del Rio Shale. *J. Paleont.* **27**, 338-46, pl. 45, 46.
- CHAPMAN, F. 1891-6. The Foraminifera of the Gault of Folkestone. *J. R. Micr. Soc.*, pts. i-x.
- CUSHMAN, J. A. 1923. The Foraminifera of the Atlantic Ocean. *Bull. U.S. nat. Mus.* **104**, pts. 1-8 (1918-31).
- 1946. Upper Cretaceous Foraminifera of the Gulf Coast Region of the United States and adjacent areas. *Prof. Pap. U.S. Geol. Surv.* **206**, 1-241, pl. 1-66.
- and OZAWA, Y. 1930. A monograph of the foraminiferal family Polymorphinidae, Recent and fossil. *Proc. U.S. nat. Mus.* **77**, 1-185, pl. 1-40.
- EGGER, J. G. 1899. Foraminiferen und Ostracoden aus den Kreidemergeln der Oberbayrischen Alpen. *Abh. bayer Akad. Wiss.* **21**, 1-230, pl. 1-27.
- FRANKE, A. 1925. Die Foraminiferen der pommerschen Kreide. *Abh. geol.-palaeont. Inst. Griefswald*, **4**, 1-96, pl. 1-8.
- 1928. Die Foraminiferen der Oberen Kreide Nord- und Mitteldeutschlands. *Abh. preuss. geol. Landesanst.* **3**, 1-208, pl. 1-18.
- GALLOWAY, J. J. 1933. *A manual of Foraminifera*. Bloomington (Indiana), 1-483, pl. 1-42.
- HOFKER, J. 1930. Die Foraminiferen aus dem Senon Limburgens: X, Die Polymorphinen der Maestrichter Kreide. *Natuurh. Maandbl., Limburg*, Jaarg. **19**.
- 1957. Foraminiferen der Oberkreide von Nordwestdeutschland und Holland. *Beih. Geol. Jb.* **27**, 1-464, 495 text-figs.
- MARIE, P. 1941. Les Foraminifères de la craie à *Belemnitella mucronata* du Bassin de Paris. *Mém. Mus. Nat. Hist. nat.*, Paris, N.S., **12**, 1-296, pl. 1-37.
- MARSSON, T. 1878. Die Foraminiferen der weissen Schreibkreide der Insel Rügen. *Mitt. naturw. Ver. Griefswald*, **10**, 115-96, pl. 1-5.
- ORBIGNY, A. D'. 1826. Tableau méthodique de la classe des Céphalopodes. *Ann. Sci. nat.* **7**, 245-314, pl. 10-17.
- 1840. Mémoire sur les Foraminifères de la Craie Blanche du Bassin de Paris. *Mém. Soc. géol. Fr.* **4**, 1-51, pl. 1-4.
- 1846. *Foraminifères fossiles du Bassin tertiaire de Vienne*. Paris, 1-312, pl. 1-21.
- REUSS, A. E. 1845. *Die Versteinerungen der böhmischen Kreideformation*. Stuttgart. **1**, 25-40, 55-58, pl. 8, 12, 13; **2**, 106-10, pl. 24.
- 1862. Les Foraminifères du crag d'Anvers. *Bull. Acad. Belg. Cl. Sci.* (2), **15**, (1863), 137-62, pl. 2, figs. 25-29.
- ROEMER, F. A. 1838. Die Cephalopoden des Nord-Deutschen tertiären Meersandes. *Neues Jb. Min. Geogn. Geol. Paläont.* 381-94, pl. 3.
- 1842. Neue Kreideforaminiferen. *Ibid.* 272-3, pl. 7.
- SCHIJFSMA, E. 1946. The Foraminifera from the Hervian (Campanian) of Southern Limburg. *Meded. geol. Sticht.*, Ser. C (5), **7**, 1-174, pl. 1-10.

- TAPPAN, H. 1940. Foraminifera from the Grayson Formation of Northern Texas. *J. Paleont.* **14**, 93-126, pl. 14-19.
- 1943. Foraminifera from the Duck Creek Formation of Oklahoma and Texas. *Ibid.* **17**, 476-517, pl. 77-83.
- TERQUEM, O. 1864. *Quatrième mémoire sur les Foraminifères du Lias. Polymorphines.* Metz, 234-308, pl. 11-14.
- 1878. Les Foraminifères et les Entomostracés — Ostracodes du Pliocène supérieur de l'Île de Rhodes. *Mém. Soc. géol. Fr.* (3), **1**, 1-133, pl. 1-14.
- VISSER, A. M. 1951. Monograph on the Foraminifera of the type-locality of the Maestrichtian (South-Limburg, Netherlands). *Leid. Geol. Meded.* **16**, 197-360, pl. 1-15.
- WILLIAMSON, W. C. 1858. On the Recent Foraminifera of Great Britain. *Ray. Soc. Publ.* 1-107, pl. 1-7.
- ZBORZEWSKI, A. 1934. Observations microscopiques sur quelques fossiles rares de Podolie et de Volhynie. *Nouv. Mém. Soc. Nat. Moscou*, **4**, 311.

TOM BARNARD
Department of Geology,
University College,
Gower Street,
London, W.C. 1.

Manuscript received 6 December 1961

CHAZYAN (ORDOVICIAN) LEPTOTRYPELLID AND ATACTOTOECHID BRYOZOA

by JUNE R. P. PHILLIPS ROSS

ABSTRACT. In Chazyan dolomitized biohermal reef complexes the bryozoans *Atactotoechus chazyensis* sp. nov. and *A. kayi* sp. nov. range throughout the standard Chazyan Series in the type section in north-eastern New York State and also occur on Isle La Motte, Vt. These primitive species of *Atactotoechus* considerably extend the geologic range of this genus (hitherto regarded as Devonian and early Carboniferous?) downward into middle Ordovician strata.

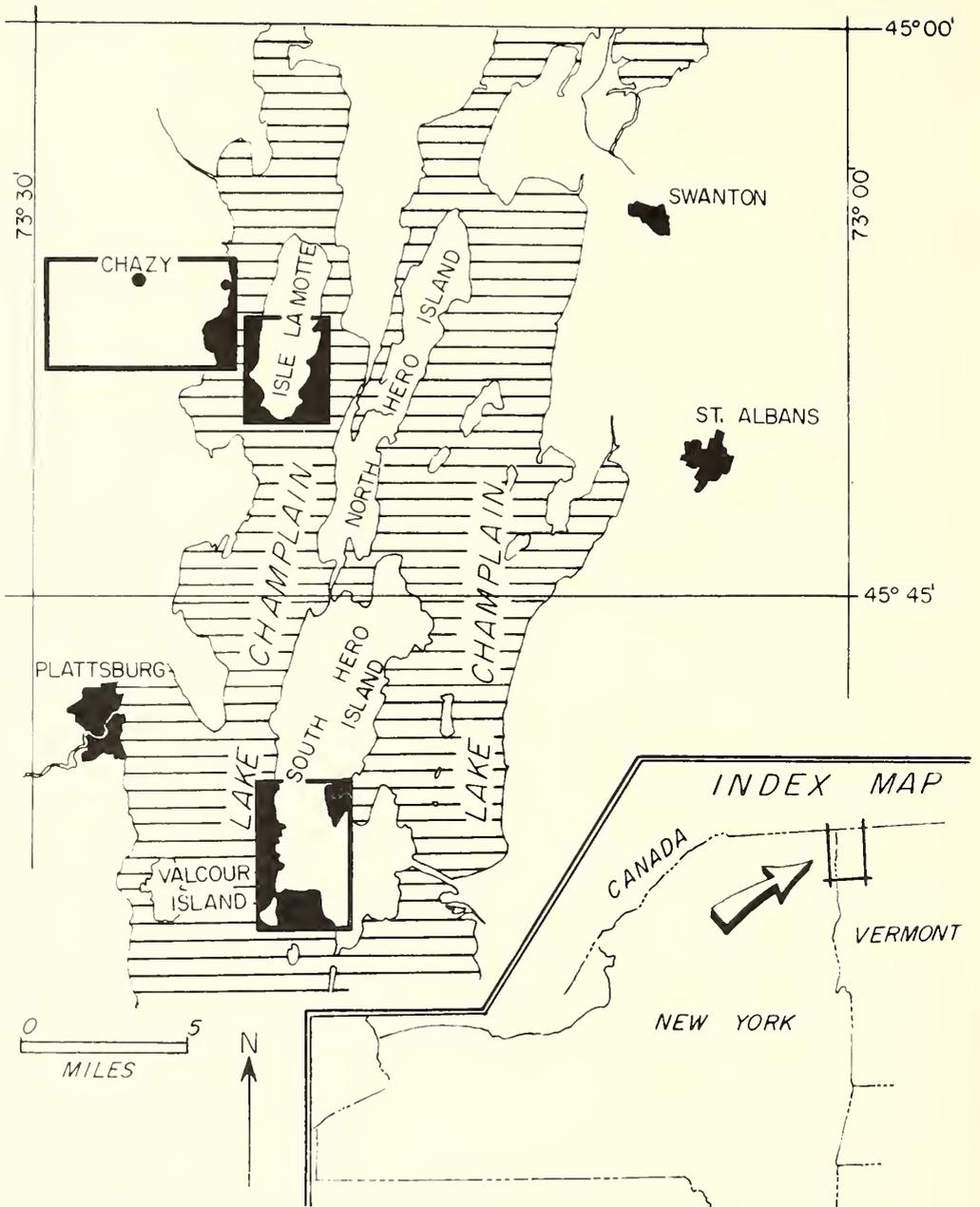
Jordanopora gen. nov. appears to be a primitive representative of the leptotrypellids and the single species, *J. heroensis* sp. nov., occurs in the Chazyan Series near Chazy, on Isle La Motte, and South Hero Island.

IN north-eastern New York State around Chazy and on Isle La Motte and South Hero Island, western Vermont (text-figs. 1-5), the Chazy Formation contains numerous trepostome and cryptostome Bryozoa (Ross, in press).

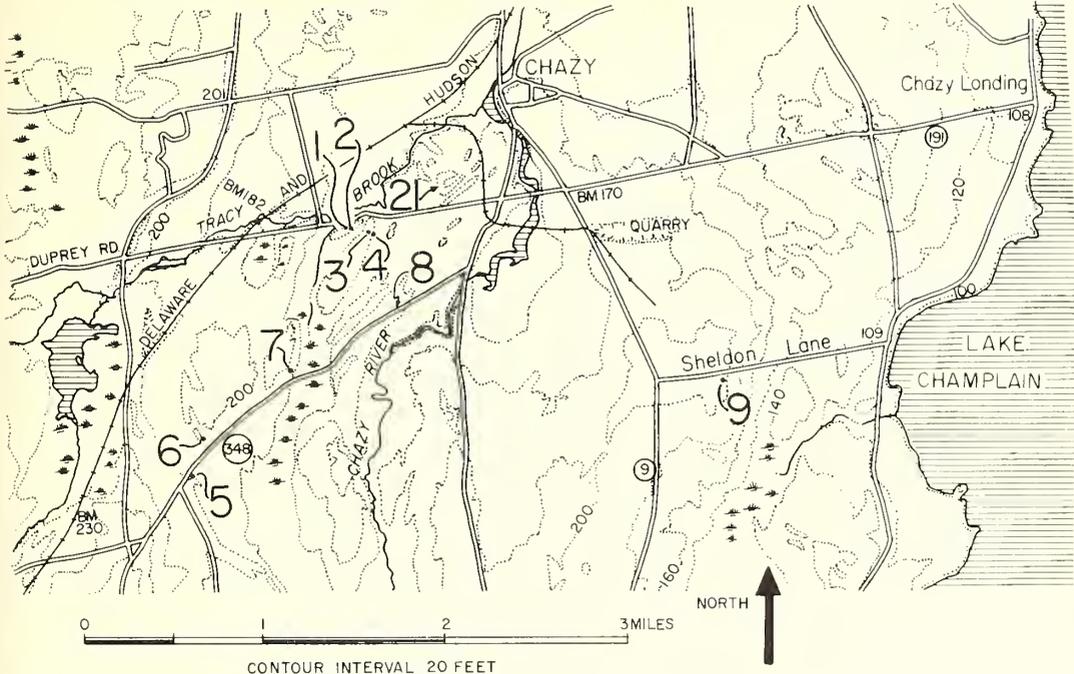
The trepostomes are well distributed through the 470 feet of strata in the type Chazy Formation (text-fig. 5). *Atactotoechus chazyensis* sp. nov., the oldest representative of this genus, ranges through member A and the lower part of member B. *A. kayi* ranges from the middle part of member B into the upper part of member C. These species occur principally in dolomitic calcarenites of a biohermal reef complex. The fragments of colonies of Bryozoa and other shell and plant material, and the poor sorting of these algal-bryozoan biosparites (limestone classification of Folk 1959), suggest shallow water deposition of the sediments in a high wave-energy environment such as on a reef flat or on the front slope of a reef. *A. chazyensis* is also present on southern Isle La Motte, and at localities 13 and 14 spectacular colonies 5 to 6 feet in diameter dominate the outcrops. Farther north, at Jordan Point, the species is abundant in a bryozoan bioherm. *A. kayi* sp. nov., which has not been found outside the type Chazy section, is the younger of the two species of *Atactotoechus* and differs from *A. chazyensis* in the sparse number of irregularly arranged diaphragms which are present only in the peripheral region and are absent in the axial region of a colony.

The new genus *Jordanopora*, which appears to be one of the earliest representatives of the leptotrypellids, has not been found in the type Chazy section but occurs in Chazyan strata at Sheldon Lane 2 miles to the east and is again found near Holcomb Point and Jordan Point, Isle La Motte, and at a single locality on South Hero Island.

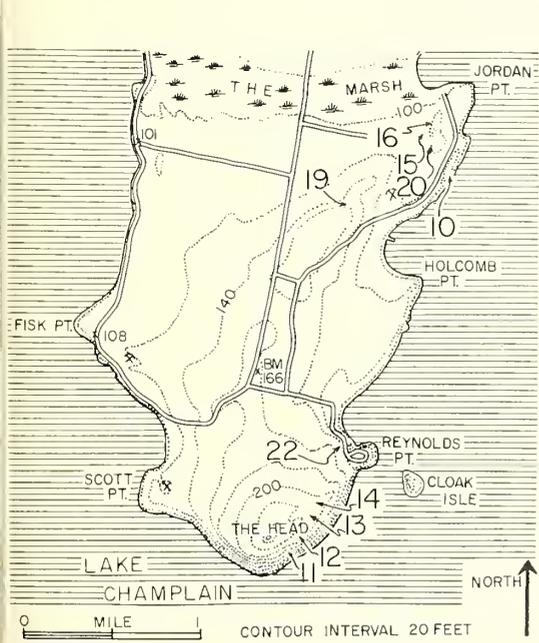
Duncan (1939) erected the family Atactotoechidae based on Devonian species of *Atactotoechus* and noted (ibid., p. 184) that this genus was allied to Ordovician and Silurian trepostomes of several different families. Boardman (1960) distinguished the atactotoechid group in his study of Devonian trepostomes from the Hamilton Group of New York State. The Ordovician species of *Atactotoechus* are similar in the microstructures of their integrate zoecial walls to the Devonian species and the morphology of the diaphragms and mesopores is also similar in the two groups of species. The Ordovician species, however, lack acanthopores with steeply inclined laminate walls which are reported in some Devonian species of *Atactotoechus*. *Amplexopora*, in which



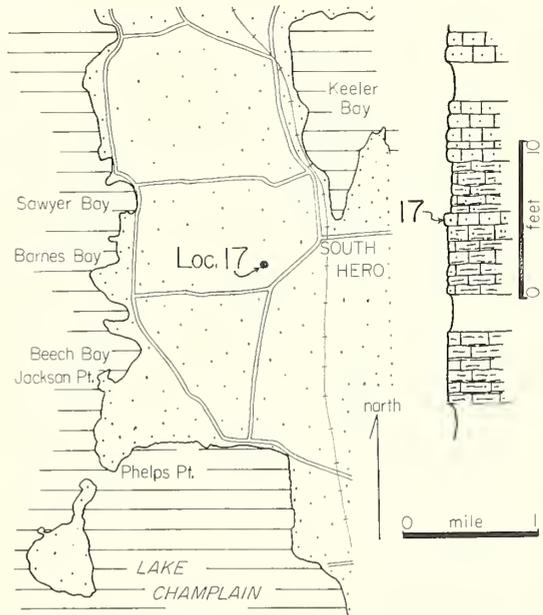
TEXT-FIG. 1. Index maps of Chazy, Isle La Motte, and South Hero Island.



TEXT-FIG. 2. Map of Chazy area showing collection localities.



TEXT-FIG. 3. Map of Isle La Motte showing collection localities.



TEXT-FIG. 4. Map of South Hero Island showing collection locality.

acanthopores are a distinct morphologic feature, appears to be a divergent lineage from the main atactotoechid group.

Jordanopora appears to be a primitive member of the leptotrypelliid group and *Anaphragma* may be a later Ordovician offshoot of this group. The main leptotrypelliid stock is well defined in the Devonian, where it is represented abundantly in such assemblages as those from the Traverse Group of Michigan (Duncan 1939) and the Hamilton Group of New York State (Boardman 1960).

Acknowledgements. I express my sincere thanks to Dr. G. A. Cooper and Dr. R. S. Boardman of the United States National Museum for the loan of bryozoan specimens and to Dr. C. A. Ross, Illinois State Geological Survey, for helpful discussions on bryozoan taxonomy. I gratefully acknowledge financial support for this study by a grant from the National Science Foundation.

Repository. Peabody Museum, Yale University (abbreviated to YPM).

SYSTEMATIC DESCRIPTIONS

Leptotrypelliid group

The microstructure of the zooecial walls was used by Boardman (1960, p. 51) to distinguish the leptotrypelliid group. The inner parts of the zooecial walls are composed of steeply inclined, distally sloping laminae which pass indistinctly into the amalgamate outer parts formed by adjacent zooecia. The amalgamate outer parts display distally convex laminae.

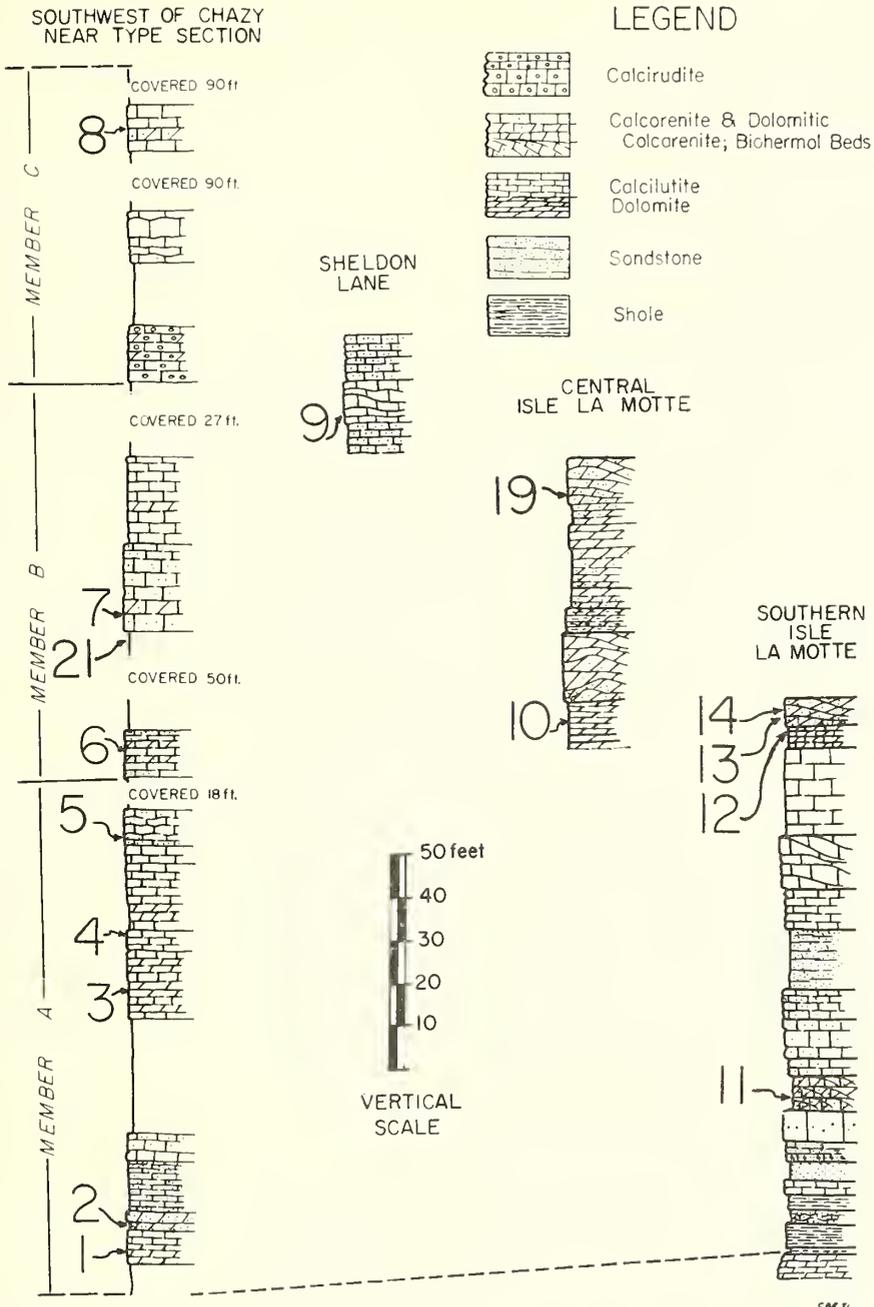
Genus JORDANOPORA gen. nov.

Type species. *Jordanopora heroensis* sp. nov.

Definition. Colonies are ramose or incrusting. Round zooecial openings are separated by wide, amalgamate laminate walls. In tangential sections the outer amalgamate parts of the zooecial walls are penetrated by very numerous small pores. Small mesopores are sparse between zooecia. In longitudinal sections the slender, crenulate, longitudinally laminate zooecial walls in the axial region pass into a narrow peripheral region of thickened zooecial walls. These thickened zooecial walls consist of laminae lying for a short distance parallel to the direction of the zooecial tube, then inclining steeply to the zooecial boundary. Near the zooecial boundary the laminae have a distally convex curvature and the boundary of adjacent zooecia consists of an intertonguing of these curved wall laminae. In the peripheral region the boundary is penetrated by small pores that have broadly curved, distally convex laminate wall structure. The laminae of the sparse diaphragms in the zooecial tubes enter the zooecial walls and follow the same pattern as other wall laminae. The numerous laminate diaphragms in the mesopores enter the zooecial walls in a similar manner.

Occurrence. Chazyan of Chazy area, N.Y., Isle La Motte, Vt., and South Hero Island, Vt.

Discussion. The wall structure in *Jordanopora* appears to be a forerunner of the more distinctive wall structure of *Leptotrypella*, in which the intertonguing distally convex laminae of the outer parts of adjacent zooecia are more clearly defined as a single unit than in *Jordanopora*. The steeply inclined laminae of the inner parts of the zooecial walls



TEXT-FIG. 5. Measured sections in Chazy Formation in Chazy area, N.Y., and Isle La Motte, Vt. Locality numbers indicate the position of collections. Members A, B, and C in the section measured at Chazy correspond to the subdivision of strata by Brainerd and Seely (1888).

in *Leptotrypella* are similar to those found in such diverse genera as *Anaphragma*, *Atactotoechus*, *Batostoma*, and *Amplexopora*.

Jordanopora heroensis sp. nov.

Plate 105, figs. 1–8; Plate 106, figs. 1–4, 6, 7

Type material. Holotype YPM 22233 and paratype YPM 22252, Chazy Formation; locality 17. Paratype YPM 22234, Chazy Formation; locality 16. Paratypes YPM 22235, YPM 22253, Chazy Formation; locality 15. Paratype YPM 22254, Chazy Formation; locality 10.

Description. The ramose colonies have slender zoarial stems of greatly variable diameter (Pl. 105, fig. 6; Pl. 106, figs. 1, 3) on which overgrowths are commonly present (Pl. 105, figs. 3, 5, 7; Pl. 106, figs. 3, 4, 6).

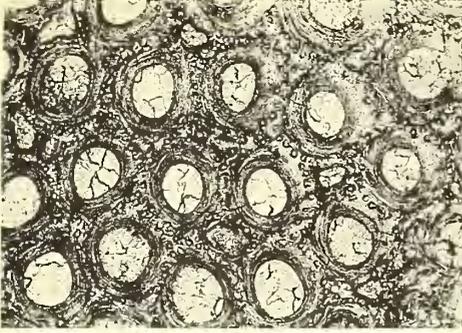
In tangential sections the amalgamate zooecial walls are almost as wide as the round zooecial openings (Pl. 105, fig. 1). Numerous very closely spaced and irregularly aligned small pores, about thirty per zooecial opening, are present in the amalgamate outer parts of zooecial walls (Pl. 105, figs. 1–3). The small pores have clear axial regions and very slender, laminate walls. Small polygonal mesopores are sparsely distributed between the zooecial openings. Very deep tangential sections (left side of Pl. 105, fig. 4) display slender walls in which laminae are indistinct and mesopores that are more distinct than in shallower tangential sections.

In longitudinal sections the zooecial walls are very slender, undulate, and longitudinally laminate in the axial region. As the walls curve gently to the periphery they thicken and mesopores appear (Pl. 105, fig. 7; Pl. 106, fig. 6). The typical laminate zooecial wall structure in the peripheral region is displayed (Pl. 105, fig. 8; Pl. 106, figs. 2, 4, 7). The flat or distally concave laminate diaphragms, which are sparse in the zooecial tubes, are commonly thin. In the mesopores, where the flat or distally concave diaphragms are more closely spaced, the laminae are thicker (Pl. 106, figs. 2, 7). The small pores are bounded by low undulations in the zooecial wall laminae (Pl. 106, fig. 2).

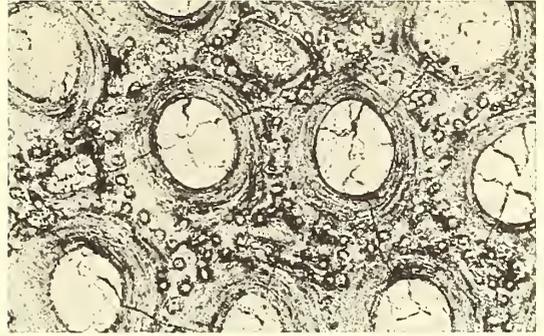
Occurrence. In the Chazy Formation *Jordanopora heroensis* is abundant at localities 16 and 22, Isle La Motte, and locality 17, South Hero Island. It is common at localities 10, 19, and 20, Isle La Motte, and rare at localities 9 and 21 near Chazy and locality 15, Isle La Motte.

EXPLANATION OF PLATE 105

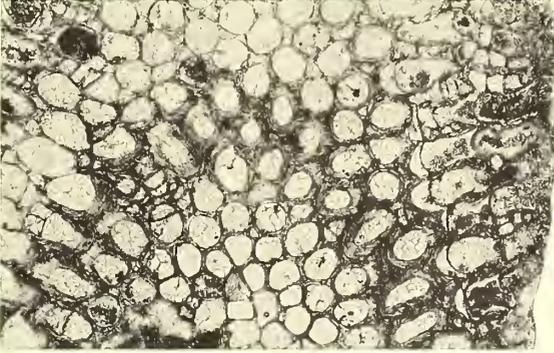
Figs. 1–8. *Jordanopora heroensis* sp. nov. 1, Shallow tangential section showing zooecial openings, mesopores, and pores, holotype YPM 22233, $\times 50$. 2, Enlarged view of tangential section showing amalgamate zooecial walls pierced by numerous pores, YPM 22233, $\times 100$. 3, Oblique transverse section showing arrangement of zooecial tubes and mesopores, YPM 22233, $\times 20$. 4, Oblique tangential section showing thin-walled zooecia and mesopores toward the base of the thickened peripheral region, YPM 22233, $\times 50$. 5, Oblique longitudinal section of a zoarial stem with an overgrowth that extends back toward the proximal part of the colony, YPM 22233, $\times 20$. 6, Longitudinal section showing tabulate mesopores in peripheral region of colony, YPM 22234, $\times 20$. 7, Longitudinal section showing slender, crenulate walls in axial region, the thickened peripheral region, and an incrustation, YPM 22233, $\times 20$. 8, Part of a longitudinal section in peripheral region showing laminate structure of zooecial walls, YPM 22233, $\times 100$.



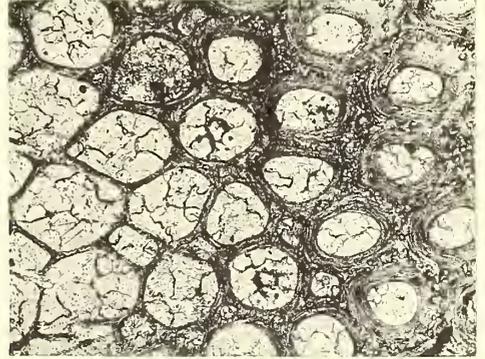
1



2



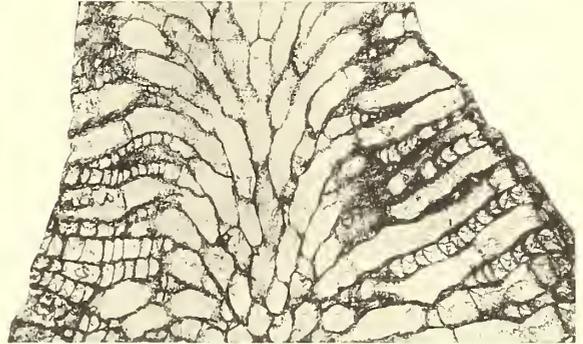
3



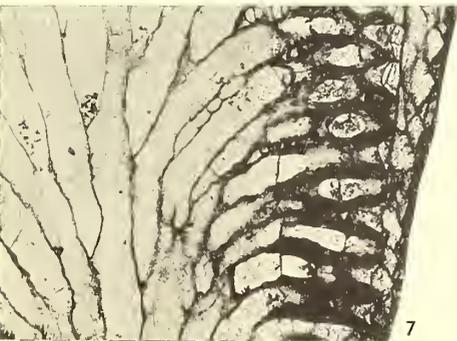
4



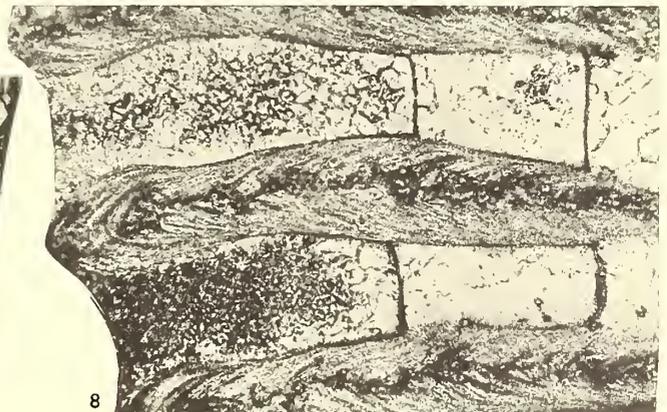
5



6



7



8

Remarks. The species is characterized by its narrow peripheral regions in which the zoecial walls are moderately but abruptly thickened; the diaphragms are sparse in the peripheral parts of the zoecial tubes, but are more numerous in the small mesopores; zoecial walls are crenulate throughout their length; and zoecia are polygonal and occasionally quadrate in the axial region.

TABLE 1

Measurements of *Jordanopora heroensis* sp. nov. in mm.

<i>Catalogue no.</i>	YPM 22233 <i>holotype</i>	YPM 22234
Diameter of zoarium	2.5 to 5.0	2.5 to 3.0
No. of zoecia per 2 mm. longitudinally	6 to 8	7 to 8
Diameter of zoecial opening	<i>max.</i> 0.15 × 0.10 <i>min.</i> 0.06 × 0.05	<i>max.</i> 0.18 × 0.10 <i>min.</i> 0.12 × 0.12
Pores per zoecium	30	30
No. of mesopores per zoecium	2 to 3	2 to 4
Diameter of mesopores	<i>max.</i> 0.08 × 0.06 <i>min.</i> 0.04 × 0.04	<i>max.</i> 0.08 × 0.08 <i>min.</i> 0.04 × 0.04
No. of diaphragms in a mesopore	7 to 12	8 to 14
No. of diaphragms in peripheral region of a zoecial tube	1 to 3	1 to 4
Width of peripheral region	0.8 to 1.0	0.8 to 1.0
Ratio: width of zoecium in peripheral region/total width of zoecium	0.40 to 0.48	0.42 to 0.44

The zoecial wall structure in *Jordanopora heroensis* appears allied to that in the leptotrypelliid group. However, the outer parts of the zoecial walls lack a wide band of convexly curved laminae. The small pores in *J. heroensis* differ markedly from the acanthopores in some Devonian species of *Leptotrypella* which have steeply inclined laminae forming their walls. Such acanthopores are absent in *Jordanopora*. Species of *Jordanopora* have a zoecial wall structure that is similar to *Anaphragma*, but they differ in lacking acanthopores with steeply inclined laminae and in having mesopores and numerous small pores.

Atactotoechid group

Emended definition. In longitudinal sections the laminae of the zoecial walls are almost parallel to the well-defined inner boundary of the zoecial tube. They extend distally and develop only a slight inclination so that laminae of adjacent zoecia abut at angles of less than ninety degrees and form a distinct boundary line. Laminae forming the diaphragms enter the zoecial walls and follow the same steep, distal inclination as the other wall laminae.

In tangential sections the walls are generally integrate but the zoecial boundary may be demarcated by a Beckè line instead of a dark boundary.

Acanthopores are sparse or lacking and, if present, are small. Diaphragms are a distinctive feature and are curved, cystoidal, or compound. Cystiphragms may be present. (After Boardman 1960.)

Genus *ATACTOTOECHUS* Duncan

1939 *Atactotoechus* Duncan, p. 190.

1960 *Atactotoechus* Duncan; Boardman, pp. 69, 70.

Type species. *Atactotoechus typicus* Duncan, 1939, p. 190.

Emended definition. Colonies are ramose, massive, or encrusting. Zoecial walls are laminate and intermittently thickened and display typical atactotoechid wall structure. Mesopores are sparse. Acanthopores having laminate wall structure are few or absent, usually restricted to monticules or groups of larger zooecia. Diaphragms commonly are curved or cystoidal and are present in varying abundance. Cystiphragms are very rare. (After Duncan 1939, and Boardman 1960.)

Range. Chazyan (Ordovician) of New York State and Vermont. Middle Devonian of New York State and Michigan. Upper Devonian of Kuznetsk Basin and Kitar, U.S.S.R. Lower Carboniferous? of the Lingling District, China.

Remarks. In a thorough study of Devonian trepostomes from the Traverse Group of Michigan Duncan (1939) noted that these Devonian trepostomes and certain Ordovician and Silurian trepostomes have various similar morphological features and that this presented possible conflicts in the systematics, depending on which structures were selected as significant. *Atactotoechus chazyensis* sp. nov. and *A. kayi* sp. nov. from the standard Chazyan are two Ordovician species that pose such taxonomic problems. They are ramose colonies which have integrate laminate zoecial walls which display microstructures similar to those observed in Devonian species from the Traverse Group, and both groups of species are closely similar in the arrangement and structure of their diaphragms and in the sparseness of mesopores and cystiphragms. The two Ordovician species lack acanthopores with steeply inclined laminate walls, which are found in some Devonian species. *A. chazyensis* and *A. kayi* appear to be early species of the genus *Atactotoechus*.

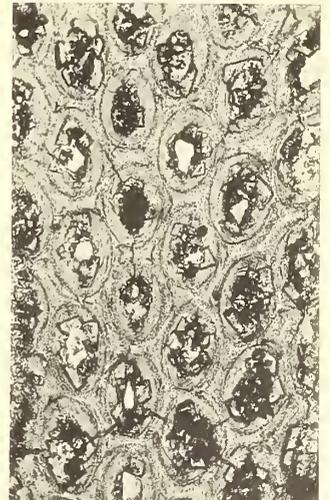
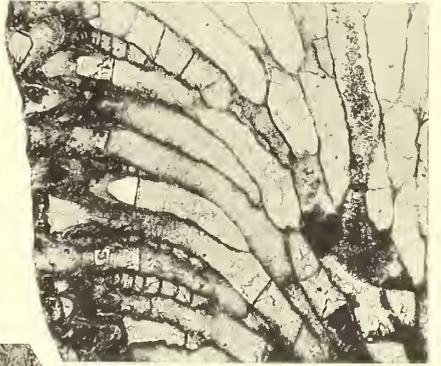
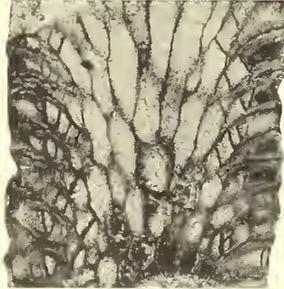
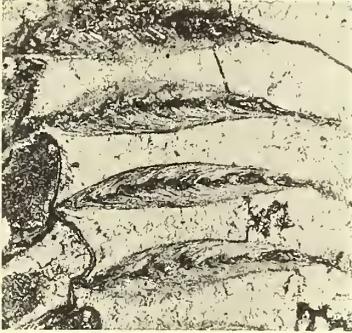
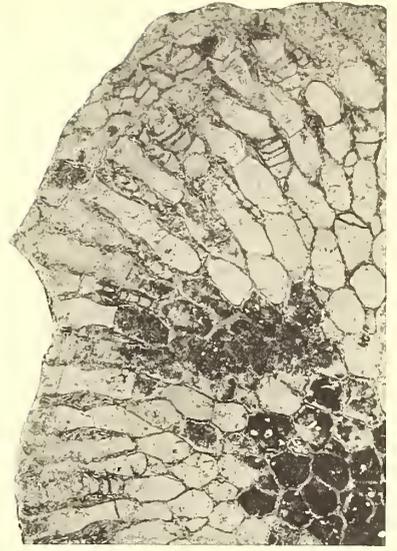
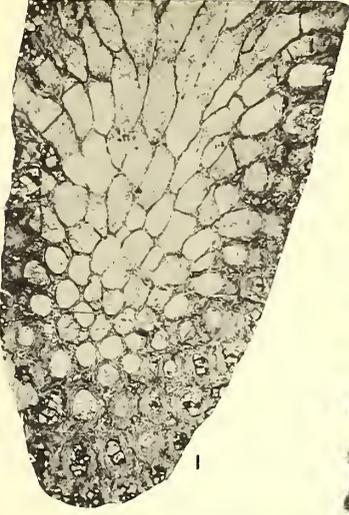
Atactotoechus chazyensis sp. nov.

Plate 107, figs. 6–10; Plate 108, figs. 1–11

Type material. Holotype YPM 22249 and paratypes 22250, 22256 to 22259, Chazy Formation; locality 13. Paratypes YPM 22240, 22246, member A of Chazy Formation; locality 1. Paratypes YPM 22260

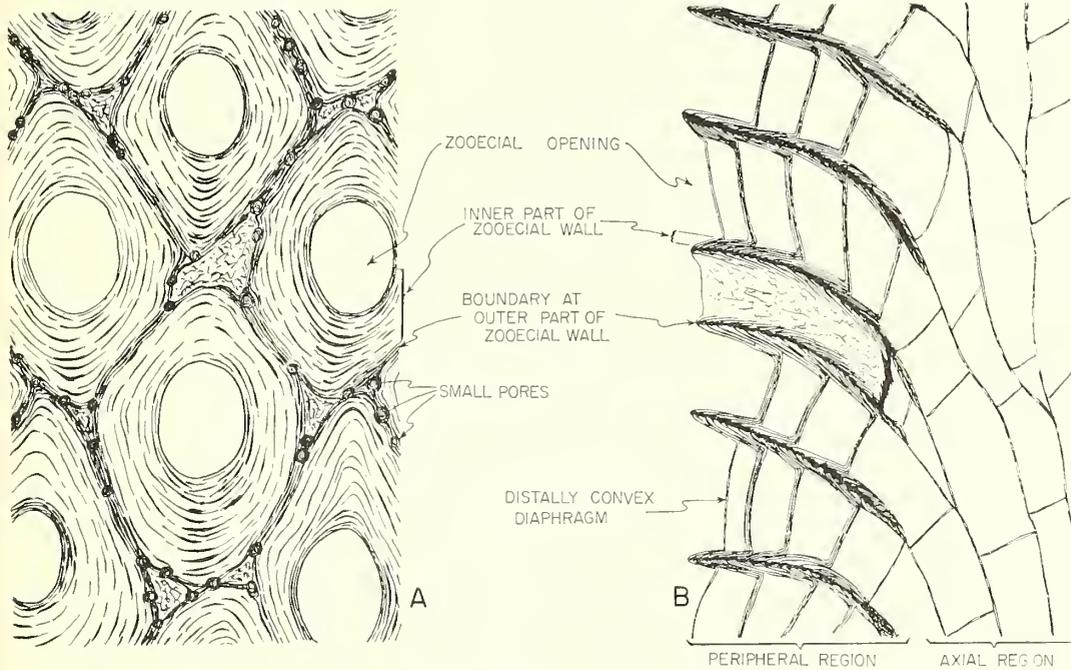
EXPLANATION OF PLATE 106

- Figs. 1–4, 6, 7. *Jordanopora heroensis* sp. nov. 1, Oblique transverse section showing narrow axial and peripheral regions of slender zoarial stem, YPM 22235, $\times 20$. 2, Oblique longitudinal section showing laminate diaphragms and pores that pierce thickened zoecial walls, YPM 22233, $\times 50$. 3, Part of a transverse section of a zoarial stem, YPM 22233, $\times 20$. 4, Laminate zoecial walls in peripheral part of colony; note overgrowth covering the zoecial openings, YPM 22233, $\times 50$. 6, Longitudinal section showing slender, undulate zoecial walls in axial region and thickened zoecial walls and mesopores in peripheral region YPM 22233, $\times 20$. 7, Part of longitudinal section at base of peripheral region showing laminate diaphragms and laminate zoecial walls, YPM 22233, $\times 100$.
- Figs. 5, 8, 9. *Atactotoechus kayi* sp. nov. 5, Longitudinal section showing irregularly arranged and sparsely distributed diaphragms in peripheral region, holotype YPM 22236, $\times 20$. 8, Oblique tangential section showing arrangement of zoecial tubes and integrate zoecial walls, YPM 22236, $\times 20$. 9, Tangential section showing laminate, integrate zoecial walls and oval zoecial openings YPM 22237, $\times 50$.



to 22263, near base of member A of Chazy Formation; locality 2. Paratypes YPM 22243, 22247, 22251, near top of member A in the Chazy Formation; locality 5. Paratypes YPM 22241, 22244, Chazy Formation; locality 11. Paratypes YPM 22248, 22264, 22265, Chazy Formation; locality 14.

Description. Colonies are ramose or incrusting. Many colonies carry overgrowths of commonly two layers and some of these overgrowths display erratic structures. In shallow tangential sections (Pl. 108, figs. 2, 3, 5; text-fig. 6A) the zooecial walls may be considerably wider than the small oval or round zooecial openings. The polygonal



TEXT-FIG. 6. Microstructures in zooecial tubes and zooecial walls of *Atactotoechus chazyensis* sp. nov. $\times 60$. A, Tangential section. B, Longitudinal section.

boundary between the laminate, integrate zooecial walls is generally identifiable as a dark, irregular line punctuated by small pores (Pl. 108, figs. 2, 3, 5; text-fig. 6A). These pores, at least ten per zooecium, may appear as dense circles (Pl. 108, fig. 2), but in some tangential sections the axial regions of those pores are clear (Pl. 108, fig. 5). In deeper tangential sections the integrate zooecial walls are very distinct and the small mesopores (four to six per 2.5 sq. mm.) are scattered between zooecia (Pl. 108, fig. 1). Acanthopores are absent.

In transverse sections a colony has varying aspects, depending on whether the colony is cut across zooecial walls (Pl. 107, fig. 9; Pl. 108, fig. 11) or across the zooecial tubes (Pl. 108, fig. 4).

In longitudinal sections the zooecial tubes in the axial region curve broadly to the periphery, where they obliquely meet the zoarial surface. In the axial region the zooecial walls are longitudinally laminate. They thicken as the tubes curve to the periphery, where

they display typical atactotoechid wall structure (Pl. 107, fig. 7; Pl. 108, fig. 7; text-fig. 6B). Flat diaphragms are regularly spaced throughout the zooecial tubes of the axial region, but become more closely spaced and include cystoidal and compound forms in the peripheral region. In colonies where the peripheral region is wide the zooecial walls are more strongly thickened (compare Pl. 107, fig. 6 and Pl. 108, figs. 8, 9, 10, with Pl. 107, fig. 7). The slender mesopores that appear in the subperipheral region and extend to the periphery have closely spaced, flat diaphragms (Pl. 107, fig. 6; Pl. 108, figs. 6, 10).

Remarks. The species is characterized by slender, ramose zoaria that have numerous, flat diaphragms in the axial region as well as in the peripheral region. Comparison with *Atactotoechus kayi* is made in remarks on that species.

Occurrence. *Atactotoechus chazyensis* is abundant at localities 1 and 5 in the type section of the formation, at localities 11, 12, 13, 14, 16, and 22 on Isle La Motte, and at locality 17 on South Hero Island. It is common at localities 2, 6, and 18 near Chazy, and at locality 15 on Isle La Motte and is rare at locality 3 in the type section near Chazy, and locality 10, Isle La Motte.

EXPLANATION OF PLATE 107

Figs. 1–5. *Atactotoechus kayi* sp. nov. 1, Part of longitudinal section showing sparsely distributed and irregularly arranged diaphragms in peripheral region, YPM 22236, $\times 50$. 2, Longitudinal section of cylindrical zoarium showing wide axial region without diaphragms, YPM 22238, $\times 20$. 3, Deep tangential section showing integrate, polygonal zooecial walls, YPM 22239, $\times 20$. 4, Part of longitudinal section showing laminate zooecial walls bounded by irregular, dark line, and cystoidal diaphragms in zooecial tubes, YPM 22238, $\times 50$. 5, Tangential section showing integrate zooecial walls forming polygons around oval zooecial openings, YPM 22237, $\times 20$.

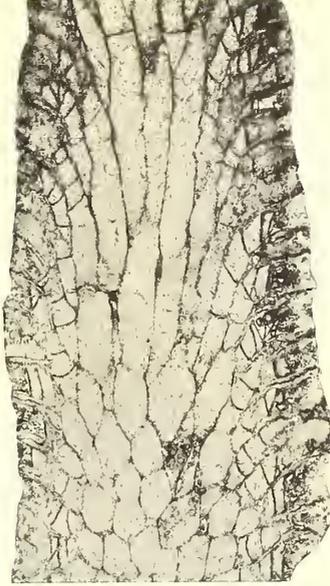
Figs. 6–10. *Atactotoechus chazyensis* sp. nov. 6, Longitudinal section showing abundant diaphragms throughout zooecial tubes, YPM 22240, $\times 20$. 7, Longitudinal section showing strongly thickened zooecial walls in peripheral region, YPM 22241, $\times 20$. 8, Oblique transverse section of slender zoarial stem, YPM 22242, $\times 20$. 9, Transverse section showing integrate zooecial walls in peripheral region, YPM 22243, $\times 50$. 10, Transverse section of cylindrical zoarium encrusted by broad laminate form, YPM 22244, $\times 20$.

EXPLANATION OF PLATE 108

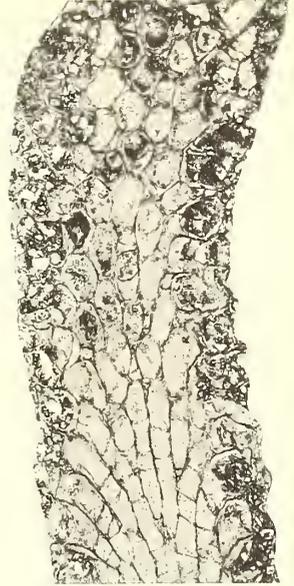
Figs. 1–11. *Atactotoechus chazyensis* sp. nov. 1, Deep tangential section showing laminate, integrate walls between zooecial tubes and mesopores, YPM 22245, $\times 50$. 2, Shallow tangential section showing dense, laminate, integrate walls and small pores penetrating zooecial boundaries, YPM 22246, $\times 50$. 3, Shallow tangential section showing arrangement of zooecia, YPM 22246, $\times 20$. 4, Transverse section showing well-defined axial and peripheral regions and numerous diaphragms (flat, curved, and cystoidal) in zooecial tubes, YPM 22247, $\times 50$. 5, Tangential section showing well-defined pores at zooecial boundaries, YPM 22248, $\times 50$. 6, Part of longitudinal section showing closely spaced diaphragms in zooecial tubes and mesopores, holotype YPM 22249, $\times 20$. 7, Part of longitudinal section showing laminate, integrate zooecial wall structure and laminate diaphragms entering into zooecial walls, YPM 22241, $\times 50$. 8, Part of longitudinal section showing flat diaphragms in axial region and flat, cystoidal, and compound diaphragms in peripheral region, YPM 22250, $\times 20$. 9, Oblique longitudinal section of slender zoarial stem, YPM 22251, $\times 20$. 10, Longitudinal section showing regular arrangement of diaphragms, YPM 22240, $\times 20$. 11, Transverse section showing laminate wall structure and distinctive zooecial wall boundaries, YPM 22255, $\times 50$.



1



2



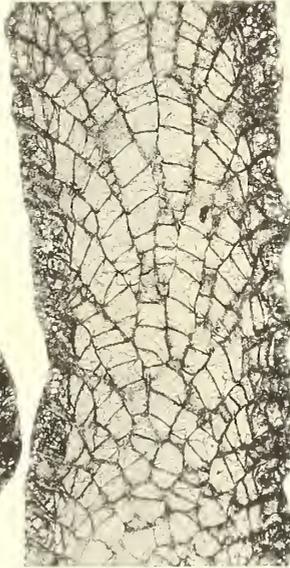
3



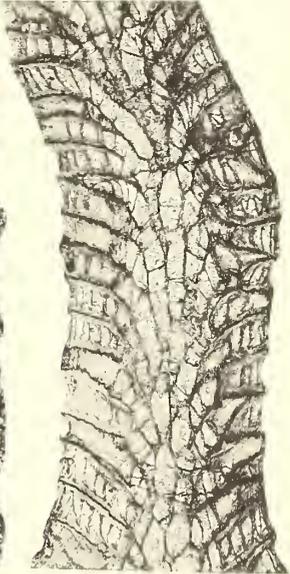
4



5



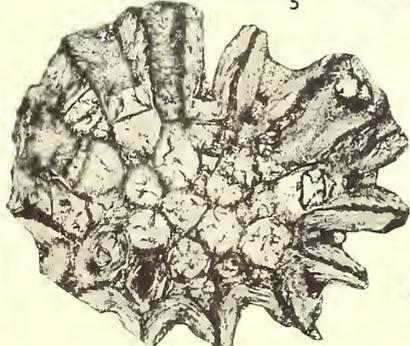
6



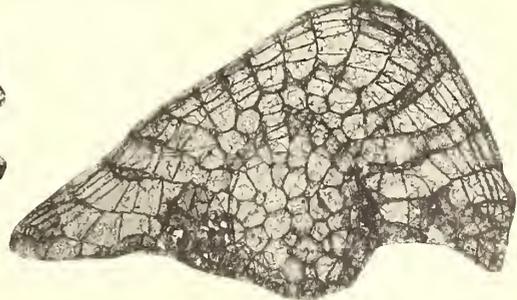
7



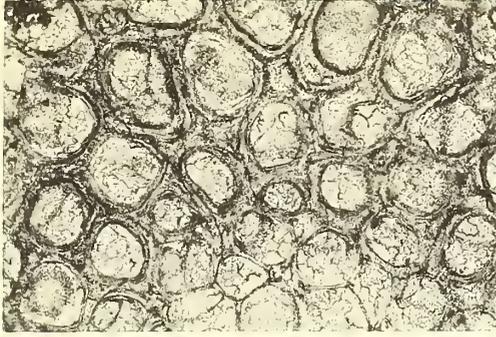
8



9



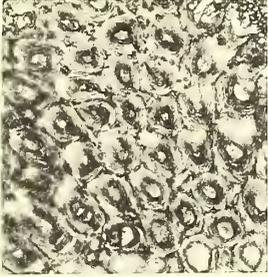
10



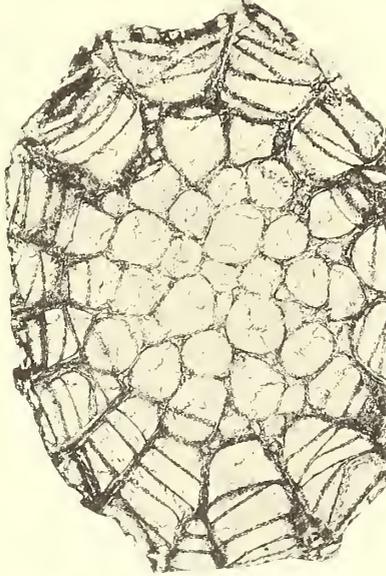
1



2



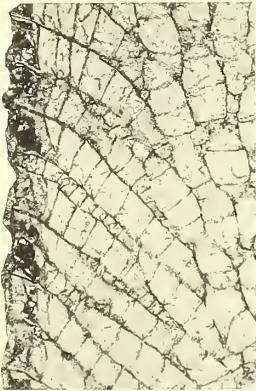
3



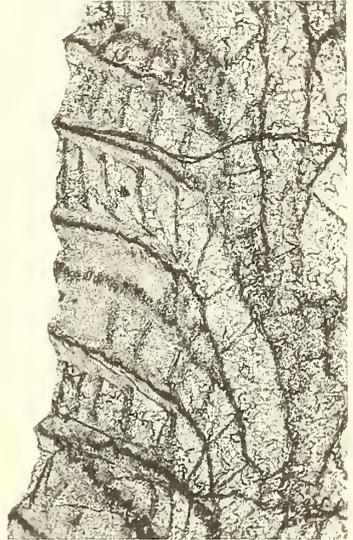
4



5



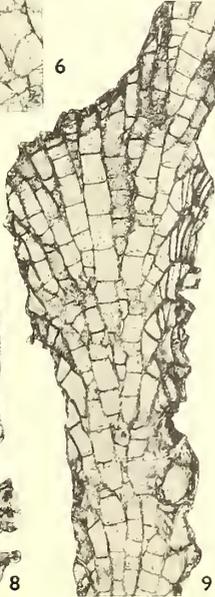
6



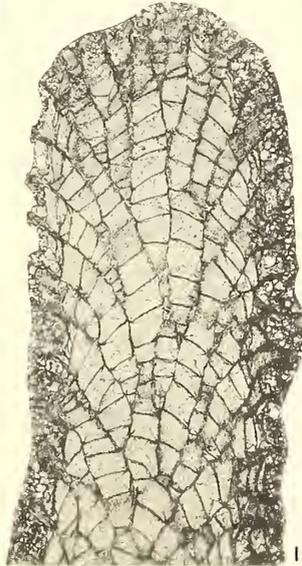
7



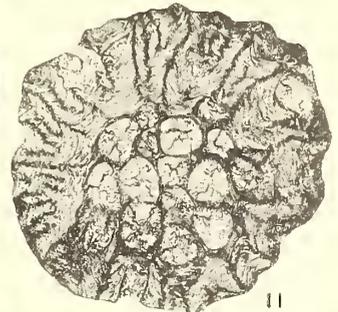
8



9



10



11

TABLE 2

Measurements of *Atactotoechus chazyensis* sp. nov. in mm.

<i>Catalogue no.</i>	YPM 22249 <i>holotype</i>	YPM 22248
Diameter of zoarium	2 to 4	2 to 2.7
No. of zooecia per 2 mm. longitudinally	7 to 8	6 to 7.5
Diameter of zooecial opening	<i>max.</i> 0.26 × 0.20 <i>min.</i> 0.17 × 0.17	<i>max.</i> 0.19 × 0.16 <i>min.</i> 0.11 × 0.05
Pores per zooecium	0 to 5	0 to 10
No. of mesopores per zooecium	0 to 3	0 to 2
Diameter of mesopores	<i>max.</i> 0.10 × 0.06 <i>min.</i> 0.08 × 0.04	<i>max.</i> 0.08 × 0.05 <i>min.</i> 0.05 × 0.04
No. of diaphragms in a mesopore	6 to 10	7
No. of diaphragms in peripheral region of a zooecial tube	5 to 8	4 to 7
No. of diaphragms in axial region of a zooecial tube	8 to 10	8 to 11
Width of peripheral region	0.44 to 0.50	0.44 to 0.47
Ratio: width of zooecium in peripheral region/total width of zooecium	0.40 to 0.45	0.33 to 0.38
Combined zooecial wall thickness between adjacent zooecial openings	0.05 to 0.09	0.06 to 0.09

Atactotoechus kayi sp. nov.

Plate 106, figs. 5, 8, 9; Plate 107, figs. 1-5

Type material. Holotype YPM 22236, member C of Chazy Formation; locality 8. Paratypes YPM 22237 and 22238, near base of member B in Chazy Formation; locality 18. Paratype YPM 22239, in member B of Chazy Formation; locality 7.

Description. Colonies are ramose (Pl. 107, figs. 2, 5) or encrusting. In tangential sections the integrate zooecial walls are narrower than the zooecial openings. Commonly the round zooecial openings are regularly arranged in longitudinal series around the zoarial stem (Pl. 106, fig. 9; Pl. 107, fig. 5). Acanthopores were not observed and mesopores, if present, are very sparse. The zooecial walls are very distinctly integrate and the boundary between adjacent zooecia is marked by a Beckè line (Pl. 106, fig. 9).

In longitudinal section in the axial region the thin, longitudinally laminate, zooecial walls are undulate and the zooecial tubes lack diaphragms (Pl. 106, fig. 5; Pl. 107, fig. 2). In the subperipheral region the zooecia arch gently and a diaphragm may be present in the zooecial tube. In the peripheral region the zooecial tubes are inclined obliquely to the zoarial surface, the thickened zooecial walls display the atactotoechid microstructure and irregularly spaced, curved, cystoidal, or compound diaphragms are present.

Occurrence. The species is common at localities 7, 8, and 18 near Chazy village.

Remarks. The colonies of *Atactotoechus kayi* are small (1.8 to 4.0 mm. diameter) for the genus. The species is characterized by undulate zooecial walls in the axial and peripheral regions; by zooecial walls that are distinctly thickened in the peripheral region; by diaphragms that are generally absent in the axial region and sparse and irregularly arranged in the peripheral regions; and by the lack of acanthopores and mesopores.

The species differs from *A. chazyensis* in lacking diaphragms in the axial region and

TABLE 3

Measurements of *Atactotoechus kayi* sp. nov. in mm.

<i>Catalogue no.</i>	YPM 22236 <i>holotype</i>	YPM 22239
Diameter of zoarium	1.8 to 2.5	2 to 2.5
No. of zooecia per 2 mm. longitudinally	8 to 9.5	8.5 to 9
Diameter of zooecial opening	<i>max.</i> 0.21 × 0.14 <i>min.</i> 0.13 × 0.10	<i>max.</i> 0.23 × 0.19 <i>min.</i> 0.12 × 0.07
Combined zooecial wall thickness between adjacent zooecial openings	0.08 to 0.13	0.10 to 0.11
Pores per zooecium	0 to 2	0 to 5
No. of mesopores per zooecium	0 to 2	0 to 2
Diameter of mesopores	<i>max.</i> 0.11 × 0.16 <i>min.</i> 0.08 × 0.05	<i>max.</i> 0.10 × 0.05 <i>min.</i> 0.03 × 0.03
No. of diaphragms in a mesopore	3 to 4	3 to 6
No. of diaphragms in peripheral region of a zooecial tube	2 to 4	6
Width of peripheral region	0.50 to 0.53	0.24
Ratio: width of zooecium in peripheral region/total width of zooecium	0.57	0.46

having only sparse distribution of diaphragms in the peripheral region. *A. kayi* also generally lacks the small pores that are present at the integrate boundaries of zooecial walls of *A. chazyensis*.

The species is named after Professor G. Marshall Kay, who has contributed so extensively to Ordovician stratigraphy in New York State.

COLLECTING LOCALITIES

CHAZY FORMATION

- 10 feet above the base of Brainerd and Seely's section no. 1 (1888, p. 326); about 50 yards south-west of intersection of Tracy Brook and Duprey Road; near base of member A. *Atactotoechus chazyensis* sp. nov.
- 16 feet above the base of Brainerd and Seely's section no. 1 (1888, p. 326); about 50 yards south-west of the intersection of Tracy Brook and Duprey Road; near the base of member A. *Atactotoechus chazyensis* sp. nov.
- 70 feet above the base of Brainerd and Seely's section no. 1 (1888, p. 326); about 220 yards south-west of intersection of Tracy Brook and Duprey Road; in member A. *Atactotoechus chazyensis* sp. nov.
- 80 feet above the base of Brainerd and Seely's section no. 1 (1888, p. 326); about 220 yards south-west of intersection of Tracy Brook and Duprey Road; near the top of member A. *Atactotoechus chazyensis* sp. nov.
- East side of N.Y. highway 348, 3 miles south-west of the centre of Chazy village; near the top of member A. *Atactotoechus kayi* sp. nov.; *A. chazyensis* sp. nov.
- West side of N.Y. highway 348, 2.5 miles south-west of the centre of Chazy village; at the base of member B. *Atactotoechus chazyensis* sp. nov.
- West side of N.Y. highway 348, 2 miles south-west of the centre of Chazy village; 78 feet above locality 5 in member B. *Atactotoechus kayi* sp. nov.
- East side of N.Y. highway 348, 1.5 miles S. 25° W. of the centre of Chazy village; in member C and 194 feet above locality 5. *Atactotoechus kayi* sp. nov.
- On the south side of Sheldon Lane, south-south-east of Chazy village, 0.3 miles east of the intersection of U.S. highway 9 and Sheldon Lane. *Jordanopora heroensis* sp. nov.

10. At lake-level (95 feet elevation) on Lake Champlain, eastern shore of Isle La Motte, 1·2 miles N. 16° E. of Holcomb Point, Isle La Motte. *Jordanopora heroensis* sp. nov.; *Atactotoechus chazyensis* sp. nov.
11. Near lake-level (95 feet elevation) on Lake Champlain, eastern shore of Isle La Motte, Vt., and $\frac{7}{8}$ mile south of Reynolds Point. *Atactotoechus chazyensis* sp. nov.
12. On the eastern slope of The Head, Isle La Motte, Vt.; $\frac{1}{4}$ mile south-west of locality 13. *Atactotoechus chazyensis* sp. nov.
13. On the north-eastern slope of The Head, Isle La Motte, Vt., and $\frac{1}{2}$ mile south-west of Reynolds Point. *Atactotoechus chazyensis* sp. nov.
14. On the north-eastern slope of The Head, Isle La Motte, Vt., and $\frac{1}{2}$ mile south-west of Reynolds Point, 100 yards north of locality 13. *Atactotoechus chazyensis* sp. nov.
15. 1 mile S. 25° E. of Isle La Motte village toward Jordan Point. *Jordanopora heroensis* sp. nov.; *Atactotoechus chazyensis* sp. nov.
16. 1 mile S. 25° E. of Isle La Motte village and 100 yards north of locality 15, toward Jordan Point. *Jordanopora heroensis* sp. nov.; *Atactotoechus chazyensis* sp. nov.
17. On eastern slope of hill, 0·6 mile south-west of Rutland railroad station, South Hero Island, Vt. *Jordanopora heroensis* sp. nov.
18. Float collected near locality 5, east side of N.Y. highway 348, 3 miles south-west of the centre of Chazy village, and near the base of member B. *Atactotoechus chazyensis* sp. nov. and *A. kayi* sp. nov.
19. On south-eastern hillslope, 1·3 miles S. 20° E. of centre of Isle La Motte village, Vt., and west of limestone quarry. *Jordanopora heroensis* sp. nov.
20. 0·95 mile S. 40° W. of Jordan Point, Isle La Motte. *Jordanopora heroensis* sp. nov.
21. From ledge in field north of Duprey road near Chazy village; in member B. *Jordanopora heroensis* sp. nov.
22. 0·17 mile N. 60° W. of Reynolds Point, Isle La Motte. *Atactotoechus chazyensis* sp. nov.

REFERENCES

- BOARDMAN, R. S. 1960. Trepostomatous Bryozoa of the Hamilton Group of New York State. *Prof. Pap. U.S. geol. Surv.* **340**, 1-87, pl. 1-22.
- BRAINERD, E., and SEELY, H. M. 1888. The Original Chazy Rocks. *Amer. Geol.* **2**, 323-31.
- DUNCAN, H. 1939. Trepostomatous Bryozoa from the Traverse Group of Michigan. *Contr. Mus. Paleont., Univ. Michigan*, **5** (10), 171-270, pl. 1-16.
- FOLK, R. L. 1959. Practical petrographic classification of limestones. *Bull. Amer. Ass. Petrol. Geol.*, **43**, 1-38, pl. 1-5.
- ROSS, J. R. P. In press. Ordovician Cryptostome Bryozoa, standard Chazy Series, New York and Vermont.

JUNE R. P. PHILLIPS ROSS
Illinois State Geological Survey,
Urbana, Illinois, U.S.A.

Manuscript received 8 January 1962

THE MORPHOLOGY OF THE BRACHIOPOD SUPERFAMILY TRIPLESIACEA

by A. D. WRIGHT

ABSTRACT. The calcareous structures of the triplesiaceid shell are discussed and interpreted in terms of the soft parts of the living animal. Special attention is paid to the pseudodeltidium, the pedicle tube, the muscle scars and pallial sinuses, which have received little consideration in the past. Relationships of the superfamily to other brachiopod stocks are considered. A new species of *Cliftonia*, *C. oxoplecioides*, from the Ashgillian, the earliest known for that genus, is described.

IN a study of the Ashgillian Brachiopoda of the Chair of Kildare Limestone, County Kildare and of the Portrane Limestone, County Dublin, Eire, material of the brachiopod superfamily Triplesiacea Cooper 1944 has been found which has yielded information hitherto unknown for the group. At the same time, this information has been supplemented by work of a somewhat broader nature, carried out by the author in preparation of the superfamily for the forthcoming brachiopod part of the Treatise on Invertebrate Palaeontology, including a study of the triplesiaceids of the Norwegian Lower Palaeozoic. Concerning the latter, a species of the genus *Streptis* has already been reassessed (Wright 1960), and a redescription of other Norwegian forms is at present in preparation.

Although species of three genera of the superfamily were known and described before the turn of the century, the only attempt at a comprehensive survey has been that of Ulrich and Cooper (1936), who dealt with the Silurian genera. While not wishing to be unduly critical of their valuable contribution, the author feels that a more interpretative approach to the group would be of value. In the present paper, this type of approach has been used, where practicable, in an attempt to reconstruct the anatomy of the animals by studying the mode of secretion of the various hard parts and the part performed by them in the living creature.

I should like to express my thanks to Professor Alwyn Williams both for reading the manuscript and for much helpful criticism and discussion; and to Dr. Gunnar Henningsmoen and my wife for reading the manuscript. I am also indebted to Dr. Vladmir Havlíček of the Ústřední Ústav Geologický, Prague, Mr. A. G. Brighton of the Sedgwick Museum, Cambridge, and Mr. J. D. D. Smith of the British Geological Survey and Museum for the loan of specimens from the collections in their care.

THE SUPERFAMILY TRIPLESIACEA

The brachiopod genera centred around the genus *Triplesia*, although only nine in number, were considered by Cooper (1944, p. 307) sufficiently different from all others to deserve superfamilial status.

The various species of the genera now placed in this superfamily were originally distributed amongst genera of widely separated brachiopod families, from *Orthis* to *Atrypa*, from *Strophomena* to *Spirifer*. This resulted from the close external resemblance between the triplesiaceids and species of these other genera. With the discovery of the internal structures of the group, it was realized that the animals all belonged to a closely

knit unit quite different in character from any of the families with which they had been previously associated, these associations being simply the result of homeomorphy. Accordingly, Schuchert (1913, p. 387) placed the genera in the Tripleciinae, as a subfamily of the Strophomenidae, but the marked differences between this subfamily and the other strophomenids prompted Öpik (1932, p. 69) to raise the group to familial level.

Following Cooper, who as stated above erected the superfamily, the status of the group was further raised to an order by Moore (1952, p. 221). This was subsequently reduced to subordinal level by Muir-Wood (1955, p. 89). The writer here follows Williams (1956, p. 285), in believing that with the present knowledge of the phylum the superfamily forms the most convenient larger unit. Williams (1956, p. 284) cites the triplesiaceids as one of the superfamilies which does not fall easily into place in his method of grouping the superfamilies around one of six well-known genera, and suggests that the Triplesiacea may belong to either the '*Orthis*' or the '*Pentamerus*' group.

Superfamily TRIPLESIIACEA Cooper 1944

Family TRIPLESIIDAE Schuchert 1913 [*nom. correct.* Quenstedt 1931 (*ex. TRIPLECIINAE* Schuchert 1913 *nom. imperf.*)]

Diagnosis. Biconvex to markedly dorsibiconvex, impunctate shells, normally with a prominent undulation in the anterior commissure. Ventral interarea with a delthyrium closed by a flat pseudodeltidium possessing a narrow median fold running anteriorly from the small apical foramen. Dorsal interarea obsolete. Cardinal process long, forked, and directed posteriorly, with a saddle or hood often developed on the posterior side of its base, and with short divergent processes on either side forming the inner boundaries to the sockets.

Range. Ordovician (Llanvirn) to Silurian (Wenlock).

Remarks. The above diagnosis emends that given by Ulrich and Cooper (1936, p. 332). Perhaps the most outstanding single feature of the family is the unusual forked nature of the long cardinal process, which is unique amongst the Brachiopoda. This feature is well developed in the earliest member of the family (Cooper 1956, p. 529) as well as in the youngest stages known in the growth of an individual (Wright 1960, p. 275). Thus no indication has been given so far of how this feature developed, or from what ancestral stock it could have arisen.

Whilst the cardinalia are very conservative features of the family, the external appearance is extremely varied, and it is this that provides the basis for generic distinction. The nine genera into which the triplesiids are at present divided are given below, together with a brief description of the generic characters.

Generic diagnoses.

BICUSPINA Havlíček 1950: transverse, uniplicate, multicostellate shells of spiriferoid appearance.

BRACHYMIMULUS Cockerell 1929: smooth, like *Triplesia* but sulcate.

CLIFTONIA Foerste 1909: subcircular outline, with strong concentric lamellae imposed on radial costellae.

ONYCHOPLECIA Cooper 1956: small, of tear-shaped outline and lenticular profile, smooth, uniplicate.

- ONYCHOTRETA Ulrich and Cooper 1936: claw-like outline with greatly elongated ventral valve and long interarea; dorsal valve short; ornament of coarse costellae.
- OXOPLECIA Wilson 1913: roundly elliptical to transverse outline, uniplicate, ornament of costellae and fine elevated concentric growth-lines.
- PLECTOTRETA Ulrich and Cooper 1936: subcircular outline, ornament of strong concentric lamellae, and strong radiating plications.
- STREPTIS Davidson 1881: small, subcircular to transverse, strong concentric lamellae and superimposed radial ribs. Uniplicate, usually with marked asymmetry.
- TRIPLESIA Hall 1859: smooth, uniplicate, strongly convex shells with marked trilobation.

THE MORPHOLOGY OF THE VENTRAL VALVE

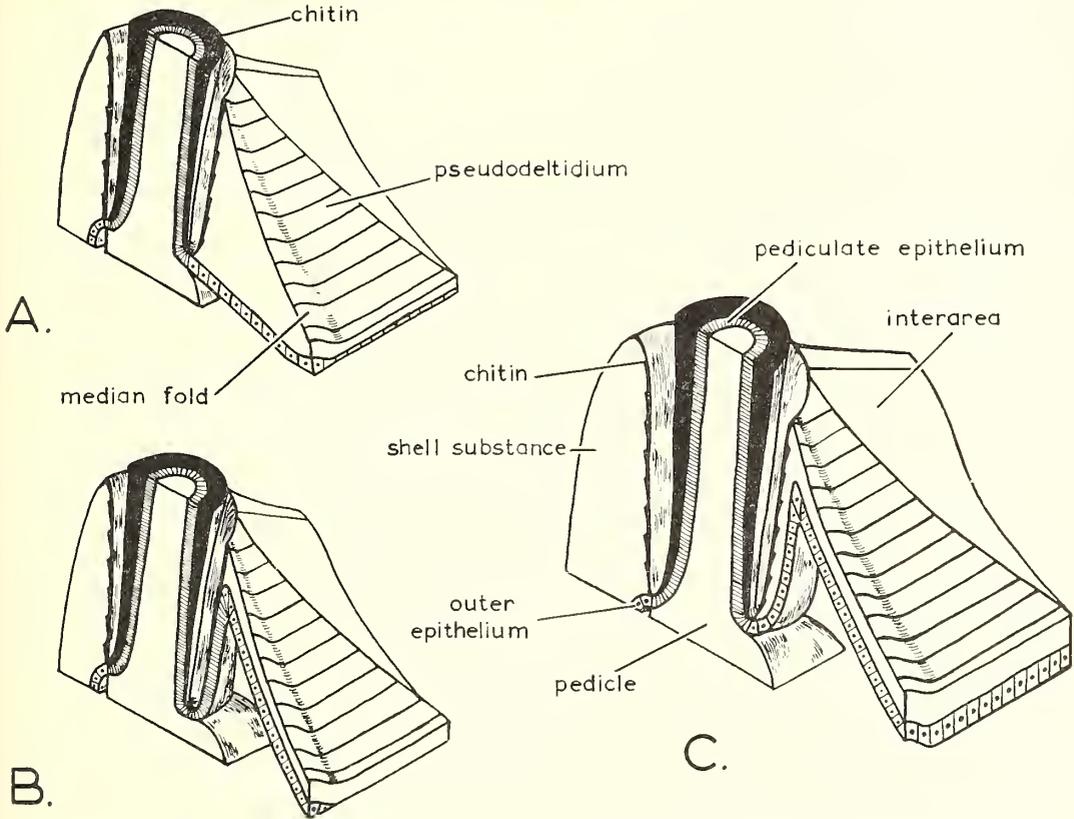
The interarea and delthyrium. All members of the superfamily are characterized by the presence of a well-developed interarea on the ventral valve which varies in attitude from orthocline to apsacline. The external surface of the interarea is flat to concave, and is usually clearly marked by growth-lines parallel to the hinge, together with striae at right angles to them. Within the triangular delthyrium, situated medianly and delimited on either side by growth-tracks of the teeth, the small pedicle foramen is restricted to the apex; it may, however, resorb part of the ventral umbo thus becoming situated anterior to the beak (Ulrich and Cooper 1936, p. 333). The remainder of the delthyrium is covered by a triangular calcareous plate which lies flush with the interarea and which possesses a narrow median fold running anteriorly from the apex to the middle of the hinge-line (Pl. 109, fig. 1). This plate has been alluded to both as a 'deltidium' and a symphytium, but it is here shown to be a pseudodeltidium which was an integral part of the interarea, and which was quite independent of the development of the pedicle.

The pedicle tube. Havlíček (1950, p. 87) in erecting his genus *Bicuspiina*, states that the essential difference between it and *Oxoplectia* is the presence of the pedicle tube in the former; this is totally lacking in the type species of *Oxoplectia*. The specimens of *Bicuspiina* in which this 'pedicle tube' has been observed are all in the form of internal moulds (e.g. Pl. 109, figs. 5, 9) where a thin rod of matrix extends from the posterior end of the adductor scars to the pedicle foramen. This type of rod is open to two interpretations; in life it may have been surrounded by a cylinder of calcite, or, alternatively, it may have been simply a cylindrical hole in a solid wedge of calcite. In both cases, the pedicle would have occupied what is now a thin rod of matrix.

Both of these interpretations of the pedicle tube are to be found within the superfamily, and diagrammatic reconstructions of these, as well as the more common type of pedicle opening, are shown (text-fig. 1). The different arrangements depend essentially on the attitude of the pediculate-outer epithelial junction. The pediculate epithelium is responsible for the secretion of cuticular chitin and the external surface of the pedicle, while the outer epithelium secretes the calcareous shell (Williams 1956, p. 255).

The more usual relationship for the triplesiaceids (as in *Triplesia* itself) is seen in text-fig. 1B. With growth of the shell, the ventral junction of the pediculate epithelium with

the outer epithelium moves anteriorly; whilst on the dorsal side, where the delthyrial cover is being secreted, the junction remains stationary at its apex. Thus, with increasing size, proliferation of pediculate or outer epithelial cells takes place without affecting the position of the junction. Thus, in the median zone a calcareous plate is secreted to fill the delthyrium, the pedicle itself being enclosed within a chitinous tube, so that when the soft parts are destroyed only the apical foramen remains.

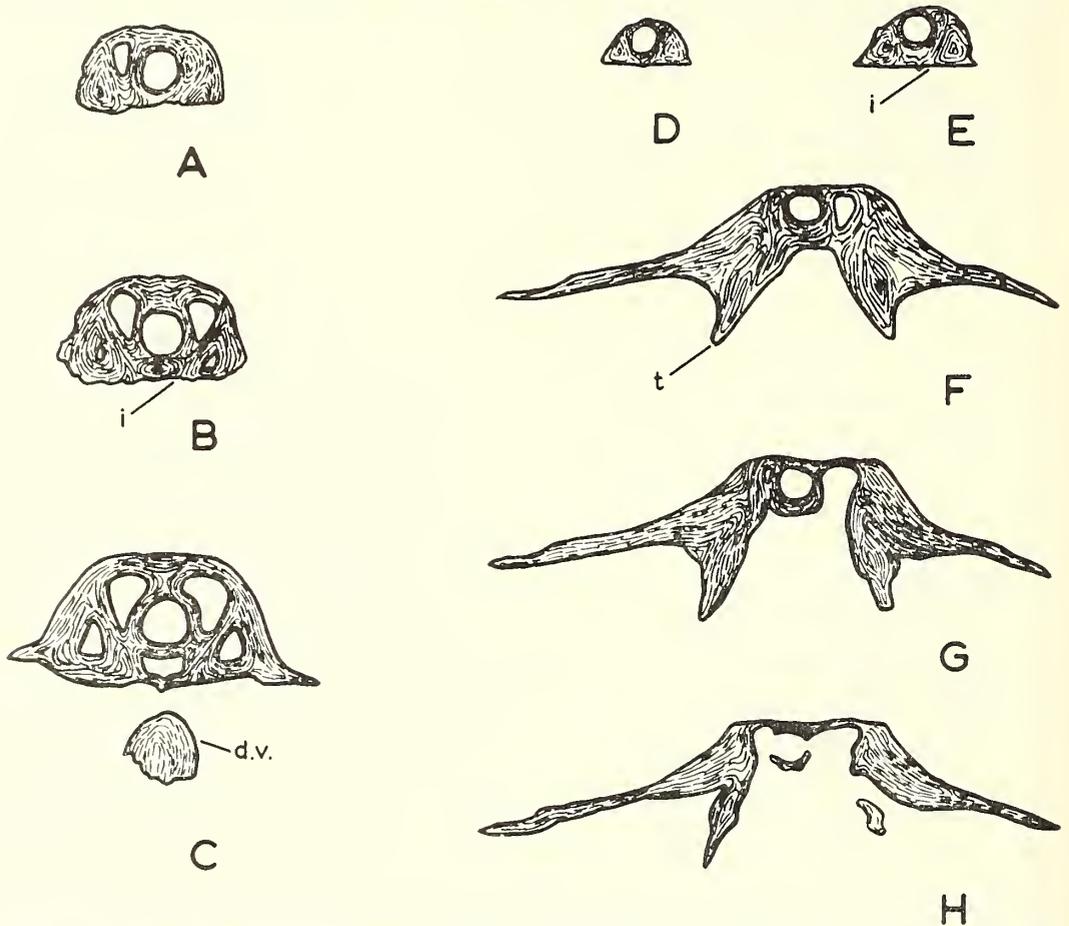


TEXT-FIG. 1. The nature of the triplesiaceid pedicle opening. Generalized block diagram reconstructions with oblique median views showing (A) development of a pedicle passage, (B) the 'normal' arrangement, (C) development of a pedicle tube.

Certain triplesiaceids show a quite remarkable thickening of the shell in the umbonal regions; the thickness of the shell in the umbo of a dorsal valve of *Triplesia ortonii* (Meek) observed by the author being about 7 mm. Young specimens are also thick, so that the thickening would seem to be a specific rather than a gerontic character, at least in this species. In the case of *Oxoplecia multicostellata* Cooper (Pl. 109, figs. 12, 15) thickening may also be observed in the umbonal regions. Here the delthyrial cover becomes very thick towards its apex, so that in these silicified specimens a neat cylindrical hole passes through the plate to connect the foramen with the interior of the valve. Text-fig. 1A shows the arrangement envisaged for this. The pediculate-outer epithelial junction advances anteriorly all round the pedicle as the animal grows, and thus the cylindrical

hole is formed with the delthyrial cover thickened on the ventral side. This cylindrical hole is here termed the *pedicle passage*.

The third variation observed is the development of the pedicle tube as used by Havlíček; whilst characterizing his genus, it is by no means restricted to it. Williams

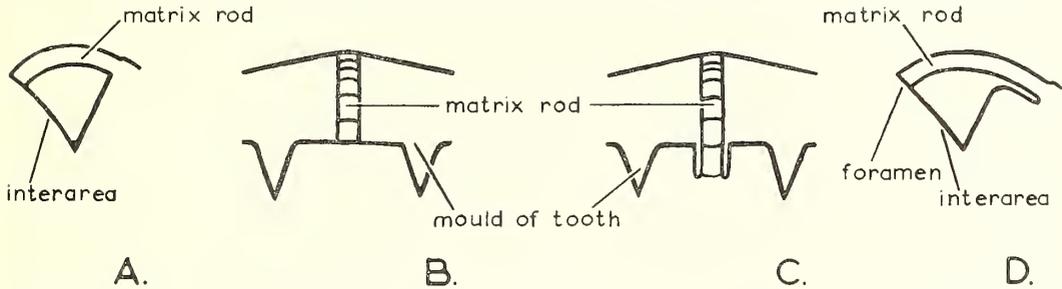


TEXT-FIG. 2. Transverse serial sections of *Cliftonia oxoplecioides* sp. nov. to show the pedicle tube. A–C: sections of a complete shell where the tube is lifted well clear of the valve floor by an isthmus of shell substance. A at 0.3, B at 0.45, and C at 0.6 mm. from the umbo. $\times 8$. D–H: sections of a ventral valve cut slightly obliquely; the tube lies much closer to the valve floor. D at 0.6, E at 0.75, F at 1.5, G at 1.65, and H at 1.8 mm. from the umbo, $\times 7.7$. d.v.—dorsal valve; i—interarea; t—tooth.

(1951, p. 105) describes a short tube in his species *Cliftonia lamellosa*, as does Wright (1960, p. 274) in *Streptis altosinuata* Holstedahl, and in *Cliftonia oxoplecioides* sp. nov. described below. This last species occurs in the form of complete shells in a limestone matrix, so that it is possible to produce serial sections. This technique gives a very satisfactory picture of the tube, substantiating the evidence obtained from the internal moulds. The ventral side of the tube (text-fig. 2) is formed by a thickening of the valve floor. The edges of this thickening are continued dorsally to form a discrete ring or

cylinder around the pedicle. The tube is usually situated close to the internal surface of the ventral valve, dependent on the somewhat variable thickening on the valve floor, which may take the form of a fairly high narrow isthmus between the valve and the pedicle. Posteriorly, the dorso-lateral sides of the tube especially tend to be in contact with the inner edges of the teeth, and the growth-lines (text-fig. 2B, C) show the two structures to be united; but anteriorly the tube becomes quite free, except for its contact with the valve floor on the ventral side (text-fig. 2H).

It will be noticed (text-fig. 2) that the pedicle tube is circular in section in *Cliftonia oxoplectioides*. Havlíček (1950, p. 88), in describing that of *Bicuspina*, says that the tube is slightly flattened in a dorso-ventral direction. Examination of a large number of specimens of *B. spiriferoides* (M'Coy) reveals that flattening may occur in the direction



TEXT-FIG. 3. Diagram showing the relationship of the rod to the surrounding matrix of internal moulds for a pedicle passage (A, B) and a pedicle tube (C, D). A, D are median longitudinal sections through the rod; B, C show the rods in ventral aspect.

indicated by Havlíček, perpendicular to it, or else there may be no indication of flattening whatever. It would seem then, that this feature is due to squashing of the matrix filling the tube; or that the flattened tubes are variants of a cylindrical tube. In any event, dorso-ventral flattening is not a diagnostic property of the tube.

The diameter of the undeformed tube appears to be fairly constant over its length in most specimens of *B. spiriferoides*, and in *C. oxoplectioides*; that of *C. lamellosa* becomes relatively rapidly larger in an anterior direction.

Text-fig. 1C is a representation of the disposition of the soft parts where a pedicle tube is developed. Whilst the delthyrial cover is of a fairly even thickness, the pediculate-outer epithelial junction moves anteriorly with growth, so that the thin calcareous tube sheaths the pedicle dorsally and laterally, passing into the shell substance of the valve floor ventrally.

Although both a pedicle passage and a pedicle tube would produce a matrix rod when the material is in the form of internal moulds, the relationship of the rod to the surrounding matrix at its anterior end enables the two forms to be differentiated (text-fig. 3). In the pedicle passage (text-fig. 3A, B), the matrix rod abuts against a flat surface of matrix which marks the internal surface of the delthyrial plate. Where a pedicle tube is developed this surface will be seen to be hollowed out around the pedicle on its dorsal and lateral sides (text-fig. 3C, D), this space being occupied in life by the calcite of the pedicle tube. Posteriorly the two matrix rods will look similar; but where there is evidence of a pedicle tube in the anterior part it is reasonable to assume that this would continue to the umbo as in *C. oxoplectioides*.

The delthyrial cover. The study of the pedicle tube, which has enabled the reconstructions of the soft parts to be produced, has, as a corollary, shed light on the nature of the delthyrial plate. The pediculate–outer epithelial junction (text-fig. 1) occupies a position in the ventral valve ventral to the delthyrial plate throughout development, with the foramen occupying an apical or supra-apical position. Thus the plate within the delthyrium is secreted by a primary isthmus of outer epithelium quite independent of the pedicle and so is a *pseudodeltidium*. That this pseudodeltidium is an integral part of the interarea is supported by the fact that growth-lines may be traced right across the pseudodeltidium on to the interareas on either side of the delthyrium.

The narrow median ridge (Pl. 109, fig. 1) on the pseudodeltidium appears to be simply a median fold of that plate; certainly the growth-lines of the pseudodeltidium pass over the fold without any break. Ulrich and Cooper (1936, p. 333) believe the narrow fold to be associated with the ‘chilidium’, but it is here considered more closely related to the highly convex and incurved dorsal umbo.

With the establishment of pseudodeltidia in the triplesiaceids, this structure is now known to be a feature of four independent stocks, the others being the strophomenoids, the thecidaceids, and the nisusiids (Williams 1956, p. 258). Differences in the various pseudodeltidia do exist; those of the thecidaceids, the nisusiids, and the earlier strophomenoids are convex, while those of the triplesiaceids are flat with a median fold, although at the same time it must be remembered that the pseudodeltidia of the later strophomenoids are also flat. Again, the foramina of the first three groups are supra-apical whereas many of the triplesiaceids possess an apical foramen, though, as already noted, the ventral umbo may be resorbed so that the foramen moves out of the apex of the delthyrium.

These differences, however, do not alter the basic features of a pseudodeltidium; in fact they serve to emphasize further the different ways in which this feature may arise and the polyphyletic nature of the structure.

The muscle scars. The pattern of the ventral muscle scars in the triplesiaceids is unknown for the majority of species. This lack of information is so real that while Ulrich and Cooper (1936, p. 331), in discussing the relative values of characters in the group, rightly stress the familial level value of characters of the region around the ventral beak and of the pallial markings of both valves, neither the muscle scars nor the pallial markings receive more than an occasional mention in the rest of their paper.

The muscle scars are completely unknown for several genera; in others, only poorly preserved scars have been described for an occasional species, so that the information is scanty and of necessity the words ‘obscure’ and ‘indistinct’ are frequently used.

The occasional species, however, does indicate the muscle distribution within the valves. Pl. 109, fig. 5 shows a clearly defined ventral muscle area in a specimen of *Bicuspina spiriferoides*. This consists of a pair of flabellate diductor scars enclosing elongatedly cordate adductor scars laterally, and almost uniting in front of the latter. The diductor scars do not coalesce, but remain separate, as may be seen more clearly in Pl. 110, fig. 7. Through the narrow space separating the two diductors passes a pair of *vascula media* which arise immediately anterior to the adductor scars. Pl. 109, fig. 5 also shows two pronounced scars within the diductor scar postero-lateral to the adductors, which mark the position of the ventral adjustor muscles.

The scars in *B. spiriferoides* appear to be better impressed than in other species of the genus (Havlíček, p. 88), but a similar muscle distribution is found in those species of the genus *Triplesia* for which muscle scars have been observed; the diductor scars are flabellate and divergent to a greater or lesser extent, while the adductors are smaller and are situated between the diductors.

Cooper (1956, p. 557), in a description of *Oxoplecia simulatrix* (Bassler), states that the diductor scars of this species are flabellate also; for the other twenty-one species of the genus described in this work, no reference is made to the muscle scars which are presumably not impressed on the valves. Whittington and Williams (1955, p. 412) in describing their species, *Oxoplecia mutabilis*, find that whilst in most specimens the muscle scars are not impressed, one specimen does show a narrow, rather long muscle scar with a median lanceolate adductor scar enclosed by narrow diductor scars. Rather narrow diductor and adductor scars have also been recorded for a species of *Streptis* (Wright 1960, p. 273).

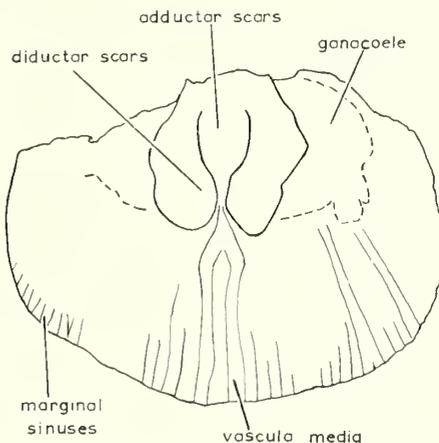
The pallial sinuses. The specimens of *Triplesia* from Kildare, which show, in the dorsal valve, by far the most complete pallial markings of any triplesiaceid known to the author, are completely devoid of these impressions in the ventral valve. Indeed, of the large number of specimens of the superfamily examined, evidence of the ventral pallial sinus patterns was only seen in four specimens of *Bicuspina spiriferoides*. The best of these is shown in text-fig. 4, and Pl. 110, fig. 7.

The branching canals take the form of grooves on the internal mould, thus the sinuses were situated on raised calcareous ridges on the inner shell surface. This indicates that the outer epithelial cells of the mantle, over which the sinuses passed, must have secreted calcite at a faster rate than in the intersinal areas.

Öpik (1934), in his outstanding work on pallial sinus patterns, is concerned principally with the clitambonitaceids and their relationships to the orthaceids, and does not mention the triplesiaceids in this connexion. Earlier, in a summary the characters of the triplesiids, he states that both the muscle scars and pallial markings to be little known for the group and ventures no further information (1930, p. 61).

The pallial markings on the specimen of *B. spiriferoides* here figured, while being clearly shown, are unfortunately incomplete. The *vascula media* arise anterior to the adductor scars, between the fronts of the diductors, and soon bifurcate. The pair diverge for a short distance, when they change direction and continue towards the anterior margin of the shell in a subparallel fashion, occupying only a relatively narrow sector of the shell.

The remainder of the pallial markings observed consist of marginal sinuses, while on the right-hand side two longer sinuses are preserved. These appear to arise at about midvalve where a shallow groove, marked in text-fig. 4 by a dashed line, is believed to



TEXT-FIG. 4. The ventral muscle scars and pallial markings of *Bicuspina spiriferoides* (M^cCoy), taken from the specimen figured in Pl. 110, fig. 7, $\times 2.4$.

mark the anterior limits of the area occupied by the gonocoeles. There is no evidence of an arcuate branch of the *vascula media* being directed in the same way as the *vascula myaria* of the dorsal valve, so it would appear that these two long sinuses form part of a series arising directly from the gonocoele as *vascula genitalia*. This is the lemniscate condition of Williams (1956, p. 275). The possibility of the two sinuses being given off from an arcuate sinus cannot entirely be ruled out due to the incomplete preservation of the pattern; but there is no trace of such a branch arising from the *vascula media*. The shallow groove, which has been taken as the anterior and lateral margin of the gonocoele, might possibly be an arcuate sinus, but its apparent termination against the lateral edge of the diductor scar, and not on the *vascula media*, would seem to make this interpretation unlikely.

THE MORPHOLOGY OF THE DORSAL VALVE

The hinge region and cardinalia. This region of the triplesiaceid shell includes the hinge-line, the 'brachiophores', the 'chilidium', and the cardinal process. Apart from these structures it is necessary here to consider the valve-opening mechanism and the role performed by the calcite processes, together with their effects on the intimately connected ventral structures (e.g. pseudodeltidium) during opening and closing of the valves.

As already stated, one of the outstanding features of the superfamily is the development of an exceedingly long, forked cardinal process (Pl. 109, fig. 14). This structure curves round backwards, from its variably thickened base at the posterior of the dorsal valve, to extend into the ventral umbo. The myophores are located on each prong at its distal end, usually as deep grooves on the dorsal surface. The actual mechanism of the muscles is discussed later.

Ulrich and Cooper (1936, p. 333) state that the cardinal process has been greatly elongated owing to the unusually great convexity of the dorsal valve.

This explanation for the development of the cardinal process is inadequate when other brachiopod stocks are considered, especially in the light of the function of the cardinal process and the leverage systems by which the valves are opened.

In such a brachiopod as *Dalmanella* Hall and Clarke, to cite a widely known stock with relatively simple organization, the cardinal process is situated posterior to the hinge-line with the myophore filling, and often protruding from, the notothyrium. This arrangement gave rise to a lever system of the first order, with the fulcrum (hinge) between the mass to be moved and the force to be applied. The required force was produced by a contraction of the diductor muscles, which pass from the cardinal process through the anterior part of the delthyrium to their ventral seat of attachment on the floor of the ventral valve in the beak region. This is a similar lever system to that found in most modern terebratulaceids and rhynchonellaceids (Thomson 1927, p. 29), the principal difference being that the muscle bases in the ventral valve are situated much further forward than in *Dalmanella*.

A first-order lever system exists also in the triplesiaceids; the *interarea* is *obsolete* in the dorsal valve, and the cardinal process projects posteriorly from the hinge into the ventral valve. This posterior growth of a cardinal process to project into the ventral umbo is by no means restricted to the Triplesiacea. Many stocks of productids develop in a similar fashion, although of course their cardinal process is bilobed and not forked. Here again it should be noted that in the majority of productids the dorsal interarea is

obsolete, as in the triplesiaceids; but when valve convexity is considered, the dorsal valve with cardinal process is flat or concave, which would instantly contradict Ulrich and Cooper's hypothesis.

The Triassic genus *Thecospira* also possesses a posteriorly directed cardinal process, combined with a concave dorsal valve and vestigial dorsal interarea. Again in some orthotetaceids, e.g. *Meekella* White and St. John, the cardinal process is directly similar. Here the convex nature of the dorsal valve would lend some support to Ulrich and Cooper's idea, although it is not developed to the extent seen in the triplesiaceids. But what would seem to be more fundamental is that, as in the productids and triple-siaceids, the development of a posteriorly directed cardinal process is found in association with the loss of interarea in the dorsal valve.

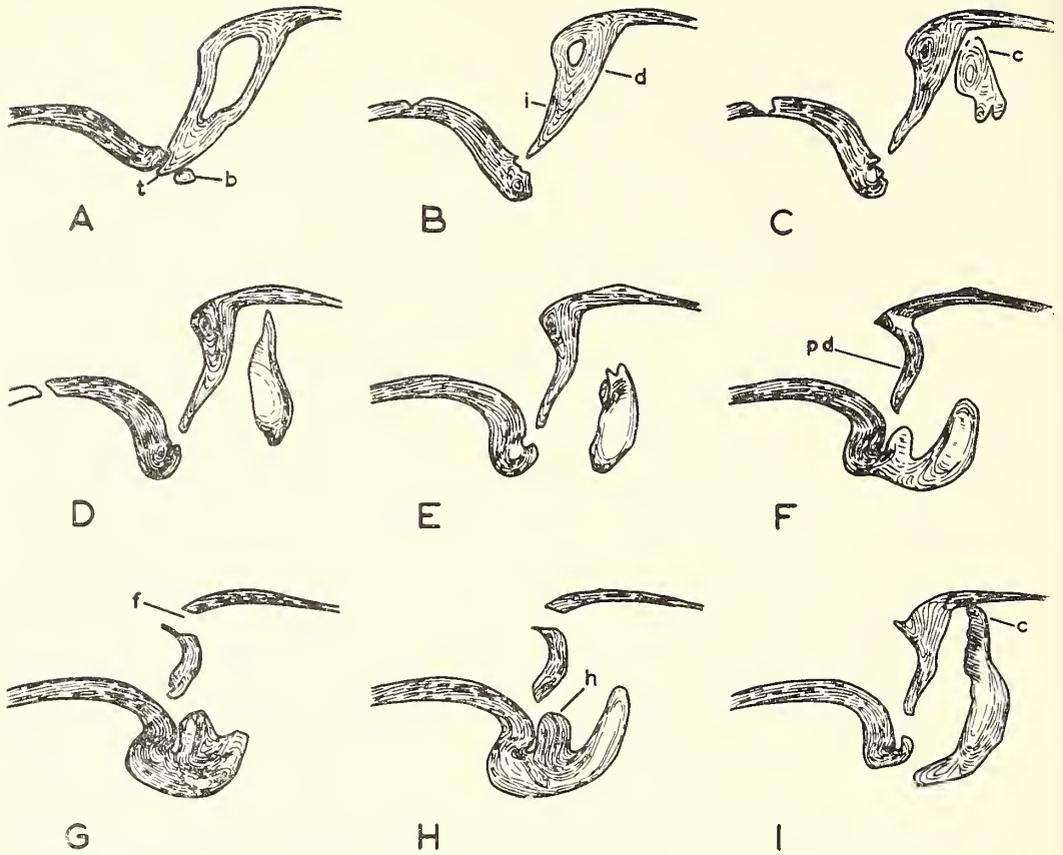
It would be unwise to say that the posterior elongation of the cardinal process was a *result* of the loss of interarea in those stocks where it is developed, as its development depends on various factors, including, for example, the growth of a sufficiently high ventral beak to accommodate this type of cardinal process. It would certainly seem, however, that there is a closer correlation between an elongated cardinal process and a reduced interarea, than between the length of the cardinal process and the convexity of the valve.

The great convexity of the dorsal valve at the umbo was, however, responsible for the median fold of the pseudodeltidium. The external edge of the pseudodeltidium (text-figs. 5A and 6A) extends straight to the hinge, where the tooth fits into the socket of the dorsal valve, bounded on the inside by the 'brachiophore'. Here the convexity of the dorsal valve is by no means marked, but it increases medianly so that the entire valve is strongly incurved in the median plane (text-figs. 5F, G, and 6B). The pseudodeltidium is now situated more dorsally (the section being through the median fold of that plate), and the dorsal umbo is in fact tucked inside the ventral valve. Thus, it becomes apparent that, if no median fold had been developed, the anterior part of the pseudodeltidium would have been jammed between the dorsal umbo and the hood of the cardinal process ('chilidium'). If the latter had not been developed, as it is envisaged below to be a complementary structure to the pseudodeltidial fold, the dorsal umbo would have been pressed against the flat pseudodeltidium and, due to its strongly convex nature and position, would certainly have impeded, if not prohibited, the opening of the valves.

To allow the dorsal umbo to be tucked into the ventral valve and also to enable the valves to open freely, it is necessary both to lift the median portion of the pseudodeltidium above the level of its lateral parts and to shorten it, producing the arrangement seen in text-fig. 5G and H.

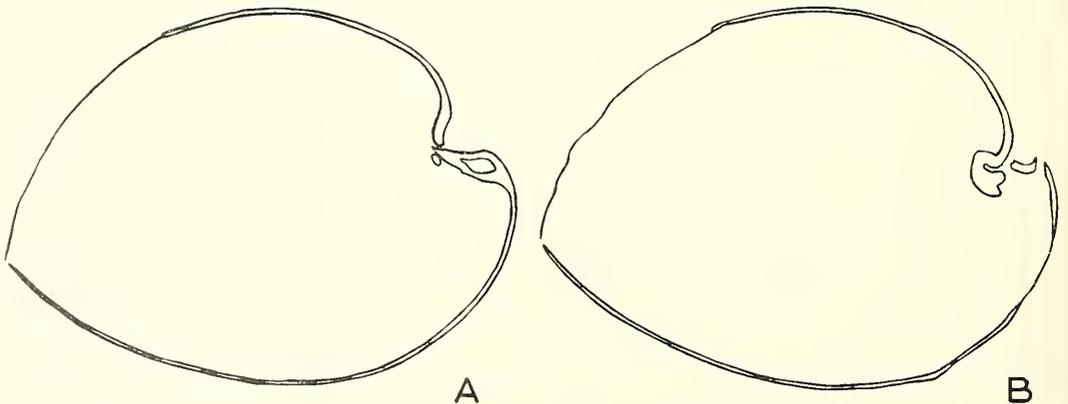
As may be observed from the longitudinal sections (text-fig. 5F, G, H) and transverse sections (text-fig. 7F, G, H) of *Triplesia extans* (Emmons), there is developed, on the posterior side of the shaft near its base, a calcareous structure which takes the form of a saddle or hood, arching over the shaft with its dorsal edge parallel with the edge of the dorsal umbo (text-fig. 7F). The actual hood may be seen in the various silicified specimens of *Triplesia* sp. from Portrane, County Dublin, figured in Pl. 109, figs. 13, 16-19.

The growth-lines, traced from photographs of cellulose peels, show that this hood is an integral part of the cardinal process. Text-fig. 5F shows the growth-lines on the hood to be abruptly truncated on the left, which is, as one would expect, at the side of the

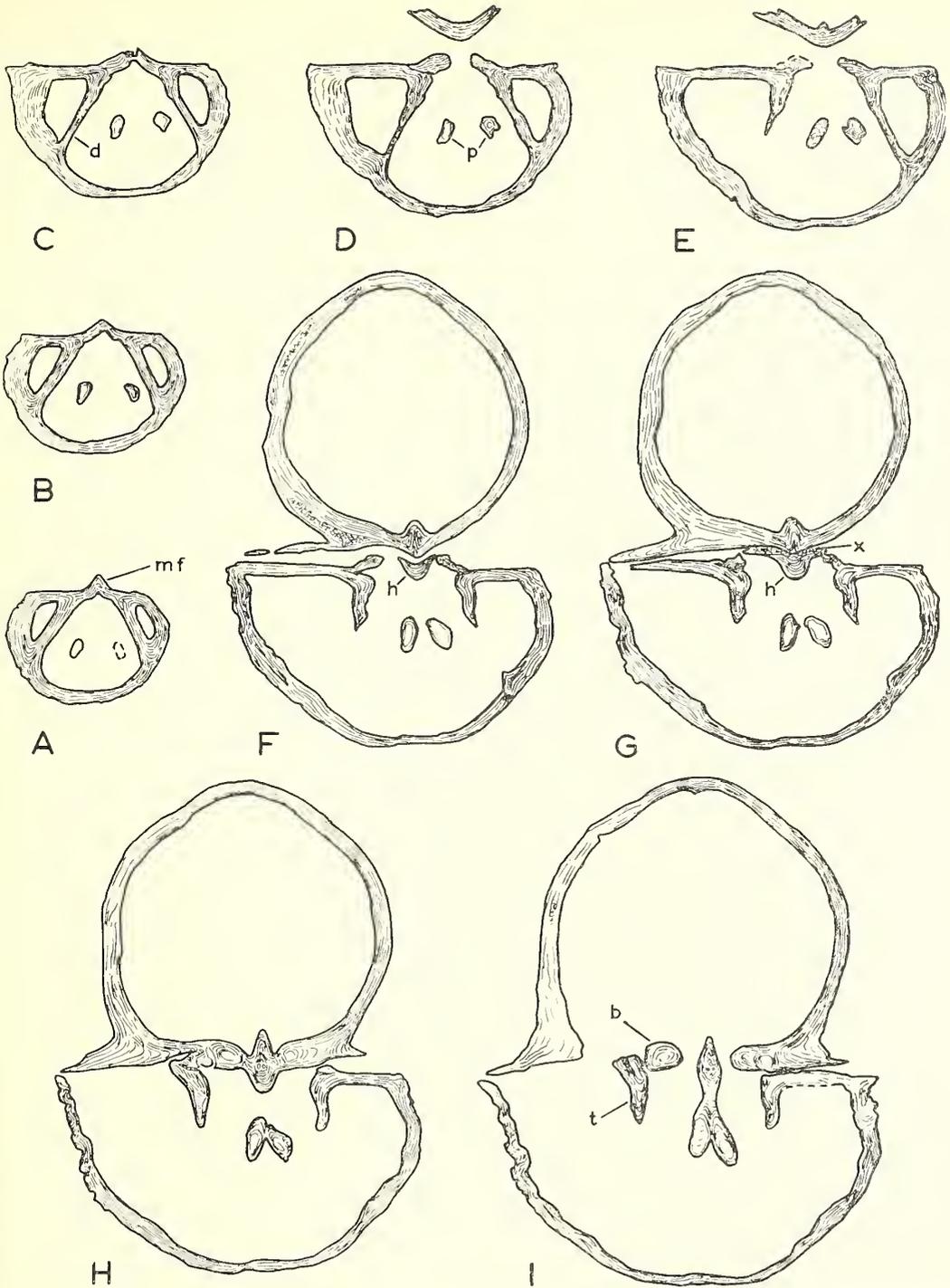


TEXT-FIG. 5. Longitudinal serial sections through a specimen of *Triplesia extans* (Emmons) to show the calcareous structures of the hinge region and their relationships. A is taken at the delthyrial edge, B at 0.5 mm. from it towards the median plane of the valve. The other peels follow B at 0.2-mm. intervals, $\times 8.1$.

b—'brachiophore'; c—distal end of cardinal process; d—dental plate; f—pedicle foramen;
h—cardinal process hood; i—interarea; pd—pseudodeltidium; t—tooth.



TEXT-FIG. 6. Longitudinal sections of *Triplesia extans* (Emmons) to show the hinge structures in relation to the rest of the valve. A and B correspond to text-fig. 5, A and G, respectively, $\times 3.3$.



TEXT-FIG. 7. Transverse serial sections of *Triplesia extans* (Emmons) at 0.15-mm. intervals, A being taken at a distance of 1.05 mm. from the ventral umbo. A-E omit, or show only part of, the dorsal valve, $\times 8.1$.

b—'brachiophore'; d—dental plate; h—cardinal process hood; mf—median fold on the pseudodeltidium; p—prongs of the forked cardinal process; t—tooth; x—crystalline calcite.

structure, while on the right the growth-lines flow smoothly into those of one of the process forks. The essential unity of the hood and the cardinal process is seen further in text-fig. 5, G and H. The sharp bend in the growth-lines at the base of the hood marks it off from the cardinal process proper, but there is no doubt that the growth-lines are continuous and that the hood is a process developing posteriorly from the cardinal process.

This hood has previously been identified as a much modified or vestigial chilidium (Ulrich and Cooper 1936, p. 333, and Muir-Wood and Cooper 1960, p. 134), but because the dorsal interarea is obsolete, and does not possess a notothyrium, it cannot possibly possess a chilidium. Moreover, the structure is an internal one, not visible on the exterior, and the growth-lines show that it is basically a development from the posterior surface of the cardinal process.

This is not to say that vestigial chilidia do not exist in some groups of brachiopods. Indeed, Williams (1953, p. 13) shows that the history of the stropheodontids exhibited a progressive reduction in the chilidium until it became obsolete. This is quite different from the triplesiaceids in which there is no such trend, for even the earliest known forms are without a dorsal interarea. Further, although the chilidium became obsolete in the stropheodontids, the dorsal interarea did not, although it may have decreased in size.

The variation in shape of the hood is discussed by Ulrich and Cooper (1936, p. 334). With respect to its function, it is here considered to be a complementary structure to the median fold of the pseudodeltidium. Lateral to the fold, where the convexity of the dorsal valve is not so pronounced, the pseudodeltidium reaches virtually to the hinge. Medianly the pseudodeltidial fold is shorter and extends towards the posterior part of the dorsal valve, rather than the hinge. This gap is closed by the hood, which appears to act rather as the anterior portion of the pseudodeltidium, which is itself unable to develop as a consequence of the highly convex dorsal umbo.

The lophophore. No direct evidence of the feeding organ of members of the superfamily is available, as calcareous supports to it of any sort are totally lacking. In other superfamilies, the so-called brachiophores have been interpreted by some authors as being the most rudimentary type of lophophore support. Williams (1956, p. 264) has shown that, in the majority of orthaceids and dalmanellaceids, these brachiophores were far too short to have functioned as a support to the lophophore. In the case of the triplesiaceids, the brachiophores are not only directed laterally and ventrally but also become curved over in a posterior direction (Pl. 109, figs. 17, 19). Hence under these conditions, it is even more apparent that these structures acted merely as the inner walls to the sockets, and have no part in supporting the lophophore, which must have developed anteriorly from the body wall.

In the absence of any calcareous supports, and, of course, the soft parts themselves, the form of the lophophore may only be postulated by a consideration of the shape of the valves. In the case of closely apposed valves, such as the concavo-convex and resupinate strophomenoids, the lophophore must of necessity be flattened ventro-dorsally, and may have taken the form of a plane-spirolophore, a ptycholo-phore (as indicated, for example, by the ridges in the dorsal valves of *Leptaenisca* and *Plectodonta*, respectively), or a simpler schizolo-phore or trocholo-phore. Biconvex valves, where this ventro-dorsal restriction to growth is absent, show a much greater range of lophophore type

from trocholophous (*Gwynia*), schizolophous (*Argyrotheca*) to spirolophous (*Hemithyris*), plectolophous (*Terebratulina*), and deutero-lophous (*Spirifer*).

Williams (1956, p. 272), in a consideration of Beurlen's (1952) classification of the articulate brachiopods (the major divisions of which are based on lophophore disposition, for which Beurlen relied principally on shell shape), demonstrates, with the Plectorthidae, the variation of shell shape within a family and the danger of homeomorphy when attempting to use this attribute as a means of classification. However, it is possible to determine some apparently valid relationships between the shape of biconvex shells and the lophophores of the animals, where the latter is known, and then apply them to extinct groups like the triplesiaceids, where the calcareous parts alone are known and do not themselves indicate the style of lophophore.

The following points are noted:

(1) In those spire-bearing brachiopods where the lophophore supports consist of spires which are directed laterally (*Athyrea*, *Spiriferacea*), the valves are more or less evenly convex.

(2) *Atrypa*, normally pronouncedly dorsi-biconvex, possesses spires which are directed dorso-medially.

(3) In the Rhynchonellacea, whose lophophore is normally a dorsally-directed spirolophore, the shells are generally deeper in the dorsal than in the ventral valve.

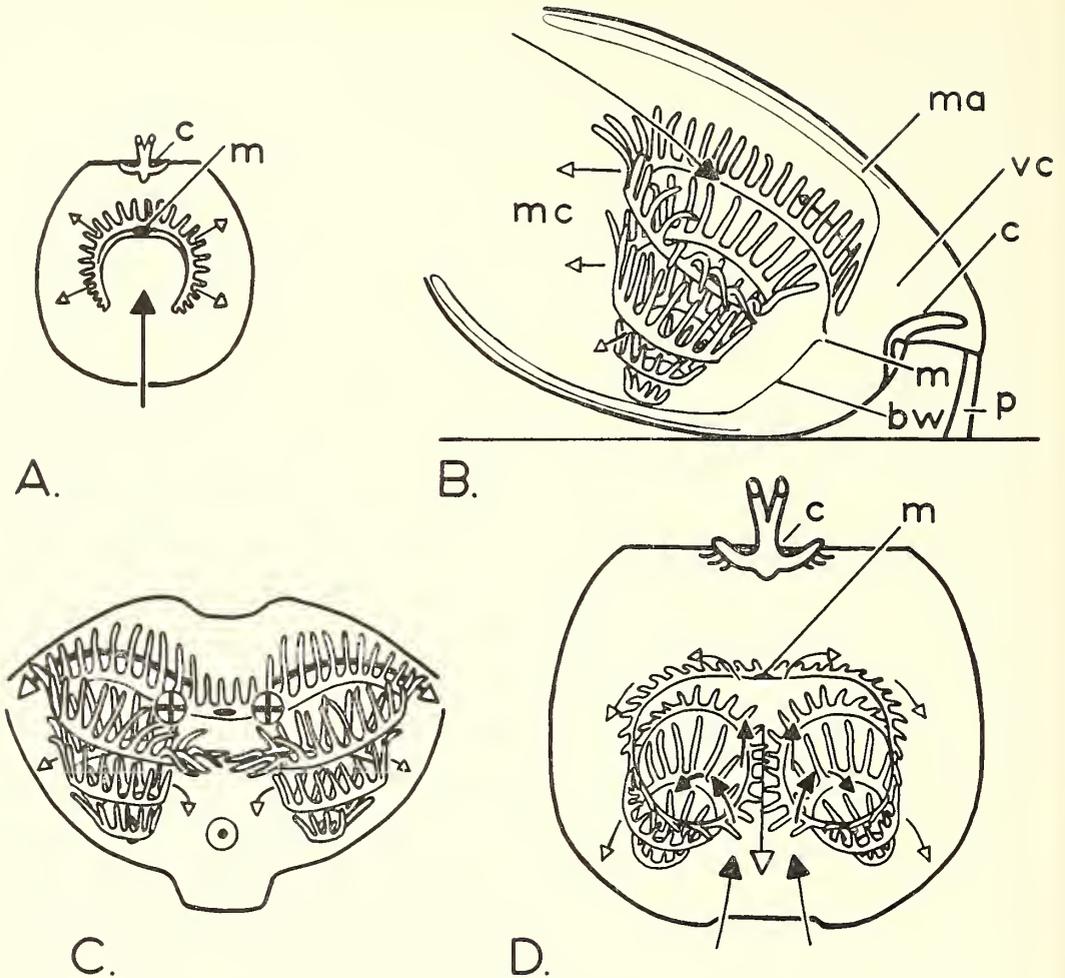
(4) The inarticulate *Crania* possesses a flat ventral valve and a more or less conical dorsal valve into which the spirolophes are directed. *Discinisca*, with its ventrally directed spires and conical dorsal valve would seem to contradict the relationship of stronger valve convexity being in the direction of coiling. However, in the anterior third of the shell, where the coils are developed, the ventral valve becomes quite strongly convex, at least as much if not more so than the dorsal valve at this point.

(5) In the '*Terebratula*' group, with their characteristically plectolophous lophophore, the ventral valve may be deeper (e.g. *Dallina*) but more commonly the valves are about evenly convex. This situation is what one might expect from a shell possessing this type of lophophore.

It would seem, from the above examples, that the convexity of the valves does bear a relation to the kind of lophophore in many instances.

The plectolophous lophophore is a very advanced form, associated with a well-developed calcareous support in the form of a loop, a septum, or both, while the valve convexity is rather variable as already noted. The Triplesiacea, however, show no calcareous support, and are all dorsi-biconvex to a greater or lesser degree. Coupling these facts with the early occurrence of the superfamily—the terebratulids had barely commenced their existence when the triplesiaceids became extinct—it would seem highly improbable that the triplesiaceids possessed this type of lophophore.

Recent brachiopods which show no calcareous support for their feeding organ are to be found in the inarticulates, while the rhynchonellaceids only possess a simple support in the form of crura. The most complicated lophophore development in both these cases is a spirolophore, and this would seem to be the type of lophophore most likely to occur in the triplesiaceids. The genera *Gwynia* and *Argyrotheca*, with their simpler lophophores, are very small forms and, as a generalization, it may be said that the much larger size of most triplesiaceid genera is possibly another point in favour of the more advanced spirolophore, although it is appreciated that a small number of



TEXT-FIG. 8. Diagrammatic reconstructions of the spirulophous lophophore and feeding currents envisaged for the Triplesiacea. (A) The trocholophous lophophore of a young individual with a median inhalant current (solid arrow), directed by the filaments to emerge as a lateral exhalant current (open arrow). The other figures represent an adult viewed, (B) laterally; (C) from the anterior commissure (posteriorly directed currents \ominus anteriorly directed currents \oplus); (D) ventrally.

bw—body wall; c—cardinalia; m—mouth; ma—mantle; mc—mantle cavity; p—pedicle; vc—visceral cavity.

larger brachiopods (e.g. *Rensselandia*) did possess a simple trocholophe in the adult stages.

The type of lophophore in Triplesiacea is considered to be that of a simple anterodorsally directed spirulophe (text-fig. 8), rather similar to that of Recent rhynchonellaceids. Now, during the early growth stages, i.e. where the trocholophous and early schizolophous condition exists, the inhalant current is a single median one, with the current then being directed through the filaments to emerge laterally (text-fig. 8A), as ascertained by Atkins (1956, 1958, 1959) for Recent brachiopods. With the development

of the spirolophore, the median inhalant current becomes divided and passes into the coils (text-fig. 8c, d). The possible advantage to certain brachiopods of a plication in the anterior commissure to assist the channelling of currents has been commented upon by Orton (1914, p. 295) and others; a plication is invariably present in the adults of the Triplesiacea. Possibly the stage of development of the lophophore associated with the division of the inhalant current is related to the appearance of the fold and sulcus. Should it be determined that the plication appeared at a definite stage in the development of the lophophore, it would prove useful in ascertaining the size attained before the development of an adult-type lophophore in the relevant extinct forms. For example, the fact that one species of *Streptis* develops its plication significantly later than another (Wright 1960, p. 269) would also mean that the former would be retarded in lophophore growth relative to the other, i.e. would possess its trocholophous stage for a longer period. As is well known, plicated commissures are far from being universal in the phylum, but it seems possible that in stocks where they are well developed, a co-ordination between the plication on the one hand and the feeding mechanism on the other may well have developed during the course of evolution.

Quite obviously this would have to be verified or disproved first of all with a sample of suitable Recent shells (rhynchonellaceids) which are unfortunately not available to the author at present.

The lophophore and current systems here envisaged for the Triplesiacea (text-fig. 8) is a mechanically efficient system (Rudwick 1960, p. 376), the filaments in the mouth region and on the first coil of the spires touching the ventral mantle to separate the inhalant and exhalant water there, whilst medianly the filaments of the first coils of the two spires interlock to separate the ventral inhalant current from the dorsal exhalant one.

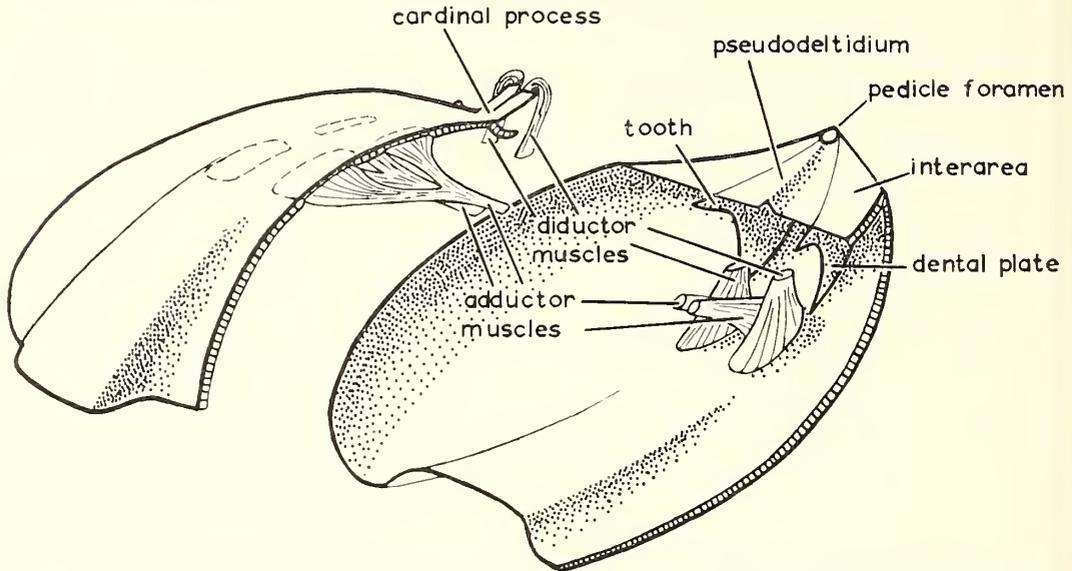
The varying outline of the valves seen in the Triplesiacea, from the almost circular *Plectotreta* to the transverse *Bicuspina* with its spiriferoid outline, would not necessitate any fundamental reorientation of the brachial apparatus or the feeding currents; in the more transverse valves the angle subtended between the two cones would merely have to be increased.

The muscle scars and muscular system. The cruciform markings found on internal moulds of specimens of *Triplesia* and *Bicuspina*, especially from the British Llandeilian and Caradocian rocks, have been known to palaeontologists for many years. The cross has been taken, quite correctly, as dividing the anterior adductor pair from the posterior adductor pair, and the left scar from the right scar of each pair. The transverse bars of the cross, here shown to be *vascula myaria*, sweep round towards the posterior margin in the form of a pair of arcs. The whole of the area bounded by these arcs, which in many specimens attain considerable dimensions, was believed to be the posterior muscle scar.

The animal would thus have possessed a large pair of posterior adductor scars of sub-circular outline, together with a smaller subtriangular anterior pair, with the apices of the triangle directed postero-medianly towards the *nodus quadrivalis* (Öpik 1934, p. 38) as in text-fig. 10D.

While agreeing with the distribution of the latter, the present study shows that it is extremely unlikely that the posterior adductor scar did in fact cover the whole of the

area delimited by the *vascula myaria*. In the first instance, while the anterior pair of adductors are to be found in the form of raised areas on the internal moulds (Pl. 110, fig. 4), indicating a deep muscle insertion, the areas defined by the *vascula myaria* are lower on the moulds and thus are areas of greater secretion on the shell interior. This is contrary to what one would expect if they, too, were muscle scars. The lower level of the posterior areas is true, except for those parts of the area just inside the boundaries formed by the vascular arcs, where one finds a raised ridge in the mould. This becomes increasingly prominent when traced anteriorly from the umbo towards the *nodus*



TEXT-FIG. 9. The muscle system of a generalized triplesiaeid. Antero-lateral view with the muscles cut and the dorsal valve lifted away from the ventral valve.

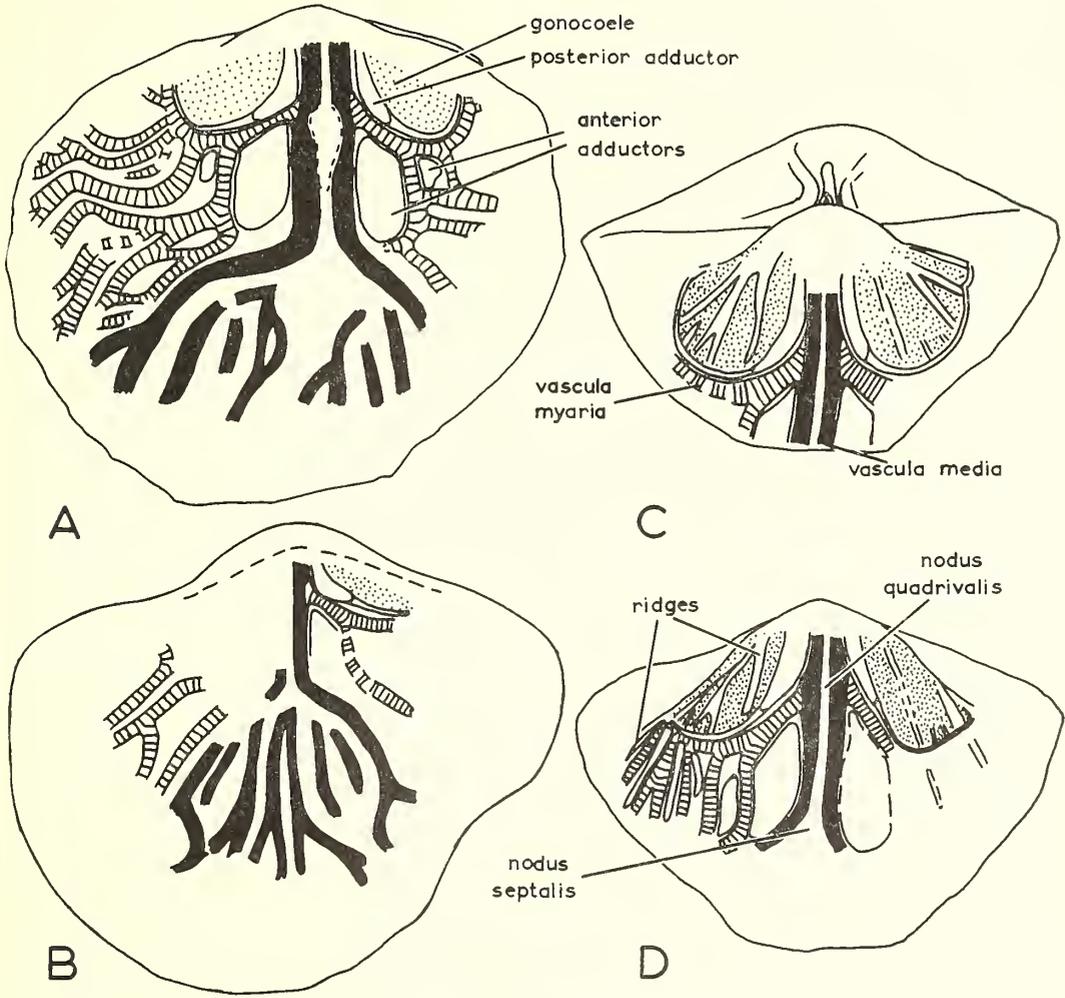
quadrivalis, where it is most marked, after which point it diminishes laterally to the valve margin. Thus on the shell interior the area is a raised one, clearly bounded anteriorly by a groove and by an area of deeper insertion postero-lateral to the 'cross' at the *nodus quadrivalis* (Pl. 109, fig. 2). These areas of deep insertion are here considered to be the location of the posterior adductor muscle attachments.

Further, while in the majority of specimens in which the subcircular area is preserved it appears to be quite smooth, an occasional shell shows a series of alternating ridges and grooves, whose disposition is roughly radial from the direction of the umbo (text-fig. 10C, D, Pl. 110, figs. 1-3). These markings have a quite different appearance from the impressions left on the valve floor by muscle attachments. Moreover, their distribution seems to be closely related to that of the branches of the *vascula myaria* anterior to them.

It is thus concluded that the subcircular areas are principally the impressions of a pair of saccate gonocoeles, while the posterior adductor scars are restricted to the median portion as indicated in text-fig. 10A.

A reconstruction of the actual muscular system for a generalized triplesiaeid is shown in text-fig. 9. The striking feature of the system when compared with other con-

temporary stocks is that the seat of attachment of the diductor muscles in the dorsal valve is situated high inside the ventral umbo, at the distal ends of the cardinal process. This would maintain an efficient valve-opening mechanism for the group.



TEXT-FIG. 10. The dorsal pallial sinus patterns in the genus *Triplesia* taken from specimens figured in Pl. 110, figs. 2-4, 6. In (A) the *vascula myaria* (ornamented by closely spaced lines) and (B) the *vascula media* (solid black) are shown more completely. (C) and (D) are postero-dorsal and antero-dorsal views of an internal mould, showing clearly defined ridges traversing the floor of the gonocoele. $\times 4.9$, $\times 4.7$, $\times 1.9$, $\times 1.9$ respectively.

The pallial sinuses. The pallial sinus patterns in the dorsal valve have been established principally from internal moulds of a species of *Triplesia* from the Kildare Limestone (text-fig. 10, Pl. 110, figs. 4-6). The gonocoeles, described above, are delimited anteriorly by a ridge on the mould, exterior to which is a groove. This groove (corresponding to a ridge in the actual shell) is produced by an arm of the main vascular canals which

branches off from the latter at the *nodus quadrivalis* to pass laterally between the posterior and anterior adductor muscles, forming an arc which follows the anterior margin of the gonocoeles. This is the principal branch of the *vascula myaria*. This branches further, the first branch (text-fig. 10A, D) passing through the region occupied by the anterior adductor scar to divide it into a larger inner and a smaller outer portion as in *Clitambonites* (Öpik 1934, p. 39). The remaining branches are somewhat shorter, carrying out their circulatory function in that region of the shell between the first branch and the main arc. Some of these branches are seen to bifurcate at the periphery of the shell to produce marginal sinuses as in the ventral valve of the specimen of *Bicuspina* shown in text-fig. 4; but in the majority of specimens examined the marginal sinuses were not sufficiently strongly impressed for them to be visible. This was the case also with the marginal sinuses of the *vascula media*.

The *vascula media* again take the form of grooves in the cast. They are first observed a short distance anterior to the umbo, the left and right ones proceeding parallel to each other anteriorly along the middle of the valve, separated by a low, but clearly defined, ridge. This pattern continues until they reach the front of the anterior adductor scars (the *nodus septalis* of Öpik) when they diverge sharply to form a characteristic inverted 'Y' shape (Pl. 110, fig. 5). While this 'Y' is often clearly defined, the anterior markings within the fork of the 'Y' are usually only faintly impressed. Where impressions are found in this position, they take the form of a series of canals as seen in text-fig. 10B. Although it is not possible to be definite in stating how these canals arise from the main *vascula media*, due to their being indistinct at crucial points, it seems most probable that they do so at the *nodus septalis*. Here, at the point of divergence of the main trunks of the *vascula media*, two smaller canals appear to form a continuance of the same parallel course taken by those sinuses up to the *nodus septalis*. These smaller canals quickly produce three branches each, some of which show further branching as the shell margin is approached. The canal system thus developed within the limits of the main *vascula media* may be compared with that present in the orthaceid *Orthostrophia* Hall 1883. In this genus it takes the form of a pair of subsidiary median gonocoeles (Williams 1956, p. 278), whose finely fingered appearance corresponds closely with that of the postero-lateral gonocoeles.

In the case of *Triplesia*, although the canals occupy the correct position to be subsidiary gonocoeles (at least where *Orthostrophia* is concerned), it is not certain whether they did actually act as such. The appearance of these canals in *Triplesia* is coarser than that of the median gonocoeles of *Orthostrophia*, and in specimens where these canals have been observed, the postero-lateral gonocoeles are smooth. This prevents a close morphological comparison. It is interesting to note that wherever ridges are developed on the postero-lateral gonocoele in *Triplesia*, they are also coarser than the corresponding ones in *Orthostrophia*. Perhaps the coarser nature of the 'median gonocoele' is a reflection of this, and these median sinuses in *Triplesia* (and in the rest of the family, if the pallial markings prove to be similar to those of the type genus) did have a sexual as well as a circulatory function.

THE RELATIONSHIPS OF THE SUPERFAMILY

The assembly of familial features characterizing the genera of the Triplesiacea enable members of this superfamily to be differentiated easily from other groups. At the same

time this distinctive combination of characters poses difficulties when the relations of the superfamily to the rest of the class Articulata are considered. The nature of the cardinalia and the postero-median part of the ventral valve is extremely unusual, and so far no brachiopod has been described which shows transitional stages in the development of these features from an ancestral stock that could be placed with certainty in another definite group of brachiopods.

However, by a consideration of the stocks (*a*) which were potentially able to develop these more distinctive single features of the superfamily (*b*) which do themselves possess other features in common with the triplesiaceids and (*c*) which are known to be in existence in rocks older than, or that were deposited contemporaneously with, those in which the earliest specimens are found, the possible ancestral stock may be suggested. With the increasing knowledge of both the triplesiaceids and the stocks from which they may have evolved, certain groups are found to have more in common with them than others, and so the number of possibilities is reduced.

When demonstrating the close relation of stocks by a process of comparative morphology, it is imperative that the time factor, i.e. the stratigraphical distribution, is kept in mind. The earliest member of the triplesiaceids, *Onychoplecia*, makes its appearance in the Llanvirn Table Head Series of Newfoundland (Cooper 1956, p. 529). Thus, although its immediate ancestors are unknown, its closest relatives may be sought in the earlier Arenig or Tremadoc or in the contemporaneous Llanvirn stocks.

Thus, from a purely chronological standpoint, the stocks which arose later than the Llanvirn may be discounted in the search for potential ancestors. This eliminates the '*Rhynchonella*', '*Spirifer*', and '*Terebratula*' groups of Williams 1956. For the remaining three groups, the '*Pentamerus*' group is represented only by the Syntrophiacea, the '*Strophomena*' group by the Plectambonitacea and some early strophomenaceids, and the '*Orthis*' group by the three superfamilies Orthacea, Dalmanellacea, and Clitambonitacea.

In carrying out a morphological comparison between these stocks and the Triplesiacea, it is essential to consider which features of the latter are of high systematic value and must therefore be searched for in the potential ancestral stocks. In the Triplesiacea, perhaps, the most important features, which are to be found in other brachiopod groups, are the impunctate shell substance and the biconvex nature of the shell. A comparison of these features with the contemporaneous members of the '*Strophomena*' group renders a close relation with this group highly improbable. Although atrophy of the caeca in punctate stocks to produce impunctate shells is suspected to occur (Williams 1956, p. 253), it seems unlikely that the Dalmanellacea could have provided the ancestors to the Triplesiacea, for, whilst they are contemporaneous, they are not known in pre-Llanvirn times. Further, in North America, where *Onychoplecia* occurs, dalmanellaceids do not appear until the Llandeilo (Ashby stage, Cooper 1956, p. 137).

The Clitambonitacea are a very specialized superfamily. Some of the early forms, however (e.g. Tritoechiidae), do not possess all of the features associated with their superfamily, and seem to be transitional from an orthaceid ancestor (Ulrich and Cooper 1938, p. 161). While these forms and the triplesiaceids may possess a common ancestor, the former are clearly intermediate between the early Orthacea and the Clitambonitacea, and not the Triplesiacea.

As stated earlier, Williams regards the superfamily as belonging to either the

'*Pentamerus*' or the '*Orthis*' group, and indeed many features present in the Triplesiacea are common to members of both the Syntrophiacea and the Orthacea—probably the latter, rather than the other two superfamilies, for reasons given above.

The external resemblance of some syntrophiaceids to triplesiaceids (e.g. *Syntrophia* Hall 1892, with *Triplesia*) is quite striking, and the two groups have often been confused. The biconvexity of the valves is also to be found in all three superfamilies, and the spirolophous lophophore, suggested for the Triplesiacea, gives no assistance in ascertaining relationships. Neither does the very distinctive pseudodeltidium or cardinalia, for both could develop equally well from the open delthyrium and simple cardinalia found in the other two stocks.

The presence of a spondylium in most Syntrophiacea, together with the general muscle distribution, would indicate that the affinities of the Triplesiacea lie rather with the Orthacea; but in the author's opinion it is the nature of the pallial sinuses, especially of the dorsal valve, which tips the balance in favour of inclusion in the '*Orthis*' group. The arcuate *vascula myaria*, curving posteriorly around saccate gonocoeles and giving off branches anteriorly, together with the branching nature of the *vascula media* possibly with subsidiary anterior gonocoeles, produces a pattern very close indeed to a lot of contemporaneous orthaceids, e.g. *Cyrtonotella*, and the later *Orthostrophia* (Williams

EXPLANATION OF PLATE 109

The photographs are not retouched, but the specimens were coated with ammonium chloride before photographing. Abbreviations of repositories: B.B. = British Museum of Natural History, London; G.S.M. = Geological Survey and Museum, London; U.U.G. = Ústřední Ústav Geologický, Prague; I.G.S. = Irish Geological Survey, Dublin.

Fig. 1. *Triplesia extans* (Emmons 1842); postero-dorsal view of a complete specimen, showing the pedicle foramen and pseudodeltidium with median fold. Caradocian (Trenton), Watertown, New York State. B.B. 28215, $\times 1.5$.

Fig. 2. *T. insularis* (Eichwald 1842); dorsal internal mould with muscle and vascular impressions. Caradocian, nr. Corwen, N. Wales. G.S.M. 10874, $\times 2.3$.

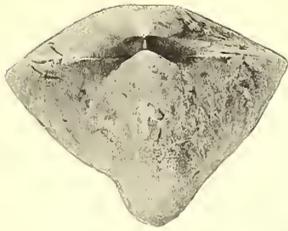
Figs. 3, 4, 6-8, 10, 11. *Cliftonia oxoplecioides* sp. nov., Ashgillian, Chair of Kildare Limestone, Kildare, Ireland. 3, 4, 8, 10, Posterior, anterior, dorsal, and lateral views of the *holotype*. B.B. 28210, $\times 1.4$. 6, Ventral valve (*paratype*). B.B. 28211, $\times 1.5$. 7, Dorsal valve (*paratype*), partly exfoliated posteriorly to reveal the muscle scars. B.B. 28212, $\times 1.5$. 11, Latex cast of an external mould, showing the strongly developed concentric ornament. B.B. 28213, $\times 3.0$.

Fig. 5. *Bicuspina spiriferoides* (M'Coy 1851); internal mould of ventral valve. Caradocian, Allt Ddu Mudstone, Y Garnedd, Bala, N. Wales. B.B. 28200, $\times 1.3$.

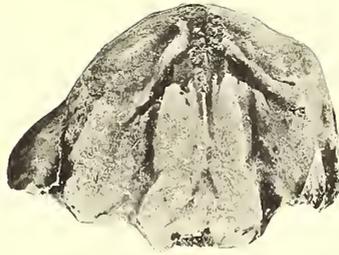
Fig. 9. *B. multicostellata* Havlíček 1950; internal mould of ventral valve. Llandeilian. Letná Beds, Chrštenice, Czechoslovakia. U.U.G. 1954. $\times 2.0$.

Figs. 12, 14, 15. *Oxoplecia multicostellata* Cooper 1956; Caradocian, Chatham Hill Formation, Sharon Springs, Virginia, U.S.A. 12, 15, Two views of a ventral valve to show the posterior thickening of the shell and the pedicle passage. B.B. 28205, $\times 2.0$. 14, View looking posteriorly into an articulated shell, showing the well-developed cardinal process directed into the ventral umbo. B.B. 28206, $\times 1.1$.

Figs. 13, 16-19. *Triplesia* sp., fragmentary silicified specimens from the low Ashgillian Limestone of Portrane, Co. Dublin, Ireland. 13, Posterior view of specimen B.B. 28209 showing cardinal process, 'brachiophores', hood, and dorsal umbo, $\times 4.8$. 16, 18, Postero-ventral and posterior views of specimen B.B. 28208 showing a medianly cleft hood to the cardinal process, $\times 5.0$. 17, 19, Oblique postero-ventral and posterior views of a specimen with a well-preserved hood (here concealing the dorsal umbo), broken cardinal process, 'brachiophore', and socket. B.B. 28207, $\times 4.7$.



1



2



3



4



5



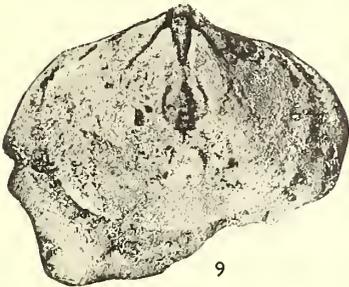
6



7



8



9



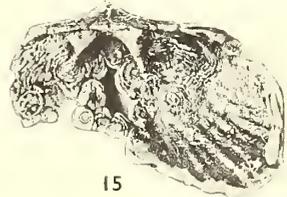
10



12



11



15



13



14



16



17



18



19

1956, p. 275, fig. 6 (3)). This is quite distinct from the digitate pattern of the Syntrophiacea.

While parallel development of this feature cannot be ruled out entirely, the present state of knowledge would suggest that the Triplesiacea developed from a stock of small biconvex orthaceids at the beginning of Ordovician times.

SYSTEMATIC PALAEOONTOLOGY

Cliftonia oxoplecioides sp. nov.

Plate 109, figs. 3, 4, 6-8, 10, 11.

Diagnosis. Dorsi-biconvex *Cliftonia*, with outline varying from subcircular to transverse, the greatest width occurring just posterior to mid-valve. Well-developed dorsal fold and ventral sulcus, very variable in shape; the fold varies in form from a flat-topped one, standing well above moderately convex flanks, to a low one, passing almost imperceptibly into very convex flanks; anterior commissure varies accordingly. Varying degree of asymmetry present in about a third of the shells examined, occasional specimens being quite contorted. Ornament of fine, concentric growth-lines, and variably developed, coarser concentric lamellae which, when indistinct, due to fine development, abrasion, or exfoliation, give the shells the appearance of *Oxoplecia*. Radial ornament of costae and costellae branching laterally or dichotomously throughout shell growth, so that one large specimen (dorsal length 16.3 mm.) has over 55 ribs at the shell margin. At a distance of 5 mm. from the dorsal umbo, the modal number of ribs on the fold is 5 or 6, with 9 on flanks, although the former may vary between 4 and 8, and the latter between 6 and 12. At 10 mm. the mode is 8 (varying between 5 and 11) on the fold, and 14 on the flanks (varying from 10 to 19). The number of dorsal valves showing a frequency of 3, 4, or 5 ribs per 2 mm. medianly at 5 mm. distance from the umbo is 26, 13, and 2; and 1, 2, 3, or 4 per 2 mm. at 10 mm. from the umbo 1, 11, 21, and 6 respectively.

Well-developed ventral interarea, pseudodeltidium with median fold and apical foramen; internally the foramen is continued in the form of a cylindrical pedicle tube (text-fig. 2).

Ventral interior with traces of muscle scars where exfoliated. Teeth supported by short dental plates.

Dorsal interior with cardinalia typical of the family; evidence of muscle scars and anterior edge of gonocoeles to be seen on some exfoliated specimens, but only sufficiently to state the pattern to be a normal one for the genus.

Type specimens (measurements in mm.):

	<i>Max. length</i>	<i>Width</i>
<i>Holotype</i> : Complete shell (B.B. 28210)	15.4	19.6
<i>Paratypes</i> : Ventral valve (B.B. 28211)	13.8	16.6
Dorsal valve (B.B. 28212)	12.4	15.7
External mould of dorsal valve (B.B. 28213)

Unfigured paratypes:

Broken ventral valve (B.B. 28214)	12.8	..
Asymmetrical complete shell (B.B. 28216)	11.6	..
Dorsal valve (B.B. 28217)	12.1	13.7
Broken dorsal valve (B.B. 28218)

Horizon and locality. Ashgillian Chair of Kildare Limestone, Chair of Kildare, Co. Kildare, Ireland.

Discussion. The valve outline of the new species varies from subrounded (typical of *Cliftonia*) to transverse (like *Oxoplecia*) with the dorsal length: valve width ranging from 91 to 70 per cent. The radial ornament distinguishes the species from the very much finer ornament of *Bicuspina*, and although both possess a pedicle tube, the stronger concentric lamellae superimposed on the growth-lines indicate that the species belongs to the genus *Cliftonia*. A pedicle tube also exists in the type species of *Cliftonia*, *C. striata* Foerste (see Ulrich and Cooper 1936, pl. 48, fig. 25), as well as in *C. lamellosa* Williams, so it would appear to characterize the genus, although suitable material for investigation of other species is so far lacking. The genus *Bicuspina*, although possessing a pedicle tube, differs in outline and ornament from *Cliftonia*.

Cliftonia oxoplecioides, the earliest species of *Cliftonia* s.s. known at present, resembles the somewhat later basal Llandovery form *C. lamellosa*. This latter differs from the new species in being much more stable in outline, having a consistently stronger concentric ornamentation, and averaging fewer ribs at the margin for specimens of similar size. Internally, the pedicle tube becomes rapidly larger anteriorly in *C. lamellosa*.

The new species exhibits variation in many features, and although specimens may be picked up which appear at first sight to be possibly a different species, a statistical assessment of a sample of seventy or so specimens showed the variation to be continuous in all characters studied.

The variation in shape of the fold between being sharp-sided and from passing evenly into the flanks seems to suggest perhaps a specific difference; but as in *Streptis* (Wright 1960, p. 267) there is continuous variation, with some specimens showing a different type of relationship on either side of the fold. Specimen B.B. 28216 has one of these asymmetric folds. Where fold asymmetry occurs, it is often evident in the rib pattern on the fold. Specimen B.B. 28217 has five ribs on the fold at a distance of 5 mm. from the umbo. Of these, three are on the left and two on the right of the median line, the third on the right-hand side being on the flank at this stage, although passing on to the fold with increased growth of the shell. Additional ribs develop on the right side only, by splitting off the existing ribs, chiefly away from the median plane (externally) so that at the commissure there are seven on the right and still three on the left side.

EXPLANATION OF PLATE 110

The photographs are not retouched, but the specimens were coated with ammonium chloride before photographing. Abbreviations of repositories as for Plate 109.

Figs. 1-3. *Triplesia anticostiensis* (Twenhofel 1914); dorso-lateral, dorsal, and postero-dorsal views of an internal mould showing the vascular markings of the dorsal valve. Upper Llandovery (C1 Beds), Sefin Footbridge, Llandovery, Wales. B.B. 28202, $\times 1.5$, 1.5 , and 1.6 respectively.

Figs. 4-6. *T. cf. insularis* (Eichwald 1842); dorsal valves from the Ashgillian Chair of Kildare Limestone, Kildare, Ireland, with the shell removed to reveal the pallial markings on the internal mould. B.B. 28203, $\times 4.6$; I.G.S., $\times 3.2$; and B.B. 28204, $\times 3.2$, respectively.

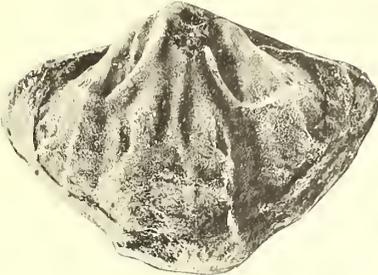
Fig. 7. *Bicuspina spiriferoides* (M'Coy 1851); internal mould showing the muscle scars and vascular markings of the ventral valve. Caradocian Horderley Sandstone, Long Lane Quarry, Craven Arms, Shropshire, England. B.B. 28201, $\times 1.7$.



1



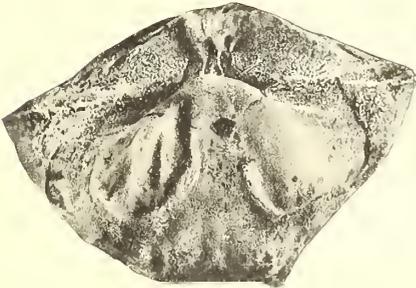
4



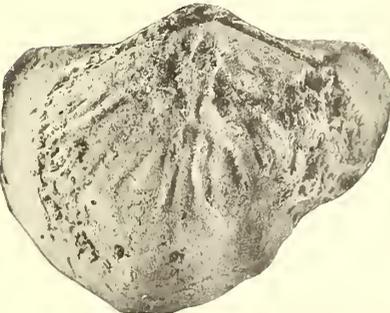
2



5



3



6



7

Five specimens, out of over 200 collected from a shell bank, show extremely pronounced concentric lamellae (Pl. 109, fig. 11) and might be thought at first to be different from the remainder. The pattern of development of the ribs is, however, identical to that of other specimens with the more usual less strongly pronounced lamellae.

Six dorsal valves with well-preserved umbonal regions showed the ribbing to originate on average at 2.15 mm. (variance 0.6) anterior of the umbo. Four primary ribs develop on the fold, the inner pair usually branching dichotomously, the outer pair externally, although branching may be delayed to a varying extent for any rib, producing a rib pattern which is almost invariably asymmetric to some degree.

Fine concentric growth-lines have been observed umbonally to number up to twenty-three per mm.; they would seem to be wider spaced in later growth (between seven and ten per mm. being observed at 10 mm. distance from the dorsal umbo), although a great deal depends on the preservation for the counting of such fine lines. The average wavelength (and variance) for the coarser concentric lamellae at 10 mm. distance from the dorsal umbo for seven specimens was 0.83 mm. (0.02).

The following statistical data were obtained for a sample of about seventy specimens:

1. 23/70 specimens showed asymmetry.
2. Shell shape: bivariate analyses of (a) ventral length : width of valve. $n = 33$; \bar{l} (var. l) = 11.58 (8.923) mm.; \bar{w} (var. w) = 13.86 (13.43) mm.; $r = 0.9249$; a (var. a) = 1.227 (0.007); $b = -0.35$.
 - (b) Dorsal length : width of valve. $n = 40$; \bar{l} (var. l) = 11.29 (8.908) mm.; \bar{w} (var. w) = 14.02 (15.63) mm.; $r = 0.9534$; a (var. a) = 1.324 (0.00577); $b = -0.93$.
 - (c) Dorsal length : thickness of complete shell. $n = 14$; \bar{l} (var. l) = 10.66 (8.55) mm.; \bar{t} (var. t) = 6.89 (5.87) mm.; $r = 0.8762$; a (var. a) = 0.8285 (0.0133); $b = -1.943$.
 - (d) Ventral length : distance anterior to ventral umbo of greatest valve width. $n = 23$; \bar{l} (var. l) = 11.8 (7.223) mm.; \bar{d} (var. d) = 5.48 (1.251) mm.; $r = 0.6763$; a (var. a) = 0.4161 (0.00447); $b = 0.57$.
3. The plication : bivariate analyses of (a) height of plication : width of plication. $n = 20$; $\bar{h}p$ (var. hp) = 3.115 (1.394) mm.; $\bar{w}p$ (var. wp) = 8.52 (3.62) mm.; $r = 0.7775$; α (var. α) = 0.602 (0.00796); $\beta = 1.458$.
 - (b) Dorsal length : height of plication. $n = 15$; \bar{l} (var. l) = 11.45 (5.72) mm.; $\bar{h}p$ (var. hp) = 2.96 (1.57) mm.; $r = 0.8046$; α (var. α) = 1.9666 (0.1048); $\beta = -3.708$.
 - (c) Dorsal length : width of plication. $n = 16$; \bar{l} (var. l) = 11.57 (5.53) mm.; $\bar{w}p$ (var. wp) = 7.98 (3.095) mm.; $r = 0.6813$; a (var. a) = 0.748 (0.0214); $b = -0.674$.
 - (d) A univariate analysis of the position of origin of the plication showed that for forty dorsal valves the mean distance anterior of the dorsal umbo (with variance) was 4.63 (1.735) mm.
4. The ribbing: the variation in numbers of ribs with shell size made it necessary for counts to be taken at a definite position on the shell surface. The rib frequencies obtained at 5 and 10 mm. from the umbos of the dorsal valves have been given above; for the ventral valve at 5 mm. the modal number of ribs in the sulcus is 5-6 (range 3-8) and 8-9 (range 4-11) on the flanks. At 10 mm. the mode is 8 ribs in the sulcus (range 6-11) and 13 on the flanks (range 9-16). The density of ribs per 2 mm. taken medianly at definite distances from the umbo has also been included in the diagnosis for the dorsal valve; for the ventral valve a frequency of 2, 3, 4, and 5 ribs was shown by 2, 19, 6, and 3 specimens at 5 mm. from the umbo; at 10 mm. 2, 3, and 4 ribs were present on 16, 10, and 3 specimens.

REFERENCES

- ATKINS, D. 1956. Ciliary feeding mechanisms of brachiopods. *Nature*, **167**, 706–7.
- 1958. A new species and genus of Kraussinidae (Brachiopoda) with a note on feeding. *Proc. Zool. Soc. Lond.* **131** (4), 559–81.
- 1959. The growth stages of the lophophore of the brachiopods *Platidia davidsoni* (EUDES DESLONG-CHAMPS) and *P. anomioides* (PHILIPPI), with notes on the feeding mechanism. *J. mar. biol. Ass. U.K.* **38**, 103–32.
- BEURLEN, K. 1952. Phylogenie und System der Brachiopoda Articulata. *Neues Jahrb. Min. Geol. Paläont. Monat.* 111–25.
- COOPER, G. A. 1944. Phylum Brachiopoda, in *Index Fossils of North America*, by H. W. Shimer and R. R. Shrock. 277–365, pl. 105–43. New York and London.
- 1956. Chazyan and related brachiopods. *Smithsonian Misc. Coll.* **127** (1–2), 1–1245, pl. 1–269.
- HAVLÍČEK, V. 1950. The Ordovician Brachiopoda from Bohemia. *Rozpr. Ústr. Úst. Geol. Praha*, **13**, 1–135, pl. 1–13.
- MOORE, R. C., LALICKER, C. G., and FISCHER, A. G. 1952. *Invertebrate Fossils*. Brachiopoda by R. C. Moore, 197–267. New York, Toronto, and London.
- MUIR-WOOD, H. M. 1955. *A history of the classification of the Phylum Brachiopoda*. 1–124. London.
- and COOPER, G. A. 1960. Morphology, classification and life habits of the Productoidea (Brachiopoda). *Geol. Soc. Amer. Mem.* **81**, 1–447, pl. 1–135.
- ÖPIK, A. 1930. Brachiopoda Protremata der Estländischen Ordovizischen Kukruse-Stufe. *Publ. geol. Inst. Univ. Tartu*, **20**, 1–261, pl. 1–22.
- 1932. Über die Plectellinen. *Ibid.* **28**, 1–85, pl. 1–12.
- 1934. Über Klitamboniten. *Ibid.* **39**, 1–239, pl. 1–48.
- ORTON, J. H. 1914. On Ciliary mechanisms in brachiopods and some polychaetes, with a comparison of the ciliary mechanisms on the gills of molluscs, protochordata, brachiopods, and cryptocephalous polychaetes, and an account of the endostyle of *Crepidula* and its allies. *J. mar. biol. Ass. U.K.* **10** (N.S.), 283–311.
- RUDWICK, M. J. S. 1960. The feeding mechanisms of spire-bearing fossil brachiopods. *Geol. Mag.* **97** (5), 369–83.
- SCHUCHERT, C. 1913. Brachiopoda, in ZITTEL, K. A. VON, edited by EASTMAN, C. R., *Textbook of palaeontology*, **1**, 355–420. London, 2nd edition.
- THOMSON, J. A. 1927. *Brachiopod morphology and genera*, 1–338. Wellington.
- ULRICH, E. O., and COOPER, G. A. 1936. New Silurian Brachiopods of the family Triplesiidae. *J. Palaeont.* **10**, 5, 331–47, pl. 48–50.
- 1938. Ozarkian and Canadian Brachiopoda. *Geol. Soc. Amer. Spec. Pap.* **13**, 1–323, pl. 1–57.
- WHITTINGTON, H. B., and WILLIAMS, A. 1955. The fauna of the Derfel Limestone of the Arênig district, North Wales. *Phil. Trans. Roy. Soc.*, ser. B, **238**, 397–430, pl. 38–40.
- WILLIAMS, A. 1951. Llandovery brachiopods from Wales with special reference to the Llandovery district. *Quart. J. Geol. Soc.* **108**, 85–136, pl. 3–8.
- 1953. North American and European Stropheodontids; their morphology and systematics. *Geol. Soc. Amer. Mem.* **56**, 1–67, pl. 1–13.
- 1956. The calcareous shell of the Brachiopoda and its importance to their classification. *Biol. Rev.* **31**, 243–87.
- WRIGHT, A. D. 1960. The species *Streptis monilifera* (M'COY). *Norsk. geol. tidsskr.* **40** (3–4), 259–76, pl. 1.

A. D. WRIGHT
 Department of Geology,
 The Queen's University,
 Belfast

SOME UPPER JURASSIC AMMONITES OF THE GENUS *RASENIA* FROM SCOTLAND

by B. ZIEGLER

ABSTRACT. Three species (one of them new) of the ammonite genus *Rasenia* from the Lower Kimeridgian of Eathie (Scotland) are described. They are of interest as being probable ancestors to different species of the one genus *Aulacostephanus*.

FOR the preparation of a monograph on the Upper Jurassic ammonite genus *Aulacostephanus* (Ziegler 1962) it was necessary to study much material from the whole of central and Western Europe. For this purpose, Dr. C. D. Waterston, Edinburgh, had the kindness to send me some specimens from the Lower Kimeridgian of Eathie (Ross-shire, Scotland). Since one of the species contained in this material was hitherto unknown and of special interest as being ancestral to some *Aulacostephanus*, it seems useful to describe the ammonite fauna briefly.

I am much indebted to Dr. C. D. Waterston for sending me the material, and to Dr. J. H. Callomon, London, and Dr. O. F. Geyer, Stuttgart, for much advice, help, and discussion. The photographs were made by Mr. J. Aichinger, Zürich. In translating the text, I was assisted by Dr. M. Schnitter and Mr. A. Somm, Zürich.

The specimens studied are part of the Hugh Miller Collection of the Royal Scottish Museum, Edinburgh. They were collected, together with other ammonites, during the last century. Stratigraphical data therefore are not given. They seem, however, to come from the limestones described by C. D. Waterston (1951) as belonging to the *walensis* Zone.

All the specimens are perfectly preserved. Often even the shell, though recrystallized, is present. The phragmocones are usually filled with white crystals of calcium carbonate; the body-chamber, however, is filled with sediment. Since parts of the body-chambers are crushed, the peristomes are never preserved. Sometimes the ammonites are accompanied by other fossils (such as *Meleagrinnella* and *Buchia*).

SYSTEMATIC DESCRIPTIONS

The ammonites are characterized by short primary, and long fine secondary, ribs crossing the venter. These features permit their classification as members of the genus *Rasenia*. Within this genus Geyer (1961) distinguishes six subgenera. Three of them (*Rasenia* s.str., including *Zonovia*, *Eurasenia*, and *Prorasenia*) bear coarse and/or sharp ribs, a fourth (*Involuticeras*) is very involute with a rather steep umbilical slope. Our ammonites, on the contrary, are finely ribbed, slightly involute to evolute and possess a gentle umbilical slope. Therefore they must be placed with the subgenera *Rasenioides* and/or *Semirasenia*.

According to Geyer a small shell is characteristic of *Rasenioides* (type: *A. striolaris*); some species (if not all) bear lappets on the peristome. Thus *Rasenioides* is a microconch (Callomon 1955). *Semirasenia*, on the other hand, seems to be a macroconch. The shell of the type species is, however, also of small size. Although its peristome is not known, it is quite probably devoid of any lappet, since the derivatives of *Semirasenia* (the subgenus *Aulacostephanoides*) do not bear lappets.

Geyer emphasizes the late appearance of the primary ribs in *Semirasenia* (in *S. möschi* the umbilical parts of the whorls remain smooth up to the body-chamber). This feature does not necessarily seem to imply subgeneric rank. Experience with the closely related genus *Aulacostephanus* shows very great variation in the appearance of the primaries.

Summarizing, it may be justifiable to classify all apparently macroconch species of *Rasenia*, with fine ribs and gentle umbilical slopes, with the subgenus *Semirasenia*. However, there is no proof or phylogenetic justification for this procedure. Since the British *Rasenia* have not been monographed it is impossible to draw lineages in any other ways than merely on morphological and arbitrary grounds.

Rasenia (*Rasenioides*) *lepidula* (Oppel)

Plate 111, figs. 1–7

1863 *Ammonites lepidulus* Oppel, p. 242, pl. 67, fig. 4.

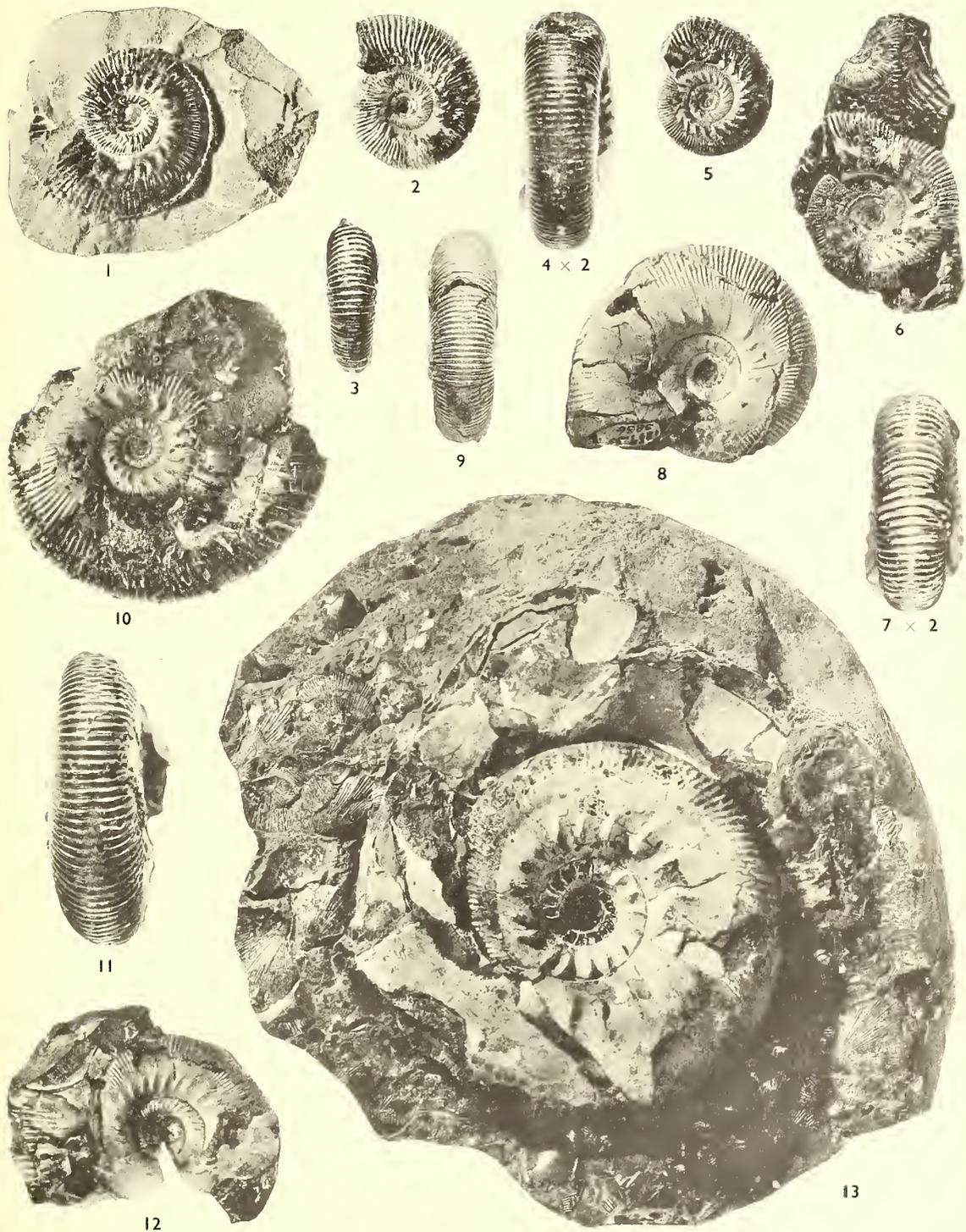
1961 *Rasenia* (*Rasenioides*) *lepidula* (Oppel 1863), Geyer, p. 112, pl. 8, figs. 5, 6.

The small shell does not exceed approximately 40 mm. in size. The body-chamber (bearing lappets at the peristome, but only partly preserved in our specimens) is about two-thirds to three-quarters of a whorl in length. The maximum diameter of the phragmocone, therefore, is about 25 mm. However, the majority of our specimens from Scotland being somewhat smaller, the diameter of the phragmocone averages about 20 mm. Often the last two or three septa are approximated (see Pl. 111, fig. 1). This may be considered a feature of adulthood.

Our shells are slightly evolute (in contrast to Geyer's statement for his central Euro-

EXPLANATION OF PLATE 111

- Figs. 1–7. *Rasenia* (*Rasenioides*) *lepidula* (Oppel); Lower Kimeridgian, *uralensis* Zone; Eathie, Ross-shire, Scotland. 1, Natural size. Diameter of the phragmocone 19 mm. Royal Scottish Museum, Department of Geology, 1859.33.3844. 2, Natural size. Diameter of the phragmocone 18.5 mm., 1859.33.3858. 3, Natural size. Ventral view. 1859.33.3858. 4, $\times 2$. Ventral view, secondary ribs diminishing in height, 1859.33.3853. 5, Natural size. Diameter of the phragmocone 15.8 mm., 1859.33.3853. 6, Natural size. Diameter of the phragmocone 28 mm. 1859.33.3859. 7, $\times 2$. Ventral view, secondary ribs interrupted by a narrow median ledge on the internal side of the shell. 1859.33.3857.
- Figs. 8–9. *Rasenia* (*Semirasenia*) cf. *möschi* (Oppel); Lower Kimeridgian, *uralensis* Zone; Eathie, Ross-shire, Scotland. Royal Scottish Museum, Department of Geology, 1859.33.3856. Natural size. 8, Lateral view, diameter of the phragmocone 35 mm. 9, Ventral view.
- Figs. 10–13. *Rasenia* (*Semirasenia*) *askepta* sp. nov.; Lower Kimeridgian, *uralensis* Zone; Eathie, Ross-shire, Scotland. All natural size. 10, Diameter of the phragmocone about 35 mm. (?). Royal Scottish Museum, Department of Geology, 1859.33.3846. 11, Same ventral view. 12, Diameter of the phragmocone about 33 mm. (?). 1859.33.3850. 13, Diameter of the phragmocone 59 mm., length of the body-chamber (crushed) more than three-quarters whorl. 1859.33.3845. Accompanying fossils: *Meleagrinnella leana* Waterston and *Bnchia concentrica* (Sowerby).



pean material). The lateral parts of the whorls are nearly flat (at least on the outer whorls), and the venter is rounded. The umbilical slope in the phragmocone and the body-chamber is gentle. As a whole the whorl section is oval.

Around the umbilicus, but somewhat removed from the umbilical seam, there are narrow, sharp but low, prorsicostate primaries. They split into rather dense, radial secondaries. These secondaries cross the venter. Only occasionally is there observed a narrow ledge in the middle of the venter on the internal surface of the shell. This ledge points to a developmental trend leading to *Aulacostephanus*. The tendency is for the siphuncle to sink more and more into the interior of the whorl. The aforesaid narrow ledge is the first step; the second step is a clear interruption of the ribs in some parts of the venter; the third step is the interruption on the whole of the venter; and the last step is a real furrow as in *Aulacostephanus eudoxus*.

Measurements:

<i>Specimen number</i>	<i>Diameter (mm.)</i>	<i>Height of whorl</i>	<i>Whorl width</i>	<i>Umbilical diameter</i>	<i>Number of primaries (at a diameter of 20 mm.)</i>	<i>Number of secondaries (at a diameter of 20 mm.)</i>
1859.33.3858	26 18	36 37	32 33	36 37	26	86 (3·3)
1859.33.3844	28·4 23	34 35		39 39	24	78 (3·25)
1859.33.3853	21·7	36	35	41	26	102 (4·4)
1859.33.3857	18	39	38	37	30	80 (2·7)
1859.33.3859	29	35	31	39	20	108 (5·4)

(at a diameter of 30 mm.)

Our specimens differ slightly from the material from central Europe described by Geyer (1961). The shells are more evolute, the number of primaries at the diameter of 20 mm. is greater, and therefore the ratio of primaries to secondaries is not the same. Most likely this is not due to specific (or subspecific) differences, but to the small number of specimens studied.

Rasenia (Semirasenia) cf. möschi (Oppel)

Plate 111, figs. 8-9

cf. 1863 *Ammonites Möschi* Oppel, p. 240, pl. 65, fig. 2.

cf. 1961 *Rasenia (Semirasenia) moeschi* (Oppel 1863), Geyer, p. 105, pl. 8, figs. 7, 8.

According to Geyer the medium size in *Rasenia möschi* is less than 70 mm. If we assume the body-chamber to be nearly a whorl in length (Oppel 1863) the mean diameter of the phragmocone would be about 30 mm. Our specimens fit these measurements quite well. Two individuals show the end of the phragmocone at 33 and 35 mm. respectively. In other specimens (most likely immature ones) the body-chamber begins at 23 and 21 mm. respectively. The shells are involute. As in *Rasenia lepidula* the umbilical slope is very gentle. The lateral parts of the whorl are very slightly vaulted, the venter is rounded.

In our specimens no peristome is preserved; but, as mentioned above, it is probable that no lappets are present. The body-chamber seems to comprise nearly a complete whorl. In our specimens, however, only the beginning of the body-chamber is to be seen.

On the inner whorls the umbilical region of the whorl is smooth. In the last half whorl of the phragmocone of our specimens, narrow somewhat elongate ribs appear. These primaries are separated from the secondaries by a smooth band. The secondaries are bent forward and arranged very densely. They cross the venter without any interruption but sometimes with an indistinct loss of relief.

Measurements:

<i>Specimen number</i>	<i>Diameter (mm.)</i>	<i>Height of whorl</i>	<i>Whorl width</i>	<i>Umbilical diameter</i>	<i>Number of primaries</i>	<i>Number of secondaries</i>
1859.33.3856	35.5	40	34	31	9	66 (7.3)
1859.33.3847	35	39	34	32	5	59 (11.8)
1859.33.3854	23.5	42	35	30	..	66
1859.33.3852	29	44	36	27	..	68

The Scottish material differs from *Rasenia möschi* (typ.) in the primaries appearing already on the phragmocone. In the type of *Rasenia möschi* and in additional (but very scanty) material, on the other hand, the primaries are restricted to the second part of the body-chamber. Therefore specific identity with our material cannot be proved.

Rasenia (Semirasenia) askepta sp. nov.

Plate 111, figs. 10-13

Holotype. Plate 111, figs. 10-11; Royal Scottish Museum, Edinburgh, 1859.33.3846.

Locus typicus. Eathie (Ross-shire, Scotland).

Stratum typicum. Lower Kimeridgian, presumably upper part of the *uralensis* Zone.

Description of the holotype. Maximum diameter 52 mm. Height of whorl 41 per cent., whorl width 31 per cent., umbilical diameter 30 per cent. Umbilical slope very gentle, lateral parts of the whorl slightly rounded, venter vaulted, whorls oval to somewhat trapezoidal. Peristome not preserved. Doubtful whether the body-chamber is present, but the state of preservation points to a maximum diameter of the phragmocone of about 35 mm. Sutures not visible.

Primaries distant from the umbilical seam, narrow, sharp, bent forward. On the last four half whorls: 8, 8, 10, and 9 primaries, respectively. Secondaries: 55, 42, and 50, respectively, on the last three half whorls, densely arranged and prorsicostate. Ribs cross the venter without interruption but slightly diminish in height. Ratio of secondaries to primaries 6.9 (at a diameter of 50 mm.), 5.3 (diameter 35 mm.), and 5.0 (diameter 25 mm.).

Remarks. Some other specimens similar to the holotype may be grouped with the same species. They differ in the number of primaries per half whorl (8-13). The number of secondaries per half whorl may reach 60, and the ratios of secondaries to primaries differ from 4.6 to 8. It seems that smaller ratios are consistent with small diameters. Another variable feature is the degree of the ribs' relief on the venter. But a clear, smooth, external band is never developed.

The diameter of the phragmocone is also variable: it measures 59 mm. (Royal Scottish Museum, 1859.33.3845), about 72 mm. (1859.33.3849), and 110 mm. (1859.33.3843), but it never seems to reach such immense dimensions as reported for *Aulacostephanus mutabilis* (Ziegler 1962).

A. mutabilis (Sowerby) is very closely related in sculpture but of greater size and with ribs interrupted on the venter. Apart from these two features there are no other differences between the two species. *A. mutabilis* occurs in younger beds, in the *mutabilis* Zone, while *Rasenia askepta* seems to be found in the upper part of the *uralensis* Zone (as proved by the accompanying species *Rasenia lepidula* and *R. cf. möschi*). It is clear that *R. askepta* and *A. mutabilis* belong to one phylogenetical lineage. It must be mentioned, however, that neither size nor sculpture of the venter of a single specimen permits specific determination. As in other cases some individuals may differ from the morphological mean of a population. Therefore only the expression of a feature found in the majority of the specimens would be of taxonomic value. Sometimes additional support may come from other contemporaneous species.

CONCLUSION

The three species described are true *Rasenia* (sensu Geyer), meaning that they bear ribs crossing the venter. They belong to the subgenera *Rasenioides* and *Semirasenia*. For each of the three species there are similar species known with clear external interruptions of the ribs. The latter are therefore grouped with *Aulacostephanus* (Ziegler 1962). The boundary between *Rasenia* and *Aulacostephanus* is arbitrary. Callomon (1963) places all individuals with *Aulacostephanus* in which the external ribs are interrupted—either on all stages or on parts of a whorl. Geyer (1961) and I prefer to interpret *Aulacostephanus* as a genus in which the majority of all individuals in every population show interruption of the external ribs throughout life.

It seems highly probable that the three *Rasenia* described are ancestral forms of the corresponding species of *Aulacostephanus*. Probable relationships are that *Rasenia lepidula* leads to *Aulacostephanus eulepidus*, *R. möschi* is ancestral to *A. variocostatus*, and *R. askepta* gives rise to *A. mutabilis*. The genus *Aulacostephanus* therefore is polyphyletic in the narrow sense of the word, but monophyletic if derivation from the one genus, *Rasenia*, is considered.

REFERENCES

- CALLOMON, J. H. 1955. The ammonite succession in the Lower Oxford Clay and Kellaway Beds at Kidlington, Oxfordshire, and the zones of the Callovian stage. *Phil. Trans. Roy. Soc. London*, B, **239**, 664, 215–64.
- 1963. Lower Kimeridgian ammonites from the Drift of Lincolnshire. *Palaeontology*, **6**.
- GEYER, O. F. 1961. Monographie der Perisphinctidae des unteren Unterkimeridgium (Weisser Jura γ , Badenerschichten) im süddeutschen Jura. *Palaeontographica*, A, **117**, 1–157.
- OPPEL, A. 1863. Über jurassische Cephalopoden (Fortsetzung). *Paläont. Mitt. k. bayer. Staat*, **1**, 3, 163–262.
- WATERSTON, C. D. 1951. The stratigraphy and palaeontology of the Jurassic Rocks of Eathie (Cromarty). *Trans. Roy. Soc. Edinburgh*, **62**, 1, 33–51.
- ZIEGLER, B. 1962. Die Ammoniten-Gattung *Aulacostephanus* im Oberjura (Taxionomie, Stratigraphie, Biologie). *Palaeontographica*, A, **119**, 1–172.

B. ZIEGLER

Paläontologisches Institut der Universität,
Zürich, Switzerland

PERMIAN HYSTRICHOSPHERES FROM BRITAIN

by DAVID WALL and CHARLES DOWNIE

ABSTRACT. Hystrichospheres are described from the Permian of Britain for the first time and are allocated to four genera and eleven species, two of which are new. Closest comparison is with other Permian assemblages but many of the hystrichospheres present appear to be virtually indistinguishable from forms known to occur in beds ranging from the Ordovician to the Eocene in age.

LARGE numbers of small hystrichospheres have recently been found in the Lower Permian Marls of Yorkshire. Hitherto, Permian hystrichospheres have only been recorded from Yugoslavia and the Sahara (Jekhowsky 1961) and from North America (Wilson 1960), although Triassic hystrichospheres have been described from Switzerland (Brosius and Bitterli 1961) and the Soviet Arctic (Kara-Murza 1957). Wilson, however, only described a single specimen, so that comparison is mainly with Jekhowsky's material. His published descriptions are restricted to a number of forms allocated to the genus *Veryhachium* and do not cover the variety of types found in the British assemblages, which belong to eleven species representing the genera *Baltisphaeridium*, *Micrhystridium*, *Veryhachium*, and *Leiofusa*.

The material was prepared according to the standard procedure for the recovery of acid-insoluble microfossils (Funkhauser and Evitt 1959); pollen and spores account for about 30 per cent. of the fossil assemblage.

Location of the samples. Sample A was collected in the Ashfield Brick Pit, Conisbrough, Yorkshire (Grid Ref. 514983), from the Lower Permian (Bed J of Gilligan 1918) and consisted of a grey marl.

Sample B came from the Ash Hill Borehole, near Sykehouse, Yorkshire (Grid. Ref. 621161) from the Lower Permian Marl at a depth of 1,006 feet.

All the specimens described are now in the collection of the Micropalaeontology Laboratory of the Department of Geology, University of Sheffield.

GENERAL CHARACTER OF THE HYSTRICHOSPHERE ASSEMBLAGE

The hystrichosphere assemblage as a whole is characterized by the small size of the individuals present. Their average size is about $15\ \mu$ and even the species of *Baltisphaeridium* present does not exceed $25\ \mu$ in test diameter.

Another feature is the variability of the hystrichospheres. Apart from four distinctive species, readily separated from each other and the remainder, all the hystrichospheres form a plexus of morphological variation transgressing the boundary between *Micrhystridium* and *Veryhachium* and including forms morphologically identical or akin to seven described species. The modal forms in this plexus must certainly be identified as *Veryhachium? irregulare* Jekhowsky and the group as a whole is referred to here as the '*V. ? irregulare*' complex (text-fig. 1a-z).

The problems of taxonomy raised by the variation within this plexus cannot be dismissed simply by uniting all the forms in a single species. To do so would cause con-

siderable confusion since homoeomorphs of many previously named species occur and the diagnoses of two genera would have to be altered in such a way as to make them largely inseparable. Furthermore, it is considered desirable to retain several specific names for the morphotypes present since it is known that similar variable groups occur at other horizons, but with an emphasis on different morphotypes.

To adapt a 'natural' classification in these circumstances would lead to confusion and the identification of single specimens or small assemblages would require prior knowledge of their geological age. It has therefore been the policy of the authors to accept the species already described as morphological entities and to identify with them, all forms having identical or closely similar shapes, irrespective of age or of gradations into other forms.

Minor variations in morphology, for example, in spine length, rigidity of spines, breadth of spine bases, have been given consideration and where it has been thought that these form an insufficient basis on which to erect new species, the specimens have been described as *formae* within the species. Species are distinguished on the basis of more obvious characters such as the number of spines and the shape of the test.

The authors would have preferred a system of classification more closely adjusted to the biological facts and have tried to restrict the number of these artificial species and *formae* to the minimum.

MICRHYSTRIDIUM AND VERYHACHIUM

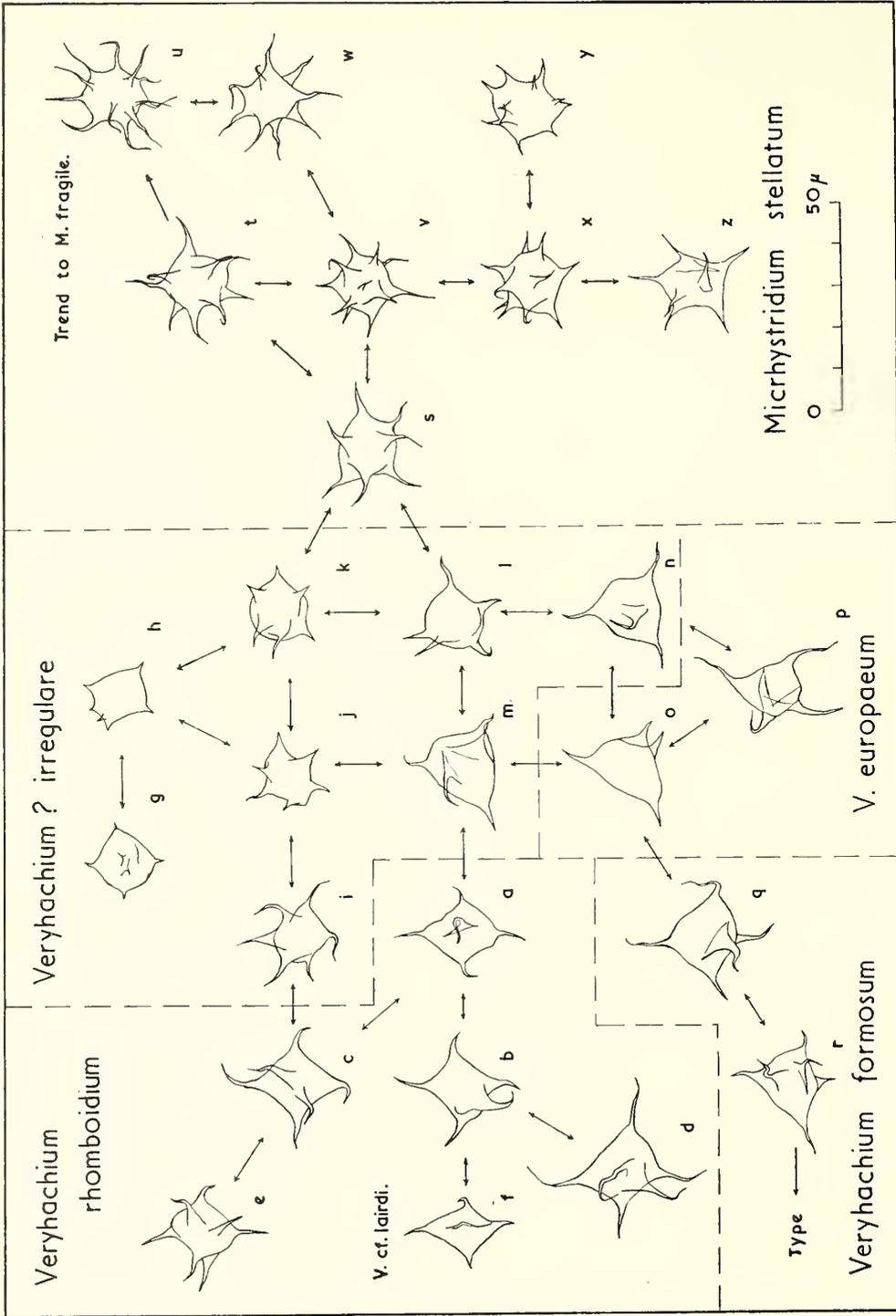
The '*V. ? irregulare*' complex includes at one extreme forms with only four processes and a polygonal test, which generally would be considered typical members of the genus *Veryhachium*; at the other extreme are small spherical hystrichospheres with as many as twenty spines, which would indubitably be placed in *Micrhystridium* by most authors. It would cause confusion to place the plexus entirely within one or other of these genera and therefore an arbitrary distinction has been made between the two.

The basis of this distinction has been the original definition of *Veryhachium* by Deunff (1945*b*), emended by the transfer of *Veryhachium monocanthum* by Downie (1960). The genus includes species with non-globose tests with three to eight spines. Some authors (Staplin, 1961) have subsequently included forms with sixteen processes, but this is not justified, although occasionally it may be necessary to include a specimen with nine or ten spines if the additional spines are 'adventitious' and do not alter the normal test shape of the species possessing eight or less spines.

In the '*V. ? irregulare*' complex the gradation between *Veryhachium* and *Micrhystridium* involves both an increase in spine number and a transition towards a globose shape. Distinction between the two genera is based on the definition of *Veryhachium* given above, so that within this genus are included forms with polygonal and subpolygonal tests with eight or less spines and a few individuals with markedly polygonal tests and additional 'adventitious' spines. *Micrhystridium* embraces that part of the complex with globose and subspherical tests generally with seven or more spines.

The systematic importance of small spines

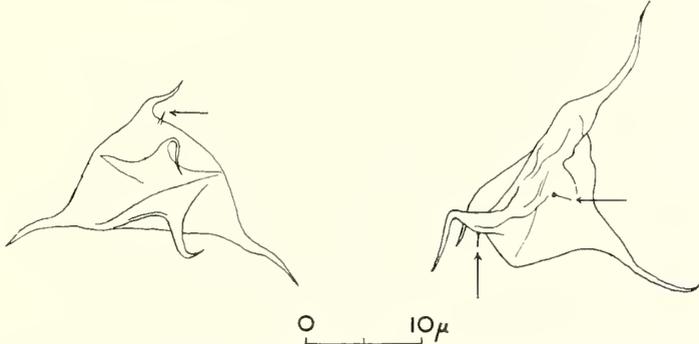
Certain specimens of *Veryhachium* occurring in the Permian have very small processes, 1 to 3 microns in length, in addition to the normal spines (text-fig. 2; Pl. 114, fig. 12).



TEXT-FIG. 1. Hystrichospheres of the 'Veryhachium? irregulare' complex from the British Permian. a-e, *V. rhomboidium*. a, Forma 1. b, c, Forma 2. d, Forma 3. e, Forma 4. f, *V. cf. lairdi*. g-n, *Veryhachium? irregulare*. g, h, Forma 1. i-k, Forma *subhexaedron*. l, m, Forma *irregulare*. n, Forma *subtetraedron*. o-p, *V. europaeum*. o, Forma 1. p, Forma 2. q-r, *V. formosum*, q, Forma 1. r, Forma 2. s-z, *Michrhystridium stellatum*. s, Forma 6. t, Forma 2. u, Forma 3. v, Forma *stellatum*. w, Form similar to forma 5 but with less-expanded spine bases. x, Form transitional between forma *stellatum* and z, Forma 1. y, Forma 4.

These small processes, which appear to be solid, are situated on the faces of the polygonal tests, either centrally or close to the main spine bases; as many as three may be present on an individual specimen.

Staplin (1961), in describing *Veryhachium* cf. *trispinosum*, noted a minute structure (presumably spinous) interpreted as a flagellar sheath. The small spines on our Permian forms cannot be interpreted in this way, for there may be up to three on an individual and their distribution on the test is random. It is considered more likely that they are underdeveloped processes. Examination of a large number of individuals shows that



TEXT-FIG. 2. *Veryhachium* sp., with small spines in addition to larger processes (examples from sample A).

some variation in spine length occurs in all specimens, and although a complete gradation in size between the small spines and the larger is not always obvious, separation of small and large spines is very subjective.

Forms of Micrhystridium in the 'V. ? irregulare' complex

All the forms of *Micrhystridium* within the complex are attributed to *M. stellatum* Deflandre, but often show slight differences from the typical Silurian material in spine length and shape. The forms described by Deflandre have globose to rather polygonal tests bearing about twelve spines, more than 50 per cent. of the diameter in length; their bases expand only slightly where they join the test. Other Silurian material described by Downie (1959) indicates that the number of spines may be as few as five in optical section and the spine length ranges from 60 to 120 per cent. of the test diameter.

Of the twelve specimens of *M. stellatum* illustrated by Stockmans and Willière (1960, pls. 1, 2), examples occur resembling both the Silurian and Permian material. Valensi (1953) and Sarjeant (1959, 1960, 1961) have also described forms of *M. stellatum* from the Jurassic of France and Britain. These are indeed similar to the Palaeozoic fossils but their spine-bases tend to be more expanded and to taper uniformly towards the tip (Sarjeant, 1959, p. 341).

In the Permian assemblage dealt with here, globose, subpolygonal, and polygonal forms occur, some of which, having expanded spine bases tapering gradually distally, are almost identical with the Jurassic forms, while others having more constricted spine bases and tapering more rapidly proximally, closely resemble the Devonian and Silurian specimens. In addition, there is a trend towards shortening of the spines and the relative length may be as low as one-third of the test diameter.

Globular forms of *M. stellatum* and polygonal forms with relatively numerous spines occurring in the Permian may also closely resemble the Mesozoic species *Micrhystridium fragile* Deflandre. Both species have spines equivalent in length and number to each other and *M. fragile* may tend to develop a polygonal test, for example those figured by Valensi (1953, pl. 5, fig. 4). The only criterion left which can usefully serve to separate the two species is the nature of the spines. *M. stellatum* possesses relatively rigid spines with expanded bases while *M. fragile* has more delicate spines without expanded bases (Valensi 1953, p. 43). Separation of the two species becomes artificial to some extent, especially in some Jurassic strata, but on this basis the Permian forms must be regarded as belonging to *M. stellatum* since their spine bases are always expanded even if the spines are not always rigid. Forms directly comparable with the holotype of *M. fragile* (Deflandre 1947, fig. 13) were not found in the Permian assemblages.

Forms of Veryhachium in the 'V. ? irregulare' complex

The remainder of the plexus consists of polygonal and subpolygonal forms, generally with four to six spines. The subpolygonal forms here have recently been described from the Permo-Trias by Jekhowsky (1961) as *Veryhachium ? irregulare*. Of the four *formae* he described, three occur in the Yorkshire Permian, only *forma pirula* being absent. The doubt expressed by Jekhowsky in attributing these forms to *Veryhachium* is understandable, since they are transitional in form to *Micrhystridium*, but in view of the distinction between the two genera discussed earlier, this question is not pursued any further here. Complete transition also occurs between the subglobular forms of *V. ? irregulare* and polygonal forms with four to six spines allocated to other species of *Veryhachium*.

With respect to the test shape of the polygonal forms, two basic series can be distinguished, one being octagonal, the other tetrahedral. Members of the first series typically have six spines projecting from their apices, but may have any number from four to nine. The second series typically has four spines but may occasionally have as many as eight spines without losing their basic tetrahedral shape.

The typical octagonal forms are very similar to *Veryhachium rhomboidium* Downie from the Silurian and may be considered as homoeomorphs of the latter. In view of their basic similarity in shape the Permian forms are allocated to this species. There are, however, slight differences which are expressed by the recognition of three new *formae*. These are not named here, but if it is subsequently found desirable to name them, this can readily be done. However, if any other new hystrichospheres are found (referable to a species within the complex) it is hoped they will be named as *formae* and not as new species based on obscure and unstated differences which might confuse morphological relationships and render identification almost impossible. It is not, however, implied that the naming of all species of microplankton should be based on such arbitrary morphological distinctions. The system applied here is considered a temporary expedient in this difficult group of hystrichospheres.

A few forms with five spines (three of which lie in an 'equatorial' region and the other two at the poles) also occur and appear to be morphologically transitional between *V. rhomboidium* and forms resembling *V. lairdi* Deunff from the Caradocian of Brittany. The latter species is characterized by four spines arranged at the apices of a rectangular or rhomboidal pad; a Permian form with four spines is compared with this species.

The typically tetrahedral forms of the second series resemble two previously recorded species in shape and spine number. These are *Veryhachium tetraëdron* Deunff and a morphologically similar but smaller species, *V. europaeum* Stockmans and Willière. The former species name was introduced by Deunff (1954a, fig. 9, p. 1065) for hystrichospheres occurring in the Devonian of Canada. No description accompanied or preceded his illustration and the species name is therefore illegitimate (Article 32, International Rules of Botanical Nomenclature). *V. tetraëdron* var. *wenlockia* Downie 1959 must also be illegitimate (Article 42, loc. cit.). The Permian forms are allocated to the legitimate species *V. europaeum* and two new *formae* are distinguished. *V. tetraëdron* var. *wenlockia* is renamed as *V. europaeum* Stockmans and Will. var. *wenlockianum* var. nov.

The remainder of the second series retains the basic tetrahedral shape but the four apical spines are augmented by processes arising from the test faces. These specimens are allocated to *V. formosum* Stockmans and Will. because of their great similarity to the Devonian species but two slightly distinct Permian *formae* are recognized. There may be up to four additional spines present bringing the total number to eight, but the test remains triangular in outline.

V. ? riburgense f. *regulare* Brosius and Bitterli from the Trias of Switzerland is to be regarded as a closely related member of this series, transitional between *V. ? riburgense* f. *irregulare* and *V. formosum*, but differing from the latter species by its inflated test and shorter spines. *V. ? riburgense* f. *irregulare* is similar to *V. ? irregulare* but has more spines.

Some forms appear to be intermediate between the octahedral and tetrahedral series, in which case their classification becomes difficult. However, in most cases these forms appear to be identifiable as specimens of *V. formosum* that have been slightly distorted during fossilization. Plate 114, fig. 7 illustrates a typical example whose outline comprises two equal and straight sides and a third longer, convex side. Since the outline is not four-sided as in *V. rhomboidium* or *V. lairdi* the specimen is allocated to *V. formosum*.

Comparison of the assemblages

A comparison of the proportional distribution of hystrichospheres in samples A and B (Table 1) reveals a considerable difference in their composition. Sample A is dominated by *V. ? irregulare*, *V. europaeum* forma 1, and *V. reductum* while *B. deblispinum* sp. nov., *V. flagelliferum* sp. nov., and *M. stellatum* dominate sample B. The prominent forms in one sample are uncommon or absent in the other.

A precise stratigraphical correlation of the two samples is not possible, but both occur within the Lower Permian Marl, which is relatively restricted in thickness (maximum 20 feet) in south Yorkshire. It is probable that the assemblages differ due to lateral rather than vertical changes in the fossil composition of the horizon. The Conisbrough assemblage (sample A) is possibly representative of a facies nearer shore since the pollen content is twice that of sample B, taken approximately 13 miles to the NNE. Furthermore, its hystrichospheres are always small subpolygonal or polygonal forms with small spires only a few microns in length, compared with the more inflated and longer-spined forms encountered in sample B; this interpretation is in agreement with other geological information.

TABLE 1. Proportional distribution of hystrichosphere species in two samples from the British Permian.

List of species	Percentage in preparation	
	Sample B	Sample A
<i>Baltisphaeridium debilispinum</i> sp. nov.	50.2	..
<i>Micrhystridium recurvatum</i> Valensi	0.4	..
<i>Veryhachium flagelliferum</i> sp. nov.	13.4	..
<i>Veryhachium reductum</i> (Deunff) Jekh.	1.1	7.8
<i>Leiofusa jurassica</i> Cookson. and Eis.	0.4	..
<i>Micrhystridium stellatum</i> f. <i>stellatum</i>	4.0	..
<i>M. stellatum</i> forma 1	6.1	0.9
<i>M. stellatum</i> forma 2	1.9	..
<i>M. stellatum</i> forma 3	1.6	..
<i>M. stellatum</i> forma 4	1.9	0.5
<i>M. stellatum</i> forma 6	2.8	..
<i>V. irregulare</i> f. <i>subhexaedron</i>	1.1	18.2
<i>V. irregulare</i> f. <i>subtetraedron</i>	0.4	2.7
<i>V. irregulare</i> f. <i>irregulare</i>	1.1	17.3
<i>V. irregulare</i> forma 1	0.4	12.3
<i>V. rhomboidium</i> forma 1	1.1	5.0
<i>V. rhomboidium</i> forma 2	0.4	..
<i>V. rhomboidium</i> forma 3	4.0	0.5
<i>V. rhomboidium</i> forma 4	1.9	0.5
<i>V. cf. lairdi</i>	..	0.5
<i>V. europaeum</i> forma 1	1.8	18.2
<i>V. europaeum</i> forma 2	..	4.1
<i>V. formosum</i> forma 1	2.1	7.8
<i>V. formosum</i> forma 2	1.9	3.7
Total percentage	100.0	100.0
Number of Hystrichospheres	277	219
Number of pollen grains	73	140
Total number of specimens counted	350	359

COMPARISON WITH OTHER ASSEMBLAGES

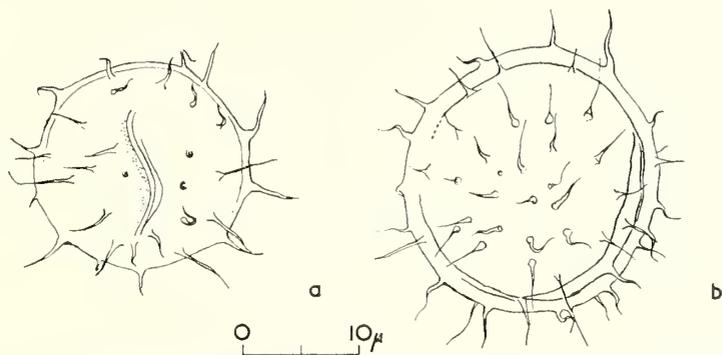
The hystrichospheres in sample A correspond most closely to those described by Jekhowsky (1961) from the Permo-Trias of Africa and Europe, although they are generally less inflated. The dominant species in sample B are new, but comparison may be possible when details of various *Micrhystridia* briefly mentioned by Jekhowsky become available. The Permian specimen from Oklahoma described by Wilson (1960) as *Hystrichosphaeridium* sp. is quite different from any seen in the British Permian.

Some Devonian species of *Veryhachium* and *Micrhystridium* illustrated by Stockmans and Willière (1960) are also very like the British Permian forms, but the Devonian assemblage is richer in species and the genera *Polyedryxium* and *Cymatiosphaera*, absent in the Yorkshire assemblages, also occur. Most of the Devonian hystrichospheres described by Staplin (1961) from Alberta also differ considerably from those in the Permian, but *Veryhachium brevitriscopinosum* Staplin and *V. sp. cf. H. trispinosum* closely resemble *V. reductum* Jekhowsky, and *V. sedecimspinosum* Staplin resembles *M. stellatum* (forma 1 below). *V. reductum* also occurs in Carboniferous marine shales from Britain (personal communication, Mr. F. Spode) and north-west Spain (personal communication, Dr. R. Neves).

The assemblage described by Brosius and Bitterli (1961) from the Trias of Switzerland comprises hystrichospheres very similar in overall morphological characteristics to the Permian forms. However, detailed comparison reveals that all the species described apart from *V. reductum* differ in some respect from the Yorkshire specimens. Additional work is necessary to prove whether or not these distinctions are always valid.

Most of the British Permian hystrichospheres persist into the Lower Jurassic and somewhat similar assemblages dominate the British Lias. Within the Middle and Upper Jurassic, however, the small forms of *Veryhachium* apparently become very rare or are entirely absent with the incoming of more complex hystrichospheres and dinoflagellates (Valensi, 1953; Sarjeant, 1959).

The assemblage is therefore composed mostly of long-ranging species, which differ only slightly in the *formae* present from counterparts in earlier and later horizons. It is noteworthy in the absence of the larger, more distinctive forms that commonly occur in the Lower Palaeozoic and Mesozoic. Whether this is characteristic of the environment or of the time is not yet known.



TEXT-FIG. 3a, b. *Baltisphaeridium debilispinum* sp. nov. a, Holotype PB/11 91.0 32.7. b, Paratype, with maximum number of spines and marginal folding of the test wall; single mount. (Both specimens from sample B.)

SYSTEMATIC DESCRIPTIONS

Order HYSTRICHOSPHAERIDEA Eisenack

Section 1. Hystrichospheres excluding the '*V. ? irregulare*' complex

Family HYSTRICHOSPHAERIDAE O. Wetzel 1933

Genus BALTISPHAERIDIUM Eisenack 1958

Baltisphaeridium debilispinum sp. nov.

Plate 112, figs. 1, 2; text-fig. 3a, b

Holotype. Slide PB/11, 91.0 32.7. Plate 112, fig. 2. Diameter 18 μ .

Diagnosis. Test spherical, smooth, relatively thick-walled; spines slender, straight or curved, with conical bases 1 μ in diameter; number of spines twenty to fifty, length 20 to 25 per cent. of the test diameter, sometimes up to 50 per cent.

Dimensions. Test diameter 16 (22) 25 μ ; test wall 1 to 2 μ thick (fifty specimens measured).

Description. The thickness of the test wall is approximately 10 per cent. of the diameter and the inner margin is frequently visible as a distinct line under the microscope. The wall often folds. The spine bases are circular, 1 to 2μ wide, but taper abruptly to form slender processes which do not appear to communicate with the test lumen. Smaller specimens tend to possess a thicker wall and fewer spines, while larger forms have relatively shorter spines and a thicker wall.

Comments. In sample B this form is abundant. *B. debilispinum* differs from *B. ehrenbergi* Defl. in that the latter is larger and possesses more numerous and longer spines and from *B. ehrenbergi* Defl. var., *brevispinosum* Sarjeant by possessing less numerous and weaker spines. *Micrhystridium* aff. *fragile* Defl. 1947 described by Brosius and Bitterli (1961) is similar but lacks the conical spine bases and relatively thick wall.

Since the test size exceeds 20μ in the majority of cases, this species is allocated to *Baltisphaeridium* but smaller examples are common.

Genus MICRHYSTRIDIUM Deflandre 1937

Micrhystridium recurvatum Valensi 1953

Several specimens of *M. recurvatum* were recorded from the Ash Hill Borehole (sample B). They correspond closely to *M. recurvatum* f. *reducta* Valensi from the Bathonian of France.

Genus VERYHACHIUM Deunff 1954

Emended diagnosis. A genus of hystrichospheres with three to eight spines; shape of the test more or less determined by the number of spines present.

Remarks. According to the original diagnosis of *Veryhachium* (Deunff 1954*b*) the number of spines present varies from one to eight. Downie (1960) created a new genus, *Deunffia*, to accommodate small hystrichospheres with only one spine, and transferred *V. monocanthum* Deunff to this genus. Hystrichospheres possessing only two spines usually belong to the genera *Leiofusa* Eisenack 1938, or *Domasia* Downie 1960, according to whether the spines are situated at opposite poles or are both at one pole respectively. In this manner, the actual lower limit for the number of spines present in the genus *Veryhachium* can be regarded as three. The upper limit for the spine number has in some cases been raised to include forms with nine spines when other characters justify their inclusion in *Veryhachium*.

EXPLANATION OF PLATE 112

All figures $\times 1,000$.

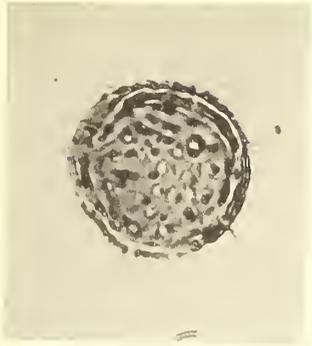
Figs. 1, 2. *Baltisphaeridium debilispinum* sp. nov. 1, Paratype; single mount. Sample B. 2, Holotype; PB/11, 91-0 32-7. Sample B.

Figs. 3-5. *Veryhachium flagelliferum* sp. nov. 3, Holotype; PB/11, 91-4 24-7. 4, 5, Paratypes; PB/11. All from sample B.

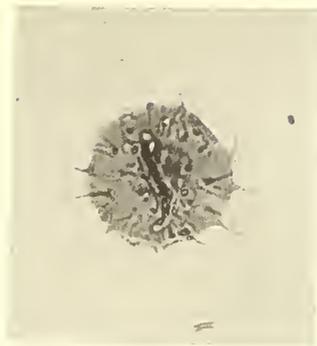
Fig. 6. *Leiofusa jurassica* Cookson and Eisenack. Sample B.

Figs. 7-9. *Veryhachium reductum* (Deunff) Jekh. 7, Forma *trispinoides*, sample B. 8, F. *reductum*; sample A. 9, F. *breve*; sample A.

Figs. 10-12. *Micrhystridium stellatum* Defl. 10, Forma *stellatum*. 11, Forma 1. 12, Transitional form between f. *stellatum* and forma 1. All from sample B.



1



2



3



4



5



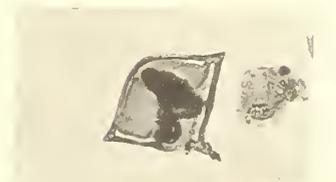
6



7



8



9



10



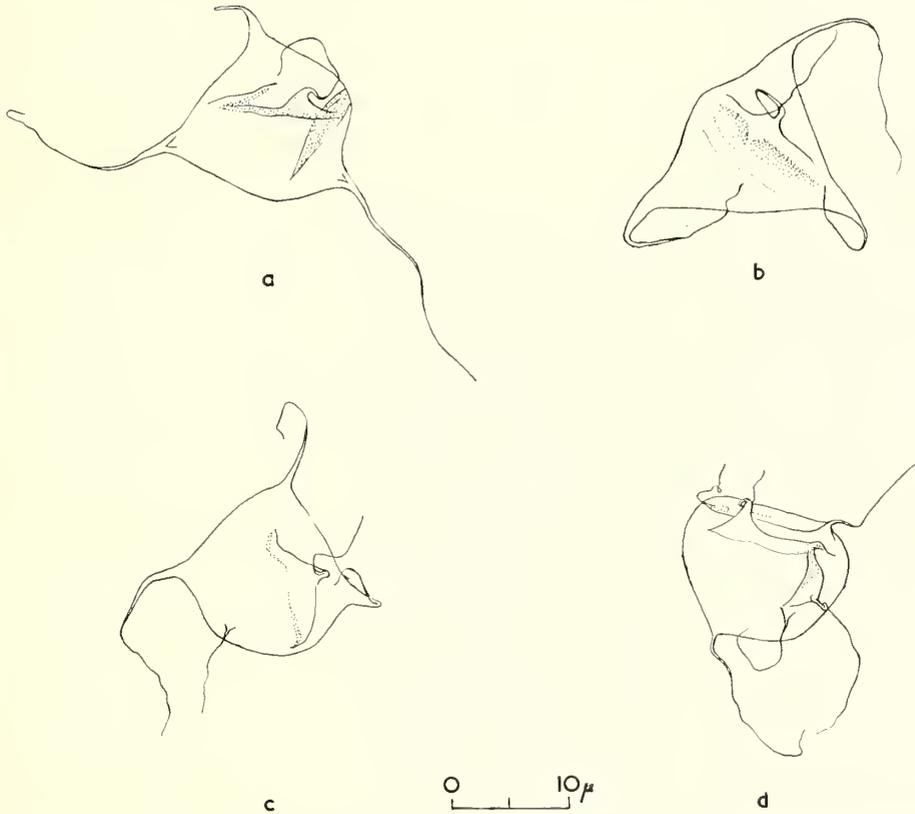
11



12

Veryhachium flagelliferum sp. nov.

Plate 112, figs. 3-5; text-figs. 4a-d

Holotype. Slide PB/11, 91·4 24·7. Plate 112, fig. 3. Test 16μ .*Diagnosis*. Test triangular to subglobose in outline, rarely with straight sides, bearing four to six long, flagellae-like processes whose length exceeds the test dimensions.

TEXT-FIG. 4a-d. *Veryhachium flagelliferum* sp. nov. a, Holotype, PB/11 91·4 24·7. b-d, Paratypes showing variation in test shape and spine number (specimens from sample B, slide PB/11, 82·5 30·7 77·1 29·3, 75·2 32·4).

Dimensions. Test 14 (16) 18μ ; spines over 24μ (twenty specimens measured).*Description*. The test is smooth, thin-walled, subtetrahedral if only four spines are present but subglobose when bearing five or six spines. The spines have restricted bases, 1 to 2μ wide, but for the most of their length they are extremely fine and flexuous and only visible at higher magnifications. They are usually colourless.*Comparisons*. The long, fine processes are a readily distinguishable feature distinct from other forms resembling *V. flagelliferum* in shape. It differs from *V. trisulcum* Deunff by possessing four to six spines and it has a smaller test.

Veryhachium reductum (Deunff 1959) Jekhowsky 1961

Plate 112, figs. 7-9

1958 *Veryhachium trisulcum* var. *reductum* Deunff.1961 *Veryhachium brevitrispinosum* Staplin.

Discussion. The three *formae* distinguished by Jekhowsky 1961 can be recognized in the British Permian. In the authors' opinion, *Veryhachium brevitrispinosum* Staplin (1961, pl. 49, fig. 1) is synonymous with *V. reductum* f. *breve* Jekhowsky (1961, pl. 2, figs. 38-44), which is senior.

Family LEIOFUSIDAE Eisenack 1938

Genus LEIOFUSA Eisenack 1938

Leiofusa jurassica Cookson and Eisenack 1957

Plate 112, fig. 6

Description. Test fusiform, 61 μ overall, central body about $32 \times 15 \mu$. Spines approximately half of the maximum test dimension, bases narrow, gradually merging with the test.

Remarks. This hystrichosphere is relatively rare in the Permian samples examined. It is apparently identical with the holotype figured by Cookson and Eisenack 1957 (pl. 10, fig. 4) from the Upper Jurassic of Western Australia.

Section 2. Hystrichospheres of the '*V. ? irregulare*' complex

Family HYSTRICHOSPHAERIDAE O. Wetzel 1933

Genus MICRHYSTRIDIUM Deflandre 1937

Micrhystridium stellatum Deflandre 1945

Diagnosis. Test more or less globose, 11 to 16 μ without the spines, often tending to be polygonal and bearing approximately a dozen strong simple spines whose length exceeds the test radius.

Remarks. The variation in morphology of this species has been discussed earlier. British Permian forms vary in size (for the test alone) from 11 to 17 μ and in spine number from six to sixteen. The spine length may be equivalent to only one-third of the test size or equal to it. Several morphotypes are recognizable in the British Permian.

Forma *stellatum* (Pl. 112, fig. 10; text-fig. 1v). Test subpolygonal, both straight and rounded sides occur in each individual; spine bases enlarged but separated, length greater than the test radius. This morphotype closely resembles the holotype (Deflandre 1942, fig. 7).

EXPLANATION OF PLATE 113

All figures $\times 1,000$.

Figs. 1-5. *Micrhystridium stellatum*. 1, Forma 2. 2, Forma 3. 3, Forma 4. 4, Form similar to typical forma 4, but with less expanded spine bases. 5, Forma 6. All from sample B.

Figs. 6-8. *V. ? irregulare* Jekh. 6, F. *subhexaedron*. 7, F. *subtetraedron*; sample B. 8, Forma 1; sample A.

Figs. 9-12. *V. rhomboidium* Downie. 9, Forma 1. 10, Forma 2. 11, Forma 2. 12, Forma 3. All from sample B.



1



2



3



4



5



6



7



8



9



10



11



12

Forma 1 (Pl. 112, fig. 11; text-fig. 1z). Test polygonal, sides straight, spine bases enlarged but separated (see Deflandre 1942, fig. 8).

Forma 2 (Pl. 113, fig. 1; text-fig. 1t). Test almost completely rounded, spine length greater than the radius, spine bases considerably enlarged but separated.

Forma 3 (Pl. 113, fig. 2; text-fig. 1u). Test polygonal or subpolygonal, spine bases only slightly enlarged, spines equal to the test diameter in length, more or less flexuous and relatively numerous (more than twelve). This morphotype closely resembles examples of *M. fragile* having subpolygonal tests but differs by its expanded spine bases.

Forma 4 (Pl. 113, fig. 3, text-fig. 1y). Test shape variable, spine length approximately one-third of the test diameter, bases expanded. This *forma* differs from *Micrhystridium sydus* Valensi by being larger and having expanded spine bases and in the latter respect it also differs from *M. parinconspicuum* Defl. It differs from *M. inconspicuum* Defl. as described by Brosius and Bitterli, 1961 (p. 40) by possessing fewer spines.

Forma 5. Test polygonal, subpolygonal, spine bases greatly expanded, almost touching, test outline concave between spines. Typical examples of this morphotype are absent in the British Permian but they are mentioned here because of their importance in comparison of Mesozoic and Palaeozoic *formae*. They appear to be restricted to the Mesozoic and have been figured by Sarjeant (1959, fig. 7c; 1961, fig. 8d) and Valensi (1953, fig. 27). The specimen figured here (Pl. 113, fig. 4) resembles the Mesozoic specimens but has less expanded spine bases.

Forma 6 (Pl. 113, fig. 5; text-fig. 1s). Test polygonal or rounded, bearing only six or seven spines, length greater than the radius, bases expanded. This form is transitional to *V. ? irregulare* f. *subhexaedron* Jekhowsky, differing by its greater spine length and additional spine.

Genus VERYHACHIUM Deunff

Veryhachium? irregulare Jekhowsky 1961

Plate 113, figs. 6-8; text-fig. 1g-n

Remarks. The British Permian hystrichospheres belonging to this species agree closely with those described by Jekhowsky. The spines are equally variable in size and may be less than $1\ \mu$ in length, but rarely exceed the test radius. One new *forma* must be distinguished to cover the range of variation shown.

Forma 1 (Pl. 113, fig. 8; text-figs. 1g, h). Test subglobular, subpolygonal possessing five or six extremely short and conical spines (1 to $3\ \mu$). This *forma* includes individuals equivalent to f. *irregulare* and f. *subhexaedron* but with shorter spines.

Veryhachium rhomboidium Downie 1959

Remarks. Many forms resembling the Silurian type material (Downie 1959) occur in the British Permian, but minor differences are recognizable. The Permian forms range from 14 to $25\ \mu$ in size (test only) and the spines vary from below 50 per cent. to a 100 per cent. of the maximum test dimensions in length and from four to nine in number. Several morphotypes are described to illustrate the variation encountered.

Forma 1 (Pl. 113, fig. 9; text-fig. 1a). Test sides straight or weakly convex, spine length less than half the test dimension, bases more or less narrow (1 to $2\ \mu$). *V. minor* Staplin may be identical with this morphotype.

Forma 2 (Pl. 113, figs. 10, 11; text-figs. 1*b*, *c*). Test more or less straight-sided, spine bases distinctly enlarged, about 50 per cent. of the test measurements in length. This form is transitional to *V. minutum* Downie but differs from it in that the spine bases are separated from one another.

Forma 3 (Pl. 113, fig. 12; Pl. 114, fig. 1; text-fig. 1*d*). Test elongate, sides more or less straight, spine length 75 to 100 per cent. of the maximum test dimension; spines slender, flexuous.

Forma 4 (Pl. 114, figs. 2, 3; text-fig. 1*e*). Test rhomboidal with typical spine arrangement, but possessing additional irregularly inserted spines; spines seven to nine in number.

Forma *rhomboidium*. The typical Silurian form does not occur in the Permian. Forma 3 closely resembles it but has more slender, flexuous spines.

Veryhachium cf. *lairdi* (Defl.) Deunff

Text-fig. 1*f*

Description. Test subquadrate, sides more or less straight, bearing four short spines with slightly enlarged bases at each corner; spine length approximately one-third of the test size. Size 17 μ (test only).

Remarks. This morphotype differs from *V. lairdi* (Defl.) Deunff 1954 by possessing restricted spine bases and from *V. minor* Staplin by only having four spines.

Veryhachium europaeum Stockmans and Willièrè 1960

Remarks. A large number of small hystrichospheres with four equal spines occur in the British Permian, although the spine length never exceeds the test size as in the typical material described by Stockmans and Willièrè 1960 from the Devonian of Belgium. The British specimens are referred to this species however and a number of morphotypes have been selected.

Forma 1 (Pl. 114, figs. 4, 5; text-fig. 1*o*). Test tetrahedral, spine length between one-third to a half of the test dimension, spine bases restricted.

Forma 2 (Pl. 114, fig. 6; text-fig. 1*p*). Test tetrahedral, spine length above 50 per cent., but not exceeding 100 per cent. of the test size, bases relatively narrow.

Forma *wenlockianum*. The forms described as *Veryhachium tetraëdron* var. *wenlockia* Downie 1959 from the Silurian of Britain are allocated to *V. europaeum* since the species *V. tetraëdron* is invalid. The type and description are those given by Downie 1959 (p. 62). This forma differs from the holotype of *V. europaeum* by its distinct and restricted spine bases and from the British Permian forms by its greater spine length (up to approximately five times greater than the test dimensions).

EXPLANATION OF PLATE 114

All figures $\times 1,000$.

Figs. 1-3. *Veryhachium rhomboidium* Downie. 1, Forma 3. 2, 3, Forma 4. All from sample B.

Figs. 4-6. *V. europaeum* Stock. and Will. 4, 5, Forma 1. 6, Forma 2. All from sample A.

Figs. 7-11 *V. formosum* Stock. and Will. 7, 8, Forma 1. 9-11, Forma 2. All from sample B.

Fig. 12. *Veryhachium* sp. showing the presence of a small spine near the centre of the test. Sample A.



1



2



3



4



5



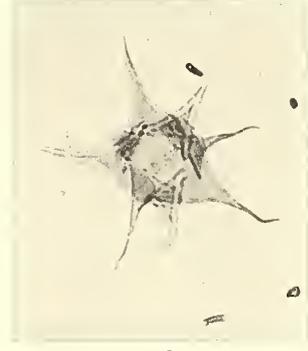
6



7



8



9



10



11



12

Comparisons. The species is here restricted to forms whose tests have more or less straight sides. Inflated, subglobular forms are referred to *V. ? irregulare* f. *subtetraedron* Jekhowsky.

Veryhachium formosum Stockmans and Willièrè 1960

Remarks. Forms allocated to this species from the British Permian differ from the holotype from the Devonian of Belgium in their shorter spine length and from *V. ? riburgense* f. *regulare* Brosius and Bitterli by their less inflated tests. They possess from five to rarely nine appendages but always maintain a triangular outline.

Forma 1 (Pl. 114, figs. 7, 8; text-fig. 1*q*). Test more or less tetrahedral, with four apical spines and one additional spine on one face. Spine length from 50 to 100 per cent. of the test size, spine bases relatively narrow. Test *c.* 15 to 20 μ .

Forma 2 (Pl. 114, figs. 9–11; text-fig. 1*r*). Test more or less tetrahedral, with four apical spines and two to four supplementary processes ornamenting the faces. Spine length less than the test size. Spine bases may be expanded. Test *c.* 15 μ .

Acknowledgements. The authors are indebted to the National Coal Board for supplying the sample from the Ash Hill Borehole and to Mr. G. S. Bryant of the Geology Department in Sheffield for technical assistance. Mr. Wall acknowledges a Shell International Oil Company Grant enabling him to do this work as part of a research project in micropalaeontology.

REFERENCES

- BROSIUS, M., and BITTERLI, P. 1961. Middle Triassic Hystrichosphaerids from salt-wells Riburg-15 and -17, Switzerland. *Bull. Ver. Schweizer, Petrol.-Geol. u. -Ing.* **28**, 74, 33–49, 2 pl.
- DEFLANDRE, G. 1937. Microfossiles des silex crétacés. Part 2. *Ann. Paléont.* **26**, 1–55, pl. 8–18.
- 1942. Sur les Hystrichosphères des calcaires siluriens de la Montagne Noire. *C.R. Acad. Sci. Paris*, **215**, 475–6.
- 1945. Microfossiles des calcaires siluriens de la Montagne Noire. *Ann. Paléont.* **31**, 41–75, pl. 1–2.
- 1947. Sur quelques micro-organismes planctoniques des silex jurassiques. *Bull. Inst. Océanogr. Monaco*, **921**, 1–10.
- DEUNFF, J. 1954*a*. Sur un microplancton du Dévonien du Canada recélant des types nouveaux d'Hystrichosphaeridés. *C.R. Acad. Sci. Paris*, **239**, 1064–6.
- 1954*b*. *Veryhachium*, genre nouveau d'Hystrichosphères du Primaire. *C.R. Soc. géol. France*, 305–6.
- DOWNIE, C. 1959. Hystrichospheres from the Silurian Wenlock Shale of England. *Palaeontology*, **2**, 56–71.
- 1960. *Deunffia* and *Domasia*, new genera of hystrichospheres. *Micropaleontology*, **6**, 2, 197–202, pl. 1.
- EISENACK, A. 1958. Mikroplankton aus dem norddeutschen Apt. *Neues Jb. Min., Geol., Palaeont.* **106**, 383–422, pl. 21–27.
- FUNKHAUSER, J. W., and EVITT, W. R. 1959. Preparation techniques for acid-insoluble microfossils. *Micropaleontology*, **5**, 3, 369–75.
- GILLIGAN, A. 1918. The Lower Permian at Ashfield Brick and Tile Works, Conisborough. *Proc. Yorks. Geol. Soc.* **19**, 289–97.
- JEKHOWSKY, B. DE 1961. Sur quelques Hystrichosphères Permo-Triassiques d'Europe et d'Afrique. *Revue de Micropaléontologie*, **3**, 207–12, pl. 1–2.
- KARA-MURZA, E. N. 1957. Hystrichosphaeridae du Crétacé supérieur et du Trias de l'Arctique soviétique. *Inst. Rech. Scient. Géol. Arctique, Rec. Articles Paléont. et Biostrat.* **4**, 64–69. Leningrad.

- SARJEANT, W. A. S. 1959. Microplankton from the Cornbrash of Yorkshire. *Geol. Mag.* **96**, 329-46, 1 pl.
- 1960. Microplankton from the Corallian Rocks of Yorkshire. *Proc. Yorks. Geol. Soc.* **32**, 4, 18, 389-408.
- 1961. Microplankton from the Kellaways Rock and Oxford Clay of Yorkshire. *Palaeontology*, **4**, 1, 90-118.
- STAPLIN, F. L. 1961. Reef-controlled distribution of Devonian microplankton in Alberta. *Ibid.* **4**, 3, 392-424, pl. 48-51.
- STOCKMANS, F., and WILLIÈRE, Y. 1960. Hystrichosphères du Dévonien belge. *Senck. leth.* **41**, 1-11.
- VALENSI, L. 1953. Microfossiles des silex du Jurassique Moyen. *Mém. Soc. géol. Fr.* **68**, 1-100, 16 pl.
- WILSON, L. R. 1960. A Permian hystrichosphaerid from Oklahoma. *Oklahoma Geol. Notes*, **20**, 7, 170.

DAVID WALL
CHARLES DOWNIE
Department of Geology,
University of Sheffield

Manuscript received 30 January 1962

THE JURASSIC ECHINOID *CIDARITES MONILIFERUS* GOLDFUSS AND THE STATUS OF *EUCIDARIS*

by G. M. PHILIP

ABSTRACT. The type specimen of the Jurassic cidarid *Cidarites moniliferus* Goldfuss, recently designated as type species of the genus *Eucidaris* Pomel 1883, is redescribed. The species is considered to be a typical member of the genus *Stereocidaris* Pomel 1883. As these two genera were published simultaneously, it is recommended that *Eucidaris* should be abandoned in favour of *Stereocidaris*.

H. L. CLARK (1926, p. 3) writes of the genus *Eucidaris* that it 'is perhaps the best known and most universally accepted genus of Cidaridae. . . .' However, like many of the earlier echinoid genera, doubt exists as to the strict application of the name.

Eucidaris was originally proposed by Pomel (1883, p. 109) as a section of the genus *Cidaris*, with the following unsatisfactory diagnosis:

Eucidaris. Tubercles à col lisse: trois espèces vivantes; presque toutes les espèces tertiaires; toutes les espèces crétacées, moins une (20); quelques jurassique seulement (*C. Morieri*, *Honorinæ*, *propinqua*, *marginata*, *monilifera*, *multipunctata*); la plupart des triasiques (7).

Döderlein (1887, p. 42), who was the next writer to use the name, employed *Eucidaris* for the living species group embracing *Cidarites metularia* Lamarck, *C. tribuloides* Lamarck, and *C. thouarsii* Valenciennes, and it is in this sense that the genus has come to be used.

The question was reviewed in a series of papers on the nomenclature of cidarid genera early this century (Bather 1908, 1908a, 1909; H. L. Clark 1908, 1909) where it was agreed that, as *Gymnocidaris* A. Agassiz 1863 (originally proposed for *C. metularia*) was a homonym of *Gymnocidaris* L. Agassiz 1838, the name *Eucidaris* Pomel should be applied to the *metularia* species group. H. L. Clark (1909) designated *C. metularia* as type species of *Eucidaris* Pomel. Bather (1909) agreed with this designation, observing that 'We may well suppose that the 'trois espèces vivantes' of Pomel's list were *Cidaris metularia*, *C. tribuloides* and *C. thouarsi*'.

And here the matter has rested for fifty years with the genus *Eucidaris* Pomel universally interpreted through *C. metularia*, a species not named in the founding of the genus, and so strictly not available for designation as type species. (Lambert and Thiéry 1910, have been the only subsequent authors who have retained *Cidaris* s.st. for the *metularia* species group, taking this view from the misinterpretation of a pre-Linnaean figure given by Rumphius, *vide* Mortensen 1910.) So well established was the generic name, particularly among neontologists, that there existed a clear case for action by the I.C.Z.N. to stabilize the genus in accordance with accustomed usage.

However, Cooke (1959, p. 8) recently noted that *C. metularia* was not among the names originally listed by Pomel, and so was not available for designation as type species of *Eucidaris*. He designated '*Cidarites monilifera* Goldfuss' as type species of the genus

Eucidaris Pomel. Since the generic relationships of *Cidarites moniliferus* Goldfuss are not apparent from the available figures and descriptions, the type material of *Cidarites moniliferus* Goldfuss is here described, together with an assessment of the generic relationships of the species.

'*Cidarites*' *moniliferus* Goldfuss

Text-figs. 1a-d; Plate 115

Cidarites moniliferus Goldfuss 1826, *Petref. Germania*, i, p. 118, pl. 39, figs. 6a-b.

Cidaris monilifera Goldfuss, Cotteau 1876, *Paléont. française, Terr. juras.* 10 (1), pp. 163-7, pls. 185-6 (*cum synon.*).

Plegiocidaris monilifera (Goldfuss), Lambert and Thiéry 1910, *Ess. nomen. rais. Échin.* ii, p. 132.

Material. The type specimen, the test originally figured by Goldfuss, is catalogued as No. 305a, in the Goldfuss Collection, Geologisch-paläontologisches Institut der Friedrich Wilhelms-Universität, Bonn. Goldfuss states that his species come from the Jurassic of Switzerland. The specimen is labelled in the collection as questionably from the Randen Malm. Two radioles (305b) from the same general locality are also in the Goldfuss Collection, identified as *Cidarites moniliferus*. As Goldfuss states that radioles of his species are unknown, these could not have been seen by him when the species was described.

Description of test. The test is rather small and depressed, with wide apical system and peristome.

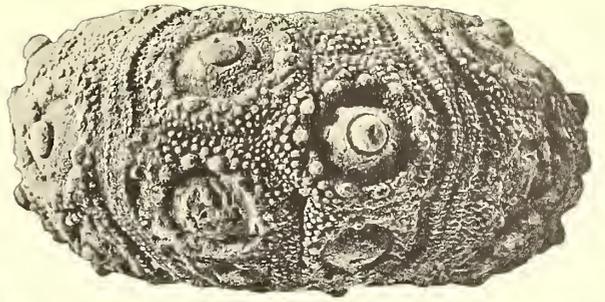
The ambulacra (text-fig. 1b) are about one-fifth of the width of the interambulacra, and are distinctly sinuate. The poriferous tract, of width similar to the interporiferous tract, is markedly sunken. The small marginal tubercles form a regular vertical series for most of the length of the ambulacra, but adorally they tend to be slightly irregular. On each ambital plate one to three small internal tubercles are present, aligned in one or two irregular vertical series. The pores are non-conjugate, with the separating wall rising to a definite elevation. They are rounded and slightly oblique, particularly adapically. The transverse ridge above the pores is low and ill defined.

Four or five interambulacral plates (nine in each interambulacral zone) are present in each vertical column. The aureoles, mounted toward the centre of each column, are rudimentary on the uppermost plate of each column of five plates. On the other plates, the aureoles are relatively small and rounded, well separated and deeply incised. The smooth, perforate, primary tubercles rise well above the level of the test. The scrobicular tubercles are large and possess aureoles elongated tangentially to the scrobicules of the primary tubercles. Outside of the scrobicular ring the interambulacra are covered with small, closely spaced secondary tubercles. The plates above the ambitus are extremely

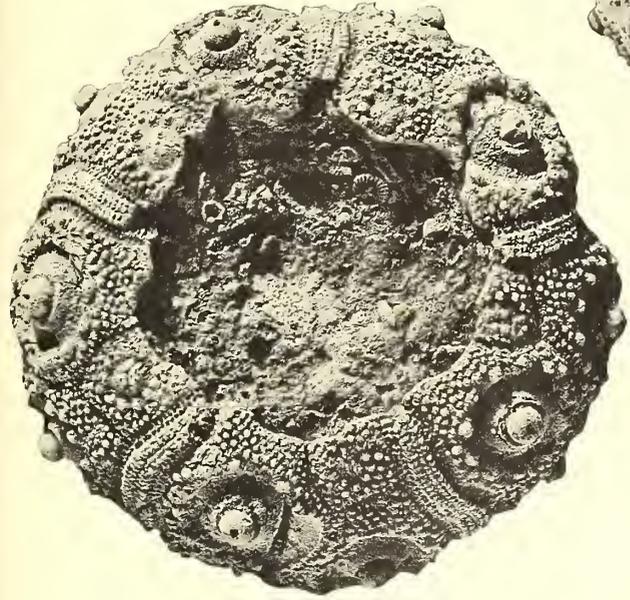
EXPLANATION OF PLATE 115

Figures unretouched, $\times 2$.

Figs. 1-6. *Cidarites moniliferus* Goldfuss. 1, Lateral, 2, adapical, 3, adoral views of holotype (Goldf. Coll. No. 305a). 4-5, Radioles (Goldf. Coll. No. 305b). 6, Oblique adaptical view of holotype, showing sunken and bare interambulacral sutures.



1



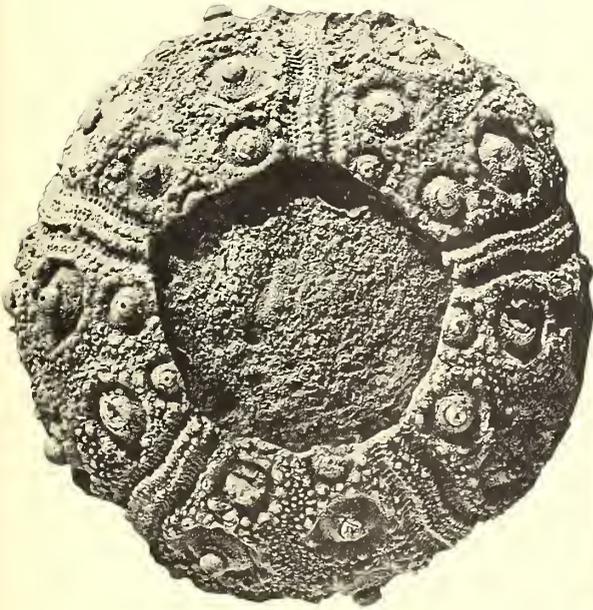
2



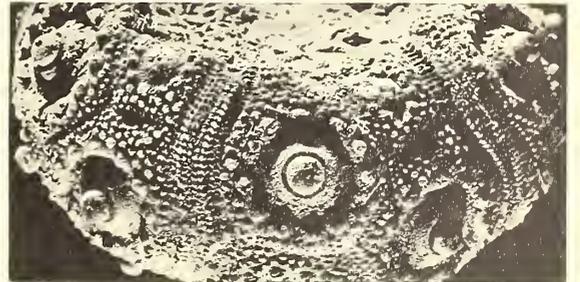
4



5



3

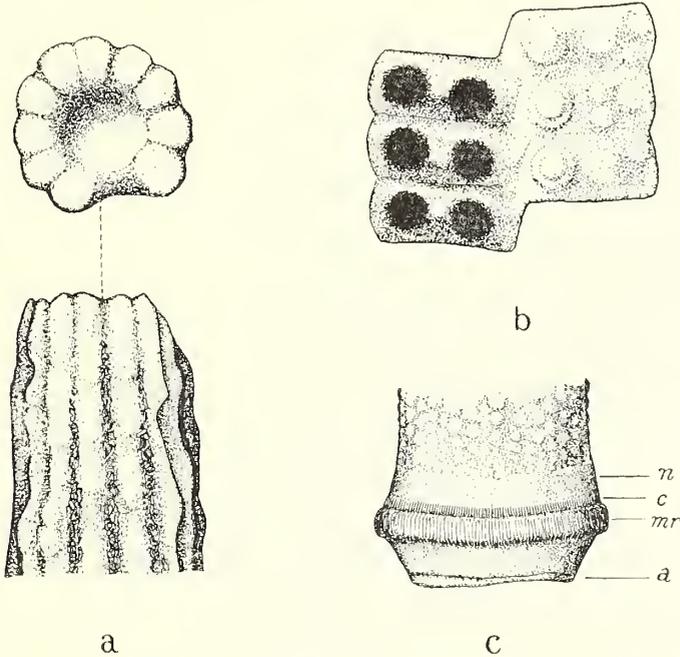


6

high. The sutures tend to be depressed and slightly incised, and the upper horizontal sutures may be bare, although pits are not developed at their admedian ends.

Measurements. H.d. 40 mm.; v.d. 19 mm.; diameter of apical system *c.* 20 mm.; diameter of peristome 17 mm. There are twenty-three ambulacral plates opposite the ambital interambulacral plates.

Radioles. The radioles are stout, cylindrical, and tapering, or slightly fusiform, with the shaft constricted above the neck. The base (text-fig. 1c) is short, and the milled ring



TEXT-FIG. 1. *Cidarites moniliferus* Goldfuss. *a*, Distal termination of radiole (Goldf. Coll. No. 305b, Pl. 115, fig. 4). Traces of the original coat of cortical hairs are shown schematically between the longitudinal ridges, $\times 6$. *b*, Composite drawing of the ambital ambulacrum of the holotype test, $\times 25$. *c*, Base of radiole (Goldf. Coll. No. 305b, Pl. 115, fig. 4). $\times 6$. *n*=neck; *c*=collar; *mr*=milled ring; *a* = acetabulum.

is not markedly expanded. The collar is extremely short, about one-third of the length of the neck, which itself is relatively short and rather poorly defined distally. The shaft is ornamented by longitudinal series of rounded warts which coalesce distally to form well-marked ridges. Between these ridges are short spicules, which are interpreted as traces of the original cortical hairs, partly obscured by matrix they have collected. They seem to have been anastomosing rather than simple. Both the radioles are distally truncated, and one (text-fig. 1a) possesses a marked distal depression. The acetabula are not well preserved, but appear to be smooth in accordance with the character of the primary tubercles of the test.

Generic relationships. The rudimentary aureoles of the tubercles of the uppermost interambulacral plates immediately suggest a relationship with the genus *Stereocidarites*

Pomel 1883 (type species *Cidaris cretosa* Mantell). This feature gives a fairly reliable guide in the identification of the genus in fossil material, as within the Cidarinae (*sensu* Mortensen 1928) it is only known outside *Stereocidaris* s.l. in the living *Stylocidaris tiara* (Anderson) and the closely related *S. effluens* Mortensen (1928, pp. 368 et seq.; pl. 37, fig. 8). It is also seen in the Cainozoic Australian species '*Goniocidaris*' *prunispinosa* Chapman and Cudmore, and other *Goniocidaris*-like forms from the same region, but here it may be taken as indicative of the derivation of these from *Stereocidaris* itself. It must be pointed out, however, that in species in which the aureole is rudimentary only on the uppermost plate of each interambulacral zone, the feature may no longer be fully diagnostic of the genus. It is well, therefore, to list the other characters of *C. moniliferus* which support the comparison with *Stereocidaris*. These are:

1. The non-conjugate pores of the sinuate ambulacra.
2. The small number of interambulacral plates, which are very high above the ambitus.
3. The small, deeply incised lower aureoles, which are widely spaced in each column.
4. The bare, incised, and slightly pitted upper horizontal interambulacral sutures.
5. The close secondary granulation.

The combination of these features leaves little doubt as to the generic affinities of the test. The only feature which seems slightly atypical for a species of *Stereocidaris* is the large size of the mamelons of the scrobicular tubercles; but in other respects these are typical for a species of *Stereocidaris*.

The radioles support this comparison with *Stereocidaris*. Although these may be simply tapered in *Stereocidaris*, they can also possess a distal cup-like termination which may even be flared, as in the living species *S. tubifera* Mortensen (1928, pl. 23), and also in such Cretaceous species as *S. gaultina* (Forbes) (Wright 1882, pl. 6, figs. 2c-e, 3a-b, 4) and *S. sceptifera* (Mantell) (Wright 1882, pl. 6, figs. 3a-c, 4a), a species very closely related to the type species of *Stereocidaris*. The collar is invariably short in *Stereocidaris*, and the neck is usually well defined and considerably longer than the collar.

The main diagnostic character of the *metularia* species group is seen in the character of the radioles. These terminate in a small flared crown, which bears an indented central prominence. Nothing similar to this is seen in the radioles ascribed to *Cidarites moniliferus*, and the test of *C. moniliferus* lacks the generalized features of the *metularia* species group. Indeed, it is doubtful whether any close congeners of *C. metularia* appeared before the Cainozoic (cf. Fell 1954).

Of interest is the fact that Cotteau (1876) included in *C. moniliferus* a number of specimens showing crenulation of the primary tubercles. This also supports the reference of the species to *Stereocidaris*, for in this genus the tubercles may be crenulate to varying degrees even in the one species.

In a reorganization of the many Mesozoic and early Cainozoic species of *Stereocidaris* s.l. (an account of the species groups within the genus is given elsewhere) *C. moniliferus* stands so close to *C. cretosa*, the type species of *Stereocidaris* Pomel, that the two must be regarded as congeneric.

It is concluded, therefore, that the genus *Eucidaris* Pomel 1883 (p. 109) should be regarded as a subjective synonym of *Stereocidaris* Pomel 1883 (p. 110). Although *Eucidaris* has page priority in Pomel, the name most certainly should not replace *Stereocidaris*

because of the great confusion which would result. The question of the generic status of the *metularia* species group is not here discussed.

I am extremely grateful to Professor H. K. Erben of the Geologisch-paläontologisches Institut der Friedrich Wilhelms-Universität, Bonn, who arranged for the specimens from the Goldfuss Collection to be entrusted to my care. I am also obliged to Mr. A. G. Brighton, who very kindly read the manuscript of this note which was prepared during the tenure of an Australian Commonwealth Scientific and Industrial Research Organization Overseas Studentship at the Sedgwick Museum, Cambridge.

REFERENCES

- BATHER, F. A. 1908. The echinoid name *Cidaris* and its modern application. *Ann. Mag. Nat. Hist.* **8**, ser. 1, pp. 284–8.
 — 1908a. The genotype of *Cidaris*. *Ibid.* **8**, ser. 2, pp. 134–6.
 — 1909. The type of *Cidaris*. *Ibid.* **8**, ser. 3, p. 88.
 CLARK, H. L. 1908. The type of *Cidaris*. *Ibid.* **8**, ser. 1, p. 532.
 — 1909. The type of *Cidaris*. *Ibid.* **8**, ser. 3, p. 88.
 — 1926. *A catalogue of Recent sea-urchins in the British Museum*. 278 pp., 12 pl. London.
 COOKE, C. W. 1959. Cenozoic echinoids of the eastern United States. *U.S. Geol. Surv. Prof. Pap.* **321**, 106 pp., 43 pl.
 COTTEAU, G. H. 1857–80. *Échinides réguliers: Paléontologie française, Terrain jurassique*, ser. 1, **10** (1), 958 pp., pl. 143–520.
 DÖDERLEIN, L. 1887. *Die japanischen Seeigel, I. Familie Cidaridae und Saleniidae*, 59 pp., 11 pl. Stuttgart.
 FELL, H. B. 1954. Tertiary and Recent Echinoidea of New Zealand. Cidaridae. *N.Z. Geol. Surv. Paleont. Bull.* **23**, 62 pp., 15 pl.
 GOLDFUSS, A. 1826. *Petrefacta Germaniæ* I. 252 pp., 71 pl. Düsseldorf.
 LAMBERT, J., and THÉRY, P. 1910. *Essai de nomenclature raisonnée des échinides* II, pp. 81–240, pl. 3–4. Chaumont.
 MORTENSEN, TH. 1910. On some points in the nomenclature of echinoids. *Ann. Mag. Nat. Hist.* **8**, ser. 5, pp. 118–19.
 — 1928. *A monograph of the Echinoidea, I, Cidaridae*. 551 pp., 88 pl. C. A. Reitzel, Copenhagen.
 POMEL, N. A. 1883. *Classification méthodique et genera des échinides vivants et fossiles*. 131 pp., 1 pl. Alger.
 WRIGHT, THOMAS. 1864–82. Monograph of the British fossil Echinodermata from the Cretaceous formations. *Palaontogr. Soc. Monogr.*

G. M. PHILIP
 Department of Geology,
 University of New England,
 Armidale, N.S.W.,
 Australia

UPPER LLANDEILO TRILOBITES FROM THE BERWYN HILLS, NORTH WALES

by A. R. MACGREGOR

ABSTRACT. Sixteen species in twelve genera are described including the following new species, *Bumastus powisensis*, *Marrolithus magnificus*, *M. lirellatus*, *Atractopyge sedgwicki*, *A. williamsi*, and *Metopolichas contractus*. The fauna was collected from three small inliers of Llandeilo rocks in the Berwyn Dome, North Wales. There is a large indigenous element in the fauna, and an exotic element, in which two species appear to be from the Appalachian province, and one might possibly be from the Bohemian province. Two species are at present cryptogenetic.

THIS paper is a systematic account of the trilobite fauna found in the three inliers of Llandeilo rocks in the Berwyn Hills, together with a discussion of that fauna. The succession within the Llandeilo rocks has been outlined in a previous paper (MacGregor 1961).

The placing of the fauna in the Upper Llandeilo is based, particularly, on the very great abundance of *Marrolithus favus* in the rocks, which both Williams (1948, p. 87) and Whittard (1956, p. 57) regard as a reliable indication of the Upper Llandeilo. The rarity in the Berwyns of marrolithids, known from Lower or Middle Llandeilo beds elsewhere, may be taken as confirmation of this, though Whittard expressed doubts on the zonal value of most other species of *Marrolithus*. Of the other established species, *Basilicus tyrannus*, *Ogygiocarella debuchii*, and *Flexicalymene cambrensis* are all known right through the Llandeilo and can, therefore, only point to a general Llandeilo age. *Marrolithoides arcuatus* s.s. is found in the *N. gracilis* graptolite zone of the Caradoc. The remainder of the fauna consists of new species not yet known elsewhere.

The material on which the paper is based was collected by the author, and is preserved as internal and external moulds, except for a small number of specimens in which shell material remains. All the figured material has been presented to the Sedgwick Museum, Cambridge, and bears the prefix A before the registered numbers. A small number of specimens referred to, or in one case figured, from other sources are prefixed as follows: GSM, Geological Survey Museum; BM, British Museum (Natural History); OUM, University Museum, Oxford; and followed by the registered number. The terminology used in the paper is that of the Treatise on Invertebrate Paleontology, Section O. Arthropoda I, except that the terms 'fixed cheeks' and 'free cheeks' have been used in preference to 'fixigenae' and 'librigenae'.

The writer thanks Professor O. M. B. Bulman and Professor W. B. R. King for their guidance throughout the work, Dr. C. J. Stubblefield and Professor A. Williams for helpful discussions, Mr. R. Johnston for assistance with the photography, and Mr. R. P. Tripp for reading the manuscript and making many helpful suggestions. The work was partly carried out during the tenure of a Carnegie Research Scholarship and the field expenses were met by grants from the Cross Trust; for both of these the writer expresses his gratitude. The writer is also grateful for permission to examine specimens in the Geological Survey Museum, the Sedgwick Museum, Cambridge, and the British Museum (Natural History), and from the University Museum, Oxford, the Geology Department, Leeds Uni-
[Palaeontology, Vol. 5, Part 4, 1962, pp. 790-816, pls. 116-118.]

versity, and the Geology Department, Birmingham University. The writer is also indebted to the Carnegie Trust for the Universities of Scotland for a grant towards the cost of the plates.

SYSTEMATIC DESCRIPTIONS

Family ASAPHIDAE Burmeister 1843
Subfamily ASAPHINAE Burmeister 1843
Genus BASILICUS Salter 1849
Basilicus tyrannus (Murchison 1839)

Plate 116, figs. 1-5

1839 *Asaphus tyrannus* Murchison, p. 648, pl. 24, fig. 4, pl. 25, fig. 1.

Material. Some forty specimens of cranidia, free cheeks and pygidia.

Localities. Widespread in all three inliers; common at SJ 12272807, 80 yards north of Nant, 1 mile north of Llanrhaiadr-ym-Mochnant, Montgomeryshire.

Horizon. Upper Llandeilo, Calcareous Ash, Limestone, and Calcareous Shale.

Description. *Cephalon:* rather more than twice as broad as long, evenly convex outline in front, more strongly curved laterally, drawn into short narrow genal spines about half length of rest of cephalon. Gently convex transversely and longitudinally, most strongly so over anterior glabellar lobe in both directions. Posterior margin straight, slightly convex backwards behind glabella. Glabella with prominent broadly clavate anterior lobe extending almost to anterior margin and about two-thirds length of glabella; tapering posteriorly. Remaining lobes ill defined and low; a pair of oblique low lobes extends outwards to join palpebral lobes, posterior lobes little more than a slight ridge parallel to posterior margin. Anterior pair of glabellar furrows behind anterior lobe converge backwards, become shallower and meet in mid-line. Next pair of furrows run straight inwards from a point level with posterior end of the eye; appear to join anterior pair about mid-line. Occipital furrow very shallow, especially in mid-line; continued laterally by posterior border furrow. Axial furrows merge with preglabellar furrow, are broad and ill defined as they diverge round anterior glabellar lobe; they become shallower, rise up to pass palpebral lobes; here they converge slightly before diverging again and become a little deeper as they drop down to posterior margin. Palpebral lobes raised above remainder of cheeks, but not as high as anterior glabellar lobe; anteriorly fixed cheek merges with narrow preglabellar field and carries a shallow continuation of preglabellar furrow. Free cheeks gently sloped outwards with large holochroal eyes standing markedly above cheeks, from which separated by shallow furrow. Faint border furrow dies out towards genal spine. Posterior border furrow also dies out towards genal spine. Genal spine sharply pointed, confluent with lateral margin of cephalon. Doublure visible on a broken free cheek, shows fine terrace lines parallel to lateral margin. Facial sutures run forward and outwards from palpebral lobes at about 50° to long axis of cephalon, so that breadth across anterior of cranidium is half as much again as that across palpebral lobes. Sutures run in this direction almost to margin of cephalon before turning to meet margin at approximate right angles. Behind palpebral lobes sutures run fairly straight outwards and backwards at about 30° to posterior margin, this angle increasing to about 45° just before suture reaches margin.

Hypostoma and thorax: not known from the Berwyns.

Pygidium: half as wide again as long, parabolic in outline, gently convex anteriorly. Convex transversely, sharply dropping to border. Axis anteriorly about one-fifth total width, tapering backwards more sharply at first so that it is about half this width about one-third way back; behind this, becomes almost parallel-sided and ends in a swollen tip some distance from posterior margin and standing above border. Axis gently convex, transversely at front, becoming more so backwards until strongly convex at tip. At least fourteen axial rings present; ring furrows shallow in mid-line, deepening outwards, but becoming shallow again before they join axial furrows. Axial furrows steeper-sided against axis than against pleurae, not sharp or deep. Pleurae, ten or eleven on each side, separated by rounded concave interpleural furrows. Pleural furrows not seen. Pleurae and furrows die out towards weakly concave border. Pleurae more strongly convex towards border, becoming more marked backwards especially adjacent to tip of axis. Border smooth apart from terrace lines arranged almost at right angles to axis. These seem to die out on to pleurae, swing forward slightly on more anterior parts of border. Doublure extends certainly beneath border, where it carries terrace lines parallel to margin of pygidium, and it may extend farther.

Remarks. This species can be readily distinguished from *B. peltastes* Salter even in isolated cranidia, free cheeks, and pygidia (Salter 1864, p. 152); though present at Llandeilo, that species is unrecorded from the Berwyn Hills.

Subfamily OGYGIACARIDINAE Raymond 1937
Genus OGYGIACARELLA Harrington and Leanza 1957
Ogygiocarella debuchii (Brongniart 1822)

Plate 116, fig. 14

1822 *Asaphus de Buchii* Brongniart, t. 2, fig. 2.

1865 *Ogygia buchi*; Salter, p. 125, pl. 14, figs. 1-7, pl. 15, figs. 1-6.

Material. One broken pygidium.

Locality. SJ 12852846, 730 yards north-west of Plas-yn-glyn, 1 mile north-north-east of Llanrhaiadr-ym-Mochnant, Montgomeryshire.

Horizon. Upper Llandeilo, Calcareous Shale.

Description. *Pygidium*: outline parabolic, very gently convex, almost flat, slightly bent down peripherally; length/breadth: seven-eighths on this single specimen; axis narrow, occupying about one-fifth total breadth at anterior, tapering backwards rapidly at first, less so towards posterior so that almost parallel-sided at tip. Axis flattened anteriorly, little higher than pleurae, but gradually rising backwards to tip, which stands distinctly above pleurae though still low. At least eight axial rings, which become less distinct towards rear; ring furrows shallow, also becoming less distinct towards rear. Axial furrows shallow and narrow at front, becoming broader and slightly deeper backwards. Eleven pleurae becoming successively weaker backwards, flat with distinct interpleural furrows, which coincide with axial ring furrows, not quite parallel-sided, expanding slightly outwards, straight-edged proximally and curving backwards distally. Pleural furrows reach almost to axial furrows and continued on axial rings by faint furrows, do

not reach so far towards margin and are much shallower than interpleural furrows. Marginally, weak concentric ridging developed, but this may be impressed from the doublure due to crushing.

Remarks. The rarity of the species in the Berwyns is remarkable in view of its abundance in the Llandeilo strata of almost all other areas of outcrop, but elsewhere the species commonly is restricted to finer-grained deposits.

Family ILLAENIDAE Hawle and Corda 1847

Subfamily BUMASTINAE Raymond 1916

Genus BUMASTUS Murchison 1839

Bumastus powisensis sp. nov.

Plate 116, figs. 6-10

Derivation of name. From Powis, the district of Wales in which the southern part of the Berwyn Hills lies.

	<i>Length</i> <i>mm.</i>	<i>Breadth</i> <i>mm.</i>
<i>Holotype.</i> A 46919, Plate 116, fig. 6. Internal mould of cranium.	14	23
<i>Paratypes.</i> 1. A 53008, Plate 116, figs. 7, 8. Broken internal mould of cranium	13	22 est.
2. A 53009, Plate 116, figs. 9, 10. External mould of hypostoma	5	7

Material. One whole and seven broken cranidia and one hypostoma.

Type localities. Holotype from SJ 07292634, 100 yards north of Llwyn-Onn Farmhouse, 3 miles west of Llanrhaiadr-ym-Mochnant; paratype 1 from SJ 12582848, roadside quarry, 450 yards south-south-west of Pen-y-graig, 1½ miles north of Llanrhaiadr-ym-Mochnant; paratype 2 from SJ 12172815, 200 yards north-north-west of Nant, 1 mile north of Llanrhaiadr-ym-Mochnant, Montgomeryshire.

Horizon. Upper Llandeilo, Calcareous Ash, Limestone, and Calcareous Shale.

Diagnosis. Cranium much wider than long, the eyes set far back and the axial furrows weak but long.

Description. *Cranidium:* much wider than long, gently convex transversely and longitudinally, but bent down vertically at front and less steeply at back. Glabella separated from fixed cheeks by weak but long axial furrows; broadest between fossulae, narrowest between palpebral lobes and broadening again slightly to base. Axial furrows shallow throughout, curved concave outwards, ending forwards in fossulae, which are a little deeper than furrow and which have a small central pustule; behind, end in pit at junction with shallow, narrow, occipital furrow, which is continued laterally by a broader, deeper posterior border furrow. Fixed cheeks about half breadth of glabella with well-defined palpebral lobes, the front of which is only one-third way from posterior to anterior margin. Cheeks slope down and back behind palpebral lobes towards posterior margin. Facial sutures run forward from palpebral lobes almost parallel to axial furrows at about 30° to long axis and then turn gradually inwards; just before the anterior of the cranium starts to steepen, sutures turn inwards, then pass over the steep margin, and are lost sight of just outside a line through the fossulae. Posterior

branches run back from palpebral lobe, swing out at about 45° to long axis, and only just short of posterior border do they swing more nearly straight back again to cut border. Surface of internal moulds smooth except near anterior margin; external moulds show surface covered with small irregular pits except anteriorly, where, as in internal moulds, concentric ridges run right across cranidium parallel to margin; these occasionally branch, are most strongly developed at margin and become fainter away from it and do not occur at more than 3 mm. from the margin; less distinct on internal moulds.

Hypostoma: subtriangular, width across anterior wings greater than length. Anteriorly gently rounded, posteriorly more strongly so; anterior wings about quarter way back, lateral margins continuous with posterior margin. Middle body: anterior lobe large, moderately swollen, more convex transversely than longitudinally; posterior lobe small,

EXPLANATION OF PLATE 116

Plates 116–18 are mainly of natural external and internal moulds and of plastic moulds made from these. They are unretouched, but the specimens were lightly coated with ammonium chloride before being photographed.

Figs. 1–5. *Basiliscus tyrannus* (Murchison). 1, From 80 yards north of Nant, 1 mile north of Llanrhaidr-ym-Mochnant, A 53006, internal mould of incomplete cranidium, $\times 1.5$. 2, 4, From 960 yards north-west of Plas-yn-glyn, 1 mile north-north-east of Llanrhaidr-ym-Mochnant. 2, A 46915, free cheek, $\times 1.5$. 4, A 53007, internal mould of pygidium, $\times 1.5$. 3, From 200 yards north-north-west of Nant, 1 mile north of Llanrhaidr-ym-Mochnant, A 46916, internal mould of pygidium, $\times 1.5$. 5, From scree 350 yards east of Llwyn-Onn, 3 miles west of Llanrhaidr-ym-Mochnant, plastic mould of A 46917, external mould of pygidium, $\times 0.75$.

Figs. 6–10. *Bumastus powisensis* sp. nov. 6, From 100 yards north-east of Llwyn-Onn, 3 miles west of Llanrhaidr-ym-Mochnant, A 46919, holotype, internal mould of cranidium, $\times 2$. 7, 8, From 960 yards north-west of Plas-yn-glyn, 1 mile north-north-east of Llanrhaidr-ym-Mochnant, dorsal and side views of A 53008, paratype 1, internal mould of incomplete cranidium, $\times 2$. 9, 10, From 200 yards north-north-west of Nant, 1 mile north of Llanrhaidr-ym-Mochnant. 9, A 53009, paratype 2 external mould of hypostoma, $\times 4.5$. 10, Plastic mould of A 53009, $\times 4.5$.

Figs. 11–13. *Proetidella* sp. 11, 12, From 80 yards north of Nant, 1 mile north of Llanrhaidr-ym-Mochnant. 11, A 53010, internal mould of pygidium, $\times 4$. 12, A 46911, free cheek, $\times 4$. 13, From 200 yards north-north-west of Nant, 1 mile north of Llanrhaidr-ym-Mochnant, A 46912, internal mould of incomplete cranidium.

Fig. 14. *Ogygiocarella debuchii* (Brongniart). From 730 yards north-west of Plas-yn-glyn, 1 mile north-north-east of Llanrhaidr-ym-Mochnant, A 46914, internal mould of incomplete pygidium, $\times 1.5$.

Figs. 15, 16. *Marrolithoides* sp. from 80 yards north of Nant, 1 mile north of Llanrhaidr-ym-Mochnant. 15, Plastic mould of A 53011, incomplete external mould of cephalon, $\times 2$. 16, Plastic mould of A 46909, incomplete internal mould of cephalon, $\times 2$.

Figs. 17–20. *Marrolithus lirellatus* sp. nov. 17, 19, From 80 yards north of Nant, 1 mile north of Llanrhaidr-ym-Mochnant. 17, A 46906, paratype 1, incomplete brim of cephalon showing ventral lamella, $\times 2$. 19, A 46907, paratype 2, internal mould of cephalon, $\times 2$. 18, From 100 yards north-east of Llwyn-Onn, 3 miles west of Llanrhaidr-ym-Mochnant, plastic mould of A 53012, holotype, external mould of incomplete cephalon, $\times 2$. 20, From 730 yards north-west of Plas-yn-glyn, 1 mile north-north-east of Llanrhaidr-ym-Mochnant, plastic mould of A 46908, external mould of incomplete cephalon, $\times 2.5$.

Fig. 21. *Marrolithoides* cf. *arcuatus* Whittard, from 80 yards north of Nant, 1 mile north of Llanrhaidr-ym-Mochnant, plastic mould of A 46910, external mould of cephalon, $\times 2$.

Fig. 22. ? *Primaspis* sp. from 200 yards north-north-west of Nant, 1 mile north of Llanrhaidr-ym-Mochnant, A 46913a, internal mould of pygidium, $\times 6$.



1



2



6



3



4



8



7



5



9



11



12



10



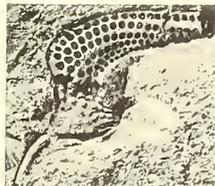
13



15



14



17



18



16



19



20



21



22

arcuate, slightly raised into weak maculae laterally. Median furrow strong in front of maculae and out to anterior wings, but weaker centrally, almost disappearing in mid-line. Lateral furrow broad and shallow after leaving median furrow, continuous with posterior furrow, which is also broad but rather deeper. Lateral and posterior border slightly raised outside furrow. Anterior wings short, almost right angles, rising sharply from lateral furrows before flattening out to be continuous with anterior lobe of middle body. Ornament of fine, roughly concentric grooves parallel to posterior and lateral margins; they branch and rejoin, most numerous in mid-line, joining and decreasing in numbers laterally; seven to eight grooves per mm.

Free cheeks, thorax and pygidium: not known.

Remarks. The only species closely resembling this is *B. fronto* Troedsson (1929) from the Upper Ordovician of Greenland, though that species shows more coarsely spaced ornament. The proportions of the cranidium are remarkably similar, but the cranidium of this species is usually about half the size of *B. fronto*, though one specimen of *B. powisensis* resembles *B. fronto* in size.

Family PROETIDAE Salter 1864
Subfamily PROETIDELLINAE Hupé 1953
Genus PROETIDELLA Bancroft 1949

Proetidella sp.

Plate 116, figs. 11–13

Material. Six cranidia, five free cheeks and one pygidium.

Localities. SJ 12272807, 80 yards north of Nant; SJ 12172815, 200 yards north-north-west of Nant, 1 mile north of Llanrhaidr-ym-Mochnant, Montgomeryshire.

Horizon. Upper Llandeilo, Calcareous Shale.

Description. *Cephalon*: approximately semicircular, convex transversely and less so longitudinally, approximately twice as broad as long. Continuous border marked off by furrow laterally and anteriorly. Glabella, just under one-third width and two-thirds length of cephalon; one-third as long again as broad, contracts slightly anteriorly, rounded in front, rises from neck furrow, very gently convex, slopes down anteriorly where it drops sharply into anterior furrow; evenly convex transversely, drops more steeply into axial furrows. Preglabellar field gently upturned, a little higher than lateral border, preglabellar furrow more rounded and broader than lateral furrow. Glabellar furrows very poorly developed and not always seen; a pair of very faint anterior furrows occasionally seen to slope backwards and inwards, inclined to axis at 45° and lying about two-fifths way back. Posterior pair of furrows curved and slope inwards and then backwards from a little more than half-way back. Lobes formed by these, roughly triangular, joined to rest of glabella posteriorly, each a little less than one-third width of base of glabella. Occipital furrow deep and swings forward to mid-line at postero-lateral angles of glabella. Occipital ring two-thirds length at sides that it is in mid-line, flattened longitudinally, gently arched transversely and lower than back of glabella; occipital node and lobes lacking. Fixed cheeks very narrow. Palpebral lobes far back, extending almost to posterior glabellar lobes; they are half the length of and only slightly lower than

glabella. Facial sutures run almost straight forward from palpebral lobes just outside axial furrows before cutting margin of cephalon almost at right angles; posterior branches run straight into posterior border furrows, then diverge strongly to cut posterior margin at about 30° half-way from axial furrow to outside lateral margin. Free cheeks rounded anteriorly, outer margin curved, becoming almost parallel to axis before passing into genal spines. Border appears to be flattened. Free cheeks quite strongly convex, bent down laterally and less strongly anteriorly. Genal angle produced into flattened triangular spine on to which lateral border furrow passes. Posterior border furrow extends across free cheek to join lateral border furrow in front of genal spine. Posterior border narrow and strongly convex. A furrow rises from posterior border furrow near axial furrow, passes round outer side of eye and dies out forwards. Eye almost semi-circular, sub-reniform, about half length of glabella, lies close to axial furrow, elevated above level of rest of free cheek.

Thorax: not known.

Pygidium: outline curved, just over twice as wide as long, slightly flattened across posterior; axis strongly convex with four clear axial rings and a nub behind these, tapers posteriorly for about two-thirds of length of pygidium, and is one-third of the breadth at anterior. Axial furrows shallow. Four pairs of pleurae present, all flattened and bent down at margin, anterior pair better defined, and have weak interpleural ridge at outer ends.

Remarks. This early British proetid species agrees with *Proetidella* in the form of the fairly long, preglabellar field and the position of the eyes, which lie close to the axial furrows and far back, being just in front of the posterior border furrows; the furrow is just lateral to the eyes and on the cheek. The form of the pygidium is also similar, though there are fewer axial rings in this species than in *P. fearnsidesi*. From the contemporary *Proetus* (?) *blandi* Cooper and *Proetus* (s.l.) *strasburgensis* Cooper from Virginia, this species differs in the form of the preglabellar field, where there is a much less sharp division between the furrow and ridge. The pygidium of this species is very similar to that of *P. (?) blandi*, however. *Ogmocnemis* from the Whittery Shales of Shropshire is markedly different, the eyes being much farther forward.

Family DIMEROPYGIDAE Hupé 1953

Genus DIMEROPYGE Öpik 1937

Dimeropyge sp.

Plate 118, figs. 20, 21

Material. One pygidium.

Locality. SJ 12272807, 80 yards north of Nant, 1 mile north of Llanrhaidr-ym-Mochnant, Montgomeryshire.

Horizon. Upper Llandeilo, Calcareous Shale.

Diagnosis. Pygidium with high vertical border beneath the pleural spines and no median indentation in the margin behind the axis.

Description. *Pygidium*: with four segments, semicircular; axis raised and rounded, higher than pleurae, sloping down backwards. Axis with three rings, and a terminal

piece seen as a pair of nodes behind third ring; does not reach posterior margin; about one-third total width at anterior; with articulating half ring. All three rings separated by well-defined transverse furrows; second and third rings with a median depression, faint on second, stronger on third and separating axis behind this into a pair of nodes. Axial furrows well defined, broader and shallower than axial ring furrows, deepen into pits at junctions with these; shallowest at posterior end. Four pairs of pleurae separated by sharp interpleural furrows continuous with axial ring furrows; weak pleural furrows near ends of pleurae. Interpleural furrows shallowest near axial furrows, deepen outwards. Pleurae broaden outwards to a series of pleural spines, then bent down sharply to a continuous vertical border. Interpleural furrows die out on this border, not reaching the bottom of it. Fourth pleurae meet in mid-line and run back almost parallel to axis, but behind it. Remaining pleurae curved to an increasing degree from front to back. Ornamentation, surface tuberculate everywhere except in furrows and on vertical border. Furrows smooth as is vertical border except for terminations of interpleural furrows. Tubercles are unevenly developed, largest round periphery overhanging border, two at end of each pleura. Larger tubercles also present on pleurae next axial furrows, one on each of first three pairs, two on each of fourth pair. Tubercles over remaining surface are considerably smaller.

Remarks. There is no close resemblance to any of the species described by Sinclair (1946). This species differs from *D. spinifera* Whittington and Evitt in having shorter tubercles, but this may be due to inferior preservation. From *D. virginiensis* of the same authors this species differs in having a higher border, while the posterior margin is not indented behind the furrow, which splits the terminal part of the axis of the pygidium. This species differs from *D. minuta* (Nieszkowski) in the absence of this indentation and in having coarser ornament. *D. minuta* appears in the Kukruse of Estonia, equated by Jaanusson and Strachan (1954, p. 693) with the *gracilis* zone in the graptolite succession. *D. spinifera* and *D. virginiensis* occur in the Lincolnshire Limestone and Botetourt Formation of the Edinburg Limestone respectively. The occurrence of *D. spinifera* seems to be about contemporary with this species, while *D. virginiensis* and *D. minuta* are slightly younger. An eastward migration seems to be indicated, with the earlier *Dimeropygiella* Ross as a possible ancestor. This specimen is slightly larger than pygidia of either *D. spinifera* or *D. virginiensis*.

Family TRINUCLEIDAE Hawle and Corda 1847

Subfamily CRYPTOLITHINAE Angelin 1854

Genus MARROLITHUS Bancroft 1929

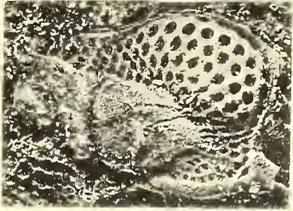
Remarks. It seems desirable that Whittard's (1956, pp. 27–29) nomenclature for the fringe formula on trinucleid brims should be adopted in the species of both *Marrolithus* and *Marrolithoides*, as it is applicable to almost all genera in the family. This still seems to be so, despite the fact that the system has one disadvantage when compared with Williams's system (1948, pp. 68–70). When noting the last radial row in which a concentric row of pits occurs, there are no difficulties in the E_1 and I_1 rows, but sometimes in the I_2 , and apparently almost always in the I_3 and subsequent rows, there is a loss of regularity, a breakdown of the concentric arrangement and possible introduction of adventitious pits. Thus it cannot with any certainty be said where a concentric row ends.

This makes the counting of pits laterally, i.e. beyond the angulation, in the more internal rows rather unreliable and therefore almost superfluous.

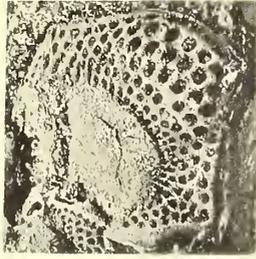
The nomenclature of the swollen area is dependent on an arbitrary delimitation of the pits within it. It was set up by Williams (1948, pp. 69–70) and was criticized by Whittard (1956, p. 51) who, however, was unable to provide a substitute or less subjective terminology. No satisfactory substitute is as yet forthcoming, but the following comments may prove useful. Although Williams states that pits on the slopes of the swollen areas should not be included in the pit count for the swollen areas, it is necessary to include pits some distance down the slopes to arrive at the counts obtained by both Williams and Whittard. To decide which pits on the slope are to be included is the most uncertain part of the procedure. Within the limitations of the system, it is possible to arrive at a fairly constant count for a specimen, based initially on counts on the holotypes. So far as pits in the I_1 row are concerned, the height above E_1 seems to be important. If the pit in I_1 is higher than the E_1 pit in the same radial row then it can be included in the swollen area. In the absence of a girder between the more internal rows, e.g. I_1 – I_2 or I_2 – I_3 , pits in the swollen area are less easily delimited.

EXPLANATION OF PLATE 117

- Figs. 1–3. *Marrolithus magnificus* sp. nov. From 730 yards north-west of Plas-yn-glyn, 1 mile north-east of Llanrhaiadr-ym-Mochnant. 1, Plastic mould of A 46902, holotype, external mould of incomplete cephalon, $\times 3$. 2, Plastic mould of A 53013, paratype 1, external mould of incomplete cephalon, $\times 3$. 3, Plastic mould of A 53014, paratype 2, external mould of incomplete cephalon, $\times 3$.
- Fig. 4. *Marrolithus inflatus maturus* Williams, from 80 yards north of Nant, 1 mile north of Llanrhaiadr-ym-Mochnant, A 46903, brim of cephalon and mould of genal spine, $\times 2$.
- Figs. 5–11. *Marrolithus favius* (Salter). 5, 6, 8, From 200 yards north-north-west of Nant, 1 mile north of Llanrhaiadr-ym-Mochnant. 5, A 46901, external mould of cephalon, $\times 3$. 6, Plastic mould of A 46901, $\times 3$. 8, Anterior view of A 53016, incomplete cephalon, $\times 2$. 7, 9–11, From 80 yards north of Nant, 1 mile north of Llanrhaiadr-ym-Mochnant. 7, Anterior view of A 53015, laterally compressed cephalon, $\times 2$. 9, A 53017a, internal mould of incomplete cephalon showing aberrant development of E_2 pits in antero-lateral corner of brim, $\times 3$. 10, Internal mould of pygidium, A 53018, showing muscle impressions on axis, $\times 4$. 11, Plastic mould of A 53019, external mould of pygidium, $\times 4$.
- Figs. 12–16. *Atractopyge williamsi* sp. nov. 12, From 200 yards north-north-west of Nant, 1 mile north of Llanrhaiadr-ym-Mochnant, A 53020, paratype 4, external mould of pygidium, $\times 6$. 13–16, From 80 yards north of Nant, 1 mile north of Llanrhaiadr-ym-Mochnant. 13, A 53021a, paratype 7, internal mould of pygidium, $\times 4$. 14, 15, Normal and posterior views of plastic mould of A 46896, paratype 5, external mould of incomplete pygidium showing doublure, $\times 6$. 16, Plastic mould of A 46895, paratype 6, external mould of pygidium, $\times 6$.
- Figs. 17, 18. *Atractopyge sedgwicki* sp. nov. From 730 yards north-west of Plas-yn-glyn, 1 mile north-north-east of Llanrhaiadr-ym-Mochnant. 17, A 46897, holotype, external mould of incomplete cranidium, $\times 3$. 18, Plastic mould of A 46897, $\times 3$.
- Figs. 19–25. *Flexicalymene cambrensis* (Salter). 19–21, 23, From 200 yards north-north-west of Nant, 1 mile north of Llanrhaiadr-ym-Mochnant. 19, A 53022, internal mould of hypostoma, $\times 5$. 20, 21, Side and normal views of A 53023, internal mould of incomplete cranidium, $\times 3$. 22, A 46898, incomplete cranidium showing shell ornament on glabella, $\times 3$. 23, A 46900a, external mould of incomplete cranidium, $\times 3$. 24, 25, From 80 yards north of Nant, 1 mile north of Llanrhaiadr-ym-Mochnant, normal and posterior views of A 53024, internal mould of pygidium, $\times 3$.



1



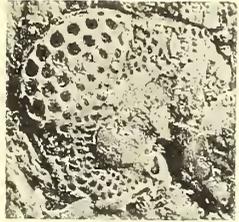
2



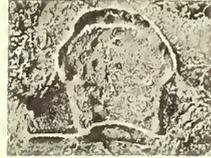
12



5



3



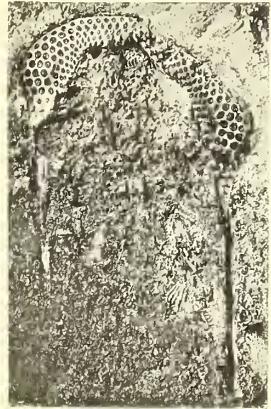
17



13



6



4



18



14



7



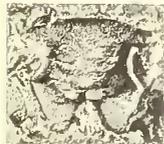
15



8



16



19



20



9



22



21



10



24



23



11



25

Marrolithus inflatus maturus Williams

Plate 117, fig. 4

1948 *Marrolithus inflatus* Williams, p. 74, pl. 6, fig. 3, text-fig. 4.1948 *Marrolithus inflatus maturus* Williams, p. 75, pl. 6, fig. 4, text-fig. 5.1956 *Marrolithus inflatus* Williams var. *maturus* Williams; Whittard, p. 56, pl. 7, figs. 2-4.

Material. Three well-preserved brims with parts of the genal spines, and one less well-preserved brim.

Locality. SJ 12272807, 80 yards north of Nant, 1 mile north of Llanrhaidr-ym-Mochnant, Montgomeryshire.

Horizon. Upper Llandeilo, Calcareous Shale.

Description. *Cephalon:* border outline smoothly convex anteriorly from one antero-lateral corner to the other, more sharply convex at corners and slightly concave laterally, passing back into very long and straight genal spines. Glabella and cheeks not known. Brim flat anteriorly, swollen antero-laterally and gently concave between these corners and cheeks; flat laterally so far as can be seen. Fringe formula: E_1 1-22, e_{10} , I_1 1-20, I_2 1-19, I_3 3-18, I_4 5(6)-17 + I_5 8-17, I_6 13-17 and I_7 present in the antero-lateral corners. The swollen areas include I_1 11-16, I_2 12-16, I_3 14-15; hexagonal patterns of tubercles occur round largest pits. Angulation occurs at 15 or 16.

Thorax and pygidium: not known from the Berwyns.

Remarks. The pitting of the brims of the Berwyn specimens compares closely with the holotype (GSM 75220), but the swollen pits in I_4 mentioned by Whittard in the Shelve material were not present, either in this material or in the holotype. *M. inflatus maturus* is distinguished from the much commoner *M. favus* in the Berwyns on the basis of the outline of the cephalon, which is more strongly convex anteriorly in this variety.

Marrolithus favus (Salter)

Plate 117, figs. 5-11

1848 *Trinucleus ornatus* var. δ *favus* Salter, p. 350, pl. 9, fig. 3.1948 *Marrolithus favus*; Williams, pp. 70-73, pl. 6, fig. 9, text-fig. 2.1956 *Marrolithus favus*; Whittard, pp. 55-57, pl. 7, figs. 6-13, text-fig. 4.

Material. Some 250 cephalons and a much smaller number of pygidia attributed to this species. Thorax not seen.

Localities. Known from all three inliers, but particularly common in the Iwrch Valley Inlier at SJ 12272807, 80 yards north of Nant; and SJ 12172815, 200 yards north-north-west of Nant, 1 mile north of Llanrhaidr-ym-Mochnant, Montgomeryshire.

Horizon. Upper Llandeilo, Limestone, and Calcareous Shale.

Description. *Cephalon:* outline subrectangular, anterior border almost straight across, but slightly convex forward in mid-line and towards antero-lateral corners. Antero-lateral corners strongly convex; lateral margin slightly concave, sloping slightly inwards and backwards; posterior margin almost straight across, slightly convex backwards laterally and behind glabella; postero-lateral corners almost right angles, only slightly rounded. Glabella strongly convex longitudinally and transversely; tapering posteriorly,

with one pair glabellar furrows in front of occipital furrow; these quite short, narrow, inclined backwards. Glabella invades fringe only slightly, front of it approximately level with angulation of antero-lateral corners. Axial furrows moderately shallow, ending forwards in fossulae. Cheeks moderately convex longitudinally and transversely with shape of quarter circle, bent down most sharply at back. Posterior border narrow, passing laterally into back of fringe. Occipital ring narrow and bearing a small occipital spine. Fringe or brim flat in front and postero-laterally, swollen in antero-lateral corners and moderately concave between these swellings and cheeks. Fringe formula of a typical example: (A 46901) E_1 0-25, e_1 i, I_1 0-25, I_2 0-22+, I_3 2-22, I_4 6-23, I_5 9-20, I_6 14-16, I_7 laterally; angulation at 16; swollen area I_1 11-20, I_2 11-17, I_3 13-16, which equals 10, 7, and 4 respectively in the I_1 , I_2 , and I_3 rows.

Remarks. As Whittard (1956, p. 56) has pointed out, the precise delimitation of the swollen area is difficult, and counts will vary from one specimen to another. Hexagonal patterns of tubercles occur round the larger of the swollen pits. There is some variation in the pattern of the pits near the mid-line especially in the E_1 row and the two specimens quoted below illustrate this. Only the first part of the fringe formula is quoted for these; they should be contrasted with specimen A 46901 quoted above.

A 53015, E_1 1-24, e_1 o, i, I_1 0-24, &c., see Plate 117, fig. 7.

A 53016, E_1 0-26, e_1 i, I_1 0-25, &c., see Plate 117, fig. 8.

The strongly marked girder on the ventral surface of the fringe referred to by Whittard (1956, p. 56) seems to be not uncommon. A specimen from the Berwyns shows the fringe to be concave in front of and behind the anterior part of the girder. The girder decreases in prominence laterally and is hardly noticeable at the swollen corner or laterally, although there is a sharp drop from the I_1 pits to the E_1 pits in the swollen corners. This sharp drop is commonly seen on the dorsal lamella. The swollen area has the following formula; I_1 7 or 8-18, I_2 11-18, I_3 14-17, that is, 11, 8, and 4 rows, which is very similar to the formula of the dorsal lamella given above.

A single specimen (A 53017a) of this variety showed the most unusual phenomenon of incipient development in the antero-lateral corners of E_2 pits (Pl. 117, fig. 9). Three of these are present, in the row containing the angulation and the two rows in front. There is no trace of E_2 development in front of the glabella as in *Costonia*. Only one specimen showing this type of aberration was collected by Williams in some 1,500 specimens from the Llandeilo of Llandeilo. In it only one E_2 pit was developed though in a similar position. It may be noted that this aberrant specimen from the Berwyns has the sharply angulated antero-lateral corner of the type seen in *M. scalpriformis* Whittard, but the amount of brim outside the E_1 pit row is greater in this specimen.

Pygidium: breadth/length: 1.5/8.0 mm. on one specimen and 2.0/6.5 mm. in another. Nine or ten axial rings, of which the anterior is more prominent; axis tapers gently to posterior margin, where it is rounded, standing high above pleurae; moderately convex transversely. Pleurae flat, rising slightly laterally; no segmentation can be seen in internal moulds, external moulds reveal weak traces of at least three pleurae with space for several more. A low, narrow brim round margin of pygidium, beyond this, pygidium bent down into a vertical flange which is deepest behind axis and decreases laterally.

Remarks. In both the Llandeilo and the Shelve areas *M. favus* occurs in the highest beds

of the Llandeilo and both Williams (1948, p. 87) and Whittard (1956, p. 57) believe that it may be taken as a good index fossil for beds of this age. It is chiefly on the very great abundance of this species that the Llandeilo rocks of the Berwyns have been placed in the Upper Llandeilo. The pygidia described above are attributed to *M. favus* because this is the most abundant marrolithid species in the Berwyns, but they have not been found attached to the remainder of the exoskeleton. There is little variation in the pygidium between most species in the genus.

Marrolithus magnificus sp. nov.

Plate 117, figs. 1-3

Derivation of name. Latin *magnificus*, noble or fine; referring to the unusually great development of the swollen areas on the brim, this species having the largest swellings so far described on the brim.

	<i>Length</i> <i>mm.</i>	<i>Breadth</i> <i>mm.</i>
<i>Holotype.</i> A 46902, Plate 117, fig. 1. External mould of part of cephalon	8	20 est.
<i>Paratypes.</i> 1. A 53013, Plate 117, fig. 2. External mould of part of cephalon	11	26 est.
2. A 53014, Plate 117, fig. 3. External mould of part of cephalon	9	20 est.

Material. Six large fragmentary cephalata.

Type locality. SJ 12852846, 730 yards north-west of Plas-yn-glyn, 1 mile north-north-east of Llanrhaidr-ym-Mochnant, Montgomeryshire.

Horizon. Upper Llandeilo, Calcareous Shale.

Diagnosis. With subrectangular outline and the swollen areas extending deep into the I₄ row of pits.

Description. *Cephalon:* outline subrectangular; anterior border slightly convex forwards centrally, more strongly so in antero-lateral corners, with a slight concavity between; antero-lateral corners quite sharply angular, though paratype 3 shows them in a rounded condition; sides slope slightly inwards and backwards to genal angles; posterior border not unlike anterior in being convex backwards centrally and postero-laterally and slightly concave between. Genal angles 90° approximately. Glabella pyriform, strongly convex longitudinally and transversely; whether any glabellar furrows are present is unknown because of poor preservation; anteriorly glabella does not invade brim to any great extent; ends a little farther forward than a line joining antero-lateral angulations. Axial furrows broad, shallow, throughout, with small fossulae. Occipital furrow and ring poorly preserved. Cheeks more strongly convex longitudinally than transversely, most strongly bent down posteriorly, approximately a quarter circle in outline. Brim (dorsal lamella) narrowest in front, broadening to a maximum antero-laterally, narrowing again behind this to pass behind cheeks almost half-way to axial furrows; flat except in swollen areas. Fringe formula E₁ 0-24, e₁0, I₁ 1-24, I₂ 1-23 or 24, I₃ 3-22+, I₄ 5-18+, I₅ 8-17+, I₆ 13-17+, and I₇ may occur in the corners. Beyond row 17 regular arrangement of pits lost inside I₂; therefore, termination of I rows inside I₂ not known with any accuracy. Angulation at row 15. Swollen area: holotype I₁ 8-17, I₂ 9-17, I₃ 10-16, I₄ 14-

16, i.e. 10, 9, 7, 3. Two other specimens gave the counts 10, 8, 6, 4 and 12, 9, 7, 4 respectively. There is clearly a slight variation in pattern, but it falls within reasonable limits. Tubercles in hexagons round larger swollen pits as in most other species. In conjunction with very great swelling in corners, I_1 row stands high above E_1 row of pits there.

Thorax and pygidium: not known.

Remarks. This new species occurs principally at one locality high in the Calcareous Shale division near the top of the Llandeilo. It occurs on the same bedding plane as the much commoner *M. favus*, and it seems likely that they are closely related, this species probably having descended from *M. favus*.

Marrolithus lirellatus sp. nov.

Plate 116, figs. 17-20

Derivation of name. Latin *lirella*, a ridge, from the narrow swollen areas on the brim, where the great majority of the swollen pits lie in a single row.

	<i>Length</i> <i>mm.</i>	<i>Breadth</i> <i>mm.</i>
<i>Holotype</i> . A 53012, Plate 116, fig. 18. External mould of part of cephalon	7	16 est.
<i>Paratypes</i> . 1. A 46906, Plate 116, fig. 17. Incomplete cephalon showing ventral lamella	7	18 est.
2. A 46907, Plate 116, fig. 19. Internal mould of cephalon	6	14

Material. Twenty-five cephalons, many of them fragmentary.

Type localities. Holotype from SJ 07292634, 100 yards north-north-east of Llwyn-Onn Farmhouse, 3 miles west of Llanrhaiadr-ym-Mochnant; paratypes 1 and 2 from SJ 12272807, 80 yards north of Nant, 1 mile north of Llanrhaiadr-ym-Mochnant, Montgomeryshire.

Horizon. Upper Llandeilo, Limestone, and Calcareous Shale.

Diagnosis. Swollen area of the brim with eight to ten swollen pits in I_1 row and usually two or less in the I_2 row; angulation of the brim level with one-third way back on the glabella; the genal angle behind the level of the occipital ring. Radial pit rows very regular.

Description. *Cephalon*: outline gently convex anteriorly, broadly rounded antero-laterally, sides straight and slightly convergent backwards; posterior margin runs straight out from occipital ring before swinging more backwards to genal angle. Genal spines variable, may point backwards, downwards, and/or outwards, sometimes being curved. Glabella clavate, strongly convex longitudinally and transversely, protruding slightly into brim; one pair glabellar furrows, little more than pits near base of glabella. Axial furrows broad and with broad, shallow fossulae, separated from brim by gently convex, low, transverse ridge. Axial furrows pass into small pits at junction with occipital furrow. Occipital ring simple, consisting mainly of base for short, thick, nuchal spine pointing backwards and upwards at about 45° . Occipital furrow shallow except at pit at junction with axial furrows, continued laterally by posterior border furrows to brim behind cheeks. Cheeks gently convex longitudinally and transversely and a quarter ellipse in outline. Brim broadens gently laterally to angulation and beyond

to genal angle; gently concave out to girder, beyond which it drops away gently. Holotype fringe formula: E_1 0–25 or 26, e_i , I_1 , 2 , and 3 1–25, I_4 4–24, I_5 13–20; swollen area I_1 12–18, I_2 18. Angulation at 18. Other specimens show that angulation may also occur at either 17 or 16. Paratype 2 and another specimen show swollen area to extend from I_1 11–17 and I_1 11–18 respectively and in both cases there are no swollen pits in I_2 row. In the ventral lamella the girder is very prominently developed, especially in front of the glabella, where it consists of a sharp ridge. The brim is more strongly concave on the proximal side of the girder than is the case on the dorsal lamella. The swollen area in paratype 1 (A 46906) has the following formula I_1 8–17, I_2 14–16, that is, 10 and 3 pits. Other specimens showing the ventral lamella indicate that there are more pits in the swollen area than occur in the dorsal lamella. The regularity of the radial rows of pits is present in both the dorsal and ventral lamellae.

Remarks. This species seems to bear out Whittard's (1956, pp. 56 et seq.) observations on the greater development of the girder on the ventral lamella of marrolithid brims. There are some resemblances to *M. bureaui* (Oehlert), particularly in the extent and nature of the swollen area in the brim. In both species there is a long row of swollen pits in I_1 with few in I_2 , but the posterior margin of this species does not run forward to the genal angle and the angulation in the antero-lateral corners is less far forward. None of the Shelve or Llandeilo species bears a close resemblance to *M. lirellatus*. This species differs from *M. craticulatus* Whittard in having the largest pits in I_1 , from *M. arenarius* Whittard in not having large numbers of auxiliary pits in E_1 , and from *M. bilinearis* Whittard in having only one row of swollen pits.

Genus MARROLITHOIDES Williams 1948

Marrolithoides cf. *arcuatus* Whittard

Plate 116, fig. 21

1956 *Marrolithoides arcuatus* Whittard, p. 64, pl. 8, figs. 16–17, pl. 9, figs. 1–2.

Material. One external mould of an almost complete cephalon.

Locality. SJ 12272807, 80 yards north of Nant, 1 mile north of Llanrhaiadr-ym-Mochnant, Montgomeryshire.

Horizon. Upper Llandeilo, Calcareous Shale.

Description. *Cephalon:* anterior margin uniformly curved, convex forward; lateral margins almost parallel, converging slightly backwards; antero-lateral corners obtusely rounded; posterior margin runs straight out from mid-line before bending slightly backwards and outwards to genal angle.

Glabella pyriform, without glabellar furrows, although there is a slight pit on one side that might be a glabellar pit or might be due to crushing of the specimen. Axial furrows straight, converging backwards, with fossulae separated from brim by low ridge; posteriorly they drop into shallow pits at junction with occipital furrow. Cheeks rounded; much lower than glabella and dropping sharply into axial furrows and posterior border furrows. Occipital ring gently curved longitudinally, with a substantial occipital spine pointing upwards and then backwards. Occipital furrow very shallow, passing laterally into slightly less shallow posterior border furrows.

Brim widest in antero- and postero-lateral corners, narrowing in front of glabella and dying out behind cheek, lobes, reaching only a short way towards axial furrows. Girder most prominent antero-laterally, slightly less prominent anteriorly, and weak laterally. Inside girder radial ridges between pits more prominent than concentric ones. Fringe formula: E_1 0-22, I_1 1-22, I_2 3-22, I_3 4-21, I_4 5-17, I_5 10-17. Angulation at 15. In antero-lateral corners there is a concentric row of small pits not corresponding to radial rows farther out, and extending from rows 15 to 22. Increase in pit size outwards very slight, I_1 pits being only slightly larger than rest.

Thorax and pygidium: not known from the Berwyns.

Remarks. The specimen from the Berwyns differs from the Shelve material in the following respects. It is half as big again, the I_5 pits appear rather sooner, the girder is low laterally, the glabella invades the border to a greater extent, and this is reflected in the pit formula in the points at which the I_2 and I_3 rows begin. In *M. simplex* Williams there are fewer concentric rows of pits, while *M. simplex elevata* Williams has the I_1 row of pits markedly raised above the E_1 and I_2 rows. This specimen occurs rather earlier in the Ordovician than the type material, which comes from the *N. gracilis* Zone Rorrington Beds of Shropshire.

Marrolithoides sp.

Plate 116, figs. 15, 16

Material. Ten incomplete cephalae.

Locality. Commonest at SJ 12272807, 80 yards north of Nant, 1 mile north of Llanrhaiadr-ym-Mochnant, Montgomeryshire.

Horizon. Upper Llandeilo, Calcareous Shale.

Description. *Cephalon*: parallel-sided and straight across front, broadly rounded antero-lateral corners and roughly right-angled postero-lateral corners; posterior margin approximately straight across as far as can be seen, but bent slightly back to genal angles. Genal spines continue line of lateral margins straight backwards. Glabella clavate, dropping steeply to brim, posterior unknown; axial furrows broad with fossulae just behind brim. Cheek lobes gently convex, lower than glabella, almost semicircular in outline. Occipital ring narrow, with nuchal spine, occipital furrow narrow, passing into a small deep pit at junction with axial furrows; continued laterally by posterior border furrows. Border narrowest anteriorly, broadening through antero-lateral corners to postero-lateral corners where widest, beyond this narrows rapidly behind cheek lobes to die out about half-way to axial furrows. Slightly concave on proximal side of girder. Only slight increase in size in brim pits outwards, most marked in antero-lateral corners. Girder is well marked on dorsal lamella. Fringe formula: E_1 1-26, I_1 1-27, I_2 1-26, I_3 3-24, I_4 4-21, I_5 11-21, I_6 16-20. One specimen showed eight accessory pits in I_7 position between 14 and 19. Angulation varies between 16 and 18. Ventral lamella; in this species, too, girder very prominent in front of glabella, continues to be so to angulation then fades away to posterior, prominent again on genal spine. Otherwise similar to dorsal lamella.

Remarks. This rather motley collection of material lacks the sharply defined angulation seen in *M. arcuatus* Whittard and has a more uniform breadth to its brim. It also has

more concentric rows of pits. Similarly, there are more concentric rows of pits than in *M. simplex* Williams. The outward increase in size of pits in the best preserved brim is not believed to justify placing this material in *Marrolithus* and indeed it is not present in the majority of the specimens. Probably more than one species is present.

Family ENCRINURIDAE Angelin 1854
 Subfamily CYBELINAE Holliday 1942
 Genus ATRACTOPYGE Hawle and Corda 1847
Atractopyge sedgwicki sp. nov.

Plate 117, figs. 17, 18

Derivation of name. After Prof. Adam Sedgwick, famous for his work on the geology of North Wales.

	<i>Length</i> mm.	<i>Breadth</i> mm.
<i>Holotype.</i> A 46897, Plate 2, figs. 17, 18. External mould of cranidium	6	7 between eyes

Material. One cranidium.

Type locality. SJ 12852846, 730 yards north-west of Plas-yn-glyn, 1 mile north-north-east of Llanrhaidr-ym-Mochnant, Montgomeryshire.

Horizon. Upper Llandeilo, Calcareous Shale.

Diagnosis. Glabella expanded forwards, with two pairs of tubercles on the anterior lobe; anterior border with eight coarse tubercles at the front and one pair laterally; anterior border furrow deep, transverse, mesially; faint laterally.

Description. *Cranidium:* glabella gently arched transversely at front, more strongly convex behind anterior lobe; weakly convex longitudinally. Axial furrows broad and shallow, almost parallel at back, diverging forward gently at first before swinging outwards sharply behind swollen frontal lobe to end in fossulae. Glabella has two pairs of prominent tubercles on frontal lobe at corners of square, another pair of tubercles lies closer together and between second and third glabellar furrows. Glabellar furrows short and transverse, posterior pair are not quite transverse, broaden inwards giving subtriangular posterior glabellar lobes, second pair parallel to posterior margin, anterior pair reduced to pits slightly elongated laterally; furrows almost obsolete laterally, deepening abruptly into transverse apodemes proximally. The fossulae lateral to and just in front of the anterior glabellar furrows, slightly elongated along axial furrows. Anterior border transverse with flattened cylindrical shape mesially, with eight coarse tubercles on dorsal surface and a number of finer ones towards front; laterally it is cylindrical, lower, inclined backwards at about 45°, smooth except for one isolated tubercle on each side lying a short distance in front of fossulae. At tubercle, anterior border more swollen again though still smaller than anteriorly. Narrows behind tubercle, becomes almost parallel to axis of glabella and dips down into fossulae. Pre-glabellar furrow deep, transverse, mesially; oblique, shallow, almost dying out laterally, but continuing as far as the fossulae. Occipital ring arched transversely, moderately flattened longitudinally, about twice as long in mid-line as adjacent to axial furrows; occipital furrow shallow, deepening towards axial furrows. Fixed cheeks rise steeply

from axial and posterior border furrows, slightly higher than glabella, much higher than posterior border; palpebral lobes rise high above cheeks, lie between posterior and second glabellar furrows, equidistant from posterior margin and axial furrows. Posterior border low, straight, and simple; posterior border furrow well developed behind fixed cheeks, parallel to posterior margin. Facial sutures run straight forward from eyes to just outside fossulae, but course of posterior branch is unknown.

Remarks. This species differs from *A. kutorgae* (Schmidt) in having a different pustule pattern on the preglabellar field, while the eyes lie slightly farther back. Compared with *A. vardiana* Männil, the glabella is broader, the axial furrows are shallower, the eyes lie farther from the axial furrows, the apodemes are deeper proximally, the preglabellar furrow is faint laterally and the pustule pattern on the preglabellar field is different. *A. sedgwicki* differs from *A. grewingki* (Schmidt) in the following respects; the axial furrows are arcuate instead of straight and the frontal lobe of the glabella is more swollen; there are more tubercles on the anterior border and the anterior border furrow is deeper mesially. A single cranidium from Nantgaredig, Carmarthenshire, JP 3821 of the Geological Survey collections, is similar. From it *A. sedgwicki* differs in not having a prominent pustule in the preglabellar furrow, in having coarser ornamentation, eye ridges are absent and the glabella is less swollen transversely, though this last point may be due to crushing.

Atractopyge williamsi sp. nov.

Plate 117, figs. 12–16; Plate 118, figs. 1–7

Derivation of name. Named after Prof. Alwyn Williams of Queen's University, Belfast.

	Length mm.	Breadth mm.
<i>Holotype.</i> A 53028, Plate 118, figs. 5, 6. Internal mould of cranidium	3·5	9·5 (crushed)
<i>Paratypes.</i> 1. A 53027, Plate 118, fig. 4. Internal mould of cranidium	3·0	4·0+ (crushed)
2. A 53025, Plate 118, figs. 1, 2. Internal mould of cranidium	3·5	7·0 est.
3. A 53029, Plate 118, fig. 7. Internal mould of cranidium	4·0	9·0
4. A 53020, Plate 117, fig. 12. External mould of pygidium	1·5	2·0 (longitudinally compressed)
5. A 46896, Plate 117, figs. 14, 15. External mould of pygidium	3·0 est.	3·5
6. A 46895, Plate 117, fig. 16. External mould of pygidium	3·0	3·1
7. A 53021a, Plate 117, fig. 13. Internal mould of pygidium	4·0	4·2

Type localities. Holotype and paratypes 3, 5, 6, and 7 from SJ 12272807, 80 yards north of Nant, 1 mile north of Llanrhaiadr-ym-Mochnant; paratypes 1, 2, and 4 from SJ 12171815, 200 yards north-north-west of Nant, 1 mile north of Llanrhaiadr-ym-Mochnant, Montgomeryshire.

Horizon. Upper Llandeilo, Calcareous Shale.

Diagnosis. With inflated, strongly convex glabella and very reduced anterior border.

Description. *Cephalon:* semicircular, breadth rather more than twice length, genal

angles bearing small fixigenal spines. Glabella strongly convex, pyriform, with bulbous anterior lobe dropping vertically or even overhanging at front; remainder of glabella strongly convex, lower than anterior lobe but merging with it, descending almost vertically to axial furrows, widening slightly across posterior glabellar lobes. Three pairs glabellar furrows, none crossing glabella completely. First two pairs very short, little more than pits, third pair longer, inclined backwards and inwards, partly cutting off very small, low, third glabellar lobes. Occipital ring slightly longer in mid-line than at sides, smooth. Anterior border discontinuous, starting as faint smooth ridge from axial furrows and dying out before reaching mid-line. Preglabellar furrow weak and shallow where present. Axial furrows run obliquely back behind anterior glabellar lobe at 30° to long axis, then swing round until parallel with it at third glabellar furrows, then swing outwards past third lobes to enter marked pit at junction with occipital furrow. Fixed cheeks strongly convex, rising steeply from axial furrows, about same height as posterior part of glabella with palpebral lobes at highest point level with second glabellar lobes; about two and a half times width of posterior part of glabella, bent down strongly to sides, dropping steeply to posterior border behind palpebral lobes, though only level with posterior border laterally. Posterior border short adjacent to occipital ring, but lengthens laterally to about twice length of occipital ring at genal angle, where it swings forward before being cut off by facial suture. Genal spine short, tapering at about 40° with outer margin parallel to long axis of glabella. Facial sutures proparian; anterior branches run forwards and outwards at 45° until level with first glabellar lobes, when they swing inwards to the axial furrows and anterior border. Posterior branches run parallel to posterior margin until almost half-way to border before curving slightly backwards to cut lateral margin a short distance in front of genal angle. Ornamentation of coarse tubercles on glabella and fixed cheeks, surface otherwise smooth. The pattern of these seems to be as follows: there is a transverse row of tubercles round the front of the glabella and low down, but on the remainder of the anterior lobe of the glabella they are scattered irregularly. A pair of tubercles is situated between each pair of glabellar lobes. On each fixed cheek there are three tubercles between the eye and the axial furrows, one a short distance in front of the eye, a second just behind it, and the third overhanging the posterior margin.

Pygidium: almost square outline, rounded in front, with slightly sigmoidal sides. Axis with eleven or twelve rings, at first almost parallel-sided, tapering gently until near posterior end, where it tapers sharply to end in a point cut off from the posterior margin by fourth pleurae, which swing round behind axis to meet just in front of posterior margin. Axial rings raised above level of pleurae, axial furrows well defined. First four axial rings completely separated by furrows, remainder by incomplete furrows seen only at sides and not crossing axis. Four pairs of pleurae, one pair arising from each of first four axial rings. These are raised, sharply defined, and with the exception of one specimen smooth, narrowest at front and broadening backwards. At first inclined outwards and backwards from axial rings, become parallel to long axis, then converge towards a point behind posterior end of axis before becoming parallel again. End in upturned points along straight posterior margin with fourth pleurae highest and immediately behind axis, and first pleurae lowest and farthest out, second and third pleurae in intermediate positions. Pleurae divided into narrow anterior bands and swollen posterior bands by

pleural furrows. These shallow throughout, long on first pleurae, shorter on second, only just present on third, and absent from fourth. Under points, posterior margin of pleurae drops almost vertically as doublure, still showing divisions into pleurae. Lower margin of doublure curved, being highest behind axis and lowest behind first pleurae, continues forward for a short distance along side of first pleurae. Whole surface faintly granular, almost smooth with the exception of one specimen (paratype 7) carrying a few tubercles on the pleurae.

Remarks. The cranidium resembles that of *Oedicybele* Whittington, but can be distinguished from it in having the eyes much farther back and much nearer the axial furrows. The pygidium differs from that of *A. kutorgae* (Schmidt) in the form of the doublure and in having fewer rings in the axis. It differs also from the pygidium of *A. grewingki* (Schmidt) in having a wider axis with fewer rings and having the pleurae reach farther back. The pygidium of *A. williamsi* is also unusual in having very narrow anterior bands on the second and third pleurae.

Family CALYMENIDAE Burmeister 1843
Subfamily CALYMENINAE Burmeister 1843
Genus FLEXICALYMENE Shirley 1936
Flexicalymene cambrensis (Salter)

Plate 117, figs. 19–24

1865 *Calymene cambrensis* Salter, pp. 98–99, pl. 9, figs. 12–14.

1931 *Calymene cambrensis* Shirley, pp. 20–22, pl. 1, figs. 11–15.

Material. Sixty cranidia, thirty pygidia, and one hypostoma.

Localities. Present in the majority of outcrops of Llandeilo rocks, but particularly common at the following localities: SJ 07292634, 100 yards north-north-east of Llwyn-Onn Farmhouse, 3 miles west of Llanrhaidr-ym-Mochnant; SJ 12172815, 200 yards north-north-west of Nant, 1 mile north of Llahraiad-ym-Mochnant; SJ 12582848, Quarry 450 yards south-south-west of Pen-y-graig, 1½ miles north of Llanrhaidr-ym-Mochnant, Montgomeryshire.

Horizon. Upper Llandeilo, Calcareous Ash, Limestone, and Calcareous Shale.

Description. *Cranidium*: arched transversely, less convex longitudinally but bent down fairly sharply in front. Glabella almost parabolic though rather flattened across front, not projecting as far forward as fixed cheeks, with weak median ridge seen only in well-preserved specimens. First (p) glabellar lobes (basal) almost quadrangular, slightly wider than axial part of glabella that lies between them and to which they are attached by low, narrow necks. Basal glabellar furrows deep, running at first in and backwards at 70° to long axis of glabella before bifurcating; anterior branch very short, shallow, swinging slightly forward and dying out; posterior branch, turning back until about parallel to long axis of glabella, remains deep until it reaches occipital furrow cutting off glabellar lobe, no intermediate lobes on even largest specimens. Second glabellar (p) lobes well developed, elongate, inclined at 60°–70° to long axis; do not project as far to side as basal pair, cut off from median part of glabella by low necks that are less prominent than those behind. Second glabellar furrows (p) broader, less deep, almost parallel to first, bending slightly back before dying out on neck of second lobes. There is a faint suggestion of an anterior branch to this furrow turning slightly forward and dying out. Third glabellar

lobes (p) small, inclined slightly back and in, nearly at right angles to axis, much lower than median part of glabella, with weak neck separating them from it. Third glabellar furrows (p) short, shallow, almost at right angles to axis, inclining slightly backwards. Very faint fourth glabellar furrows (p) in front of this, barely discernible and leaving axial furrows just behind fossulae. Anterior lobe of glabella semicircular, rather straight across the front. Axial furrows run forwards and outwards from occipital furrow, farthest apart across middle of basal glabellar lobes, then converge forward, deepest here also, become shallower forwards towards second glabellar lobes (p) before deepening slightly to fossulae; beyond this, shallower and broader before merging into preglabellar furrow; narrowest at middle of basal glabellar lobes, very gradually widen forwards. Preglabellar furrow shallow and, like the anterior border, which is unbroken and rises gently forward, is affected considerably by compression of individual specimen. Occipital ring about twice as long in mid-line as behind glabellar lobes, extends laterally not quite as far as first glabellar lobes; about same height as first glabellar lobes in mid-line and lower behind them; none of the Berwyn specimens showed the median knob seen in the types. Occipital furrow deepest behind glabellar lobes and shallower and broader in mid-line where it swings some distance forward. Fixed cheeks much lower than median part of glabella, palpebral lobes about same height as second glabellar lobes, which they are opposite; cheeks slope steadily outwards and downwards towards genal angles, gently convex longitudinally. Posterior border broadens steadily outwards from axial furrows to genal angles while bending gently backwards; at genal angle it begins to turn forward before being cut off by gonatoparian facial suture. Facial sutures run almost straight forward from eye to anterior border, posterior branches swing outwards and backwards to most posterior part of border furrow before cutting genal angle. Free cheeks not known.

Hypostoma: subquadrate outline, middle body ovate, uniformly swollen, middle furrow curved, crossing middle body to divide it into a U-shaped posterior lobe and an ovate, globose, anterior lobe. Lateral border separated from middle body by broad lateral furrow running from anterior wing, where narrow, back parallel to border and broadening out to posterior wing where deepest; here, lateral furrows merge into posterior furrow, also broad. Anterior margin ventrally flexed centrally and slightly convex forward; anterior furrow broad, shallow. Anterior wings small, gently flexed dorsally, slightly backwards. Posterior wings obtusely pointed, lying about two-thirds way back. Posterior forks acutely rounded on either side of median notch, which extends forward to cut posterior furrow.

Pygidium: almost diamond-shaped outline, strongly convex transversely, nearly flat longitudinally, bent down sharply beyond tip of axis. Eight axial rings and short unsegmented portion beyond, seven pairs of pleurae. Axis three-sevenths of width at front, narrowing rapidly for first four rings then more gently to posterior part of axis; strongly arched transversely, anterior rings flattening out towards axial furrows. Ring furrows become shallower backwards, all crossing axis; articulating half ring present. Axial furrows deepest opposite fifth axial ring, become shallower backwards and forwards, unite at tip of axis, which does not quite reach posterior margin. Pleurae strongly convex, bent down most strongly at posterior, becoming more flattened distally; pleural furrows faint, but extending from axial furrows to margin, dividing pleurae into slightly

larger anterior and smaller posterior portions; interpleural furrows well developed. Pleurae behind sixth pair ill defined but space for a further two pairs before mid-line in post-axial area. Margin of pygidium rises posteriorly to almost meet tip of axis. Laterally bent down.

Remarks. This material corresponds closely with the description of the species by Shirley (1931). The anterior border is the area most meriting comment. Here it varies from one-third to one-quarter or even one-fifth of the length of the glabella, and so far as can be seen this figure depends chiefly on the amount of compression that the specimen has undergone, and the direction taken by that compression relative to the long axis of the specimen. Those compressed perpendicularly to the long axis have the longest anterior border (up to one-third length of the glabella) while those compressed along the length of the specimen have much shorter anterior borders. In the latter specimens the anterior border also takes on a slightly bent appearance producing a condition approaching that seen in the anterior border of *Reacalymene*. The break seldom goes as far as is seen in that genus, but the intermediate stages seem well represented. A more extreme condition of compression is illustrated alongside more normal specimens (Pl. 117, fig. 22).

The description of the pygidium is rather more detailed than that of Shirley, and the hypostoma is described for the first time.

Family LICHIDAE Hawle and Corda 1847
Subfamily LICHINAE Hawle and Corda 1847
Genus METOPOLICHAS Gürich 1901

Metopolichas contractus sp. nov.

Plate 118, figs. 8-17

Derivation of name. Latin *contractus*, narrow, from the narrow central lobe in the glabella.

	Length mm.	Breadth mm.
<i>Holotype.</i> A 46894, Plate 118, figs. 8-10. Internal mould of cranium	13	14 est.
<i>Paratypes.</i> 1. A 46893b, Plate 118, figs. 11, 12. Fragmentary internal mould of cranium.	9.5+	9+
2. A 53030, Plate 118, figs. 13, 14. Internal and external moulds of hypostoma	4	5.5
3. A 53031, Plate 118, figs. 15-17. Internal and external moulds of pygidium	4.5	9

Material. Two incomplete cranidia, one hypostoma, and one pygidium.

Type localities. Holotype from SJ 12582848, 450 yards south-south-west of Pen-y-graig, 1 $\frac{2}{3}$ miles north of Llanrhaiadr-ym-Mochnant; paratypes from SJ 12272807, 80 yards north of Nant, 1 mile north of Llanrhaiadr-ym-Mochnant, Montgomeryshire.

Horizon. Upper Llandeilo, Calcareous Shale.

Diagnosis. Glabella with elongate and narrow central lobe which is lower than the bicomposite lobes at its narrowest point, and with occipital ring hardly extending beyond the occipital lobes; pygidium with axis dying out gradually and reaching well towards the posterior margin, which has a slight median embayment.

Description. *Cranidium*: gently convex transversely, strongly so longitudinally, anterior margin rounded and slightly arched in centre. Anterior border well defined continuing on to front of free cheek. Glabella, widest across bicomposite lobes; central lobe flattened posteriorly, curved downward in front; longer than wide, gently rounded transversely in front with acutely rounded antero-lateral extremities; greatest width of central lobe in front of bicomposite lobes, then narrowing posteriorly to about one-quarter of maximum width and parallel-sided about half-way back along bicomposite lobes; gently widening behind this so that between basal lateral glabellar lobes, from which separated by very shallow depressions, it is about half maximum width at anterior. Anterior of central lobe strongly convex longitudinally and transversely, downward slope to front starting from a level about half-way along bicomposite lobes; narrow neck gently convex longitudinally and transversely and slightly lower than bicomposite lobes; posterior part gently convex transversely and with an even slope backwards. Longitudinal furrows start at front of bicomposite lobes and lead inwards at right angles to length of specimen, then gradually curve backwards and converge until level with front of fixed cheeks where they are parallel to long axis. A short distance in front of the narrowest part of central lobe, the longitudinal furrows have slight notches on their outer sides; these represent relics of first glabellar furrows. Behind the narrowest part of the central lobe they gradually diverge to become the basal lateral furrows behind bicomposite lobes; these turn sharply outwards and, just before dying out, swing forwards, not joining axial furrows. Bicomposite lobes slightly kidney-shaped, semi-oval, rather broader at anterior end, which is bluntly pointed; about two and a half times as long as broad; moderately convex, posteriorly just coalescing with basal lateral glabellar lobes, almost cut off by basal lateral furrows. Basal lateral glabellar lobes quadrilateral, outline almost diamond-shaped, weakly marked off from base of central lobe and coalescing with bicomposite lobes. Occipital lobes almost triangular with side against occipital ring and two almost equal sides against fixed cheek and basal lateral glabellar lobe, all three being slightly convex outwards. Occipital ring longest between occipital lobes, slightly convex forwards; behind occipital lobes narrows to about half this length and bends gently round lobes; passes laterally for only a very short distance beyond occipital lobes, continued behind fixed cheeks, by posterior border, which it only just touches. Fixed cheeks long, narrowly pointed anteriorly extending forward half-way along bicomposite lobes, widening backwards with palpebral lobes lying level with basal lateral glabellar lobes; continuing backwards to occipital lobes, occipital ring and posterior border; not known completely. Axial furrows convex outwards to narrowest part of glabella then gently concave outwards as far as occipital lobes, then diverging strongly and skirting occipital lobes. Occipital furrow very slightly convex forward centrally, almost parallel to posterior margin, shallower and broader than other furrows, dividing laterally round occipital lobes with anterior branch also broad, shallow; posterior narrow and deeper until it joins axial furrow and broadens. Posterior border furrow broad and shallow as far as seen. Cheeks only partly seen. Posterior part of palpebral lobe separated from fixed cheek by a shallow broad furrow, concave outwards, which continues forward, becomes deeper and swings inwards to join axial furrow. Anterior part of free cheek also preserved, continues forwards as far as anterior of bicomposite lobes; remainder unknown.

Hypostoma: convex longitudinally and transversely, roughly polygonal in outline but

with indented posterior margin and rounded in front. Middle body about as long as wide, rounded in front, sides slightly divergent backwards, posterior margin gently undulating, almost straight across. Middle furrow incomplete, lying nearer posterior margin, consisting of a curved furrow on each side, converging posteriorly, but not joining in mid-line. Middle body ends sharply backwards at posterior furrow, which resembles middle furrow in consisting of two crescentic furrows, convex backwards, but these do join in mid-line making a slight forward notch in middle body. Lateral furrows broad and fairly deep, almost straight, parallel to long axis; appear from beneath anterior part of middle body and run back to middle furrow where they follow a slightly curved course, convex outwards, back to posterior furrow; beyond this flatten out with a posterior branch continuing on to posterior wing and a faint anterior branch passing outwards behind anterior wing. Anterior border if present is hidden, dorsal to front of middle body. Anterior wings rounded, raised sharply above lateral furrow, sloping more gently posteriorly and merging into much larger, flatter posterior wings, which are also rounded and with faint terrace lines; joined by posterior border, which is raised above their level, but which is not as high as posterior of middle body. Posterior margin straight across except for a central semicircular embayment of about half width of middle body.

Pygidium: semicircular in outline, almost exactly twice as wide as long. Axis about two-thirds length and anteriorly just under one-third breadth, tapers posteriorly, markedly raised above pleurae and with well-defined axial furrows which die out two-thirds way to posterior margin after diverging; posteriorly dropping to level of pleurae and flattening without a sharp termination. Marked anteriorly by two or three ring furrows, first strongly developed, second much less so, a possible third faintly developed behind that. Owing to preservation not known whether any or all of these furrows cross axis. Three pairs of pleurae occur, first being separated from second by sharp interpleural furrow, second from third by a weak interpleural furrow. Anterior pleurae are only slightly

EXPLANATION OF PLATE 118

- Figs. 1-7. *Atractopyge williamsi* sp. nov. 1, 2, and 4, From 200 yards north-north-west of Nant, 1 mile north of Llanrhaiadr-ym-Mochnant. 1, 2, Normal and anterior views of A 53025, paratype 2, internal mould of incomplete cranidium, $\times 6$. 4, Side view of A 53027, paratype 1, internal mould of incomplete cranidium showing fixigenal spine, $\times 6$. Figs. 3 and 5-7, From 80 yards north of Nant, 1 mile north of Llanrhaiadr-ym-Mochnant. 3, A 53026, internal mould of incomplete cranidium, $\times 6$. 5, 6, Normal and anterior views of A 53028, holotype, internal mould of cranidium, $\times 6$. 7, A 53029, paratype 3, internal mould of cranidium, $\times 6$.
- Figs. 8-19. *Metopolichas contractus* sp. nov. 8-10, From 960 yards north-west of Plas-yn-glyn, 1 mile north-north-east of Llanrhaiadr-ym-Mochnant, side, normal, and anterior views of A 46894, holotype, internal mould of incomplete cephalon, $\times 3$, $\times 2$, and $\times 2$ respectively. 11, 12, From 200 yards north-north-west of Nant, 1 mile north of Llanrhaiadr-ym-Mochnant, normal and side views of A 46893a, paratype 1, internal mould of incomplete cranidium, $\times 3$. Figs. 13-17, from 80 yards north of Nant, 1 mile north of Llanrhaiadr-ym-Mochnant. 13, Internal mould of A 53030a, paratype 2, hypostoma, $\times 4$. 14, External mould of A 53030b, hypostoma, $\times 4$. 15, A 53031a, internal mould of paratype 3, pygidium, $\times 3$. 16, 17, A 53031b, and plastic mould from A 53031b, external mould of pygidium, $\times 3$. 18, 19, Locality unknown, OUM B 122b, and plastic mould from OUM B 122b, external mould of pygidium, $\times 1.5$.
- Figs. 20, 21. *Dimeropyge* sp. from 80 yards north of Nant, 1 mile north of Llanrhaiadr-ym-Mochnant. 21, A 53032, external mould of pygidium, $\times 4$. 20, Plastic mould from A 53032, $\times 4$.



1



3



5



2



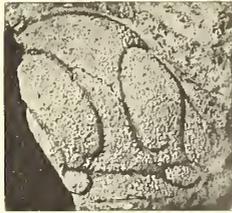
4



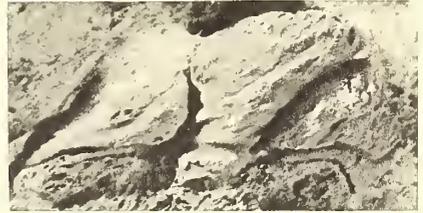
6



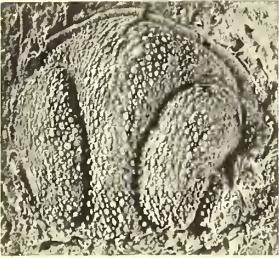
8



9



7



11



10



18



12



15



13



16



19



14



17



20



21

inclined back until about one-third way from axis, then bend back more sharply and narrow to form pleural spines, pleural furrow dividing each pleura dies out between this bend and pleural spine. Second pleurae inclined at smaller angle to axis and widen more than first; the bend towards pleural spine less sharp, spine broader and pleural furrow shorter. Third pleurae much shorter, lie at about 30° to axis and slightly wider again, merging with post axial region beyond where axial furrows die out. The pleural furrows yet shorter, barely reaching half-way to margin. Behind third pleurae posterior margin has a slight median embayment. Periphery of pygidium bent down at about 45° ; breadth of this flange at maximum behind axis, being about one-third length; decreasing laterally to about one-ninth of total width on each side. A comparison of the type pygidium with the specimen OUM B 122*a, b* suggests that this flange may be due to crushing or distortion of some kind, and that an uncrushed specimen may have had only a gentle concentric ridge behind the axis and dying out laterally. Doublure extending below flange, with fine, concentric, terrace lines. Surface of cephalon and pygidium covered with fine tubercles except in furrows; larger tubercles separated by smaller ones between.

Remarks. The genus occurs in the Lower and Middle Ordovician of Scandinavia and the Middle Ordovician of the British Isles. *M. patriarchus* (Wyatt-Edgell) occurs in the Llanvirn of Llandeilo and the Llandeilo of Shelve; in both areas it is rare. *M. contractus* differs from it in the following respects: in the cranidium the median lobe of the glabella is more elongate, is narrower between the bicomposite lobes and is lower than these lobes at its narrowest point; the occipital ring does not extend so far laterally beyond the occipital lobes. The hypostoma is not tuberculate, is more inflated and has an unbranched middle furrow; the anterior wings are much smaller and more rounded and the posterior wings are also smaller. The pygidium is not so flattened and the axis stands higher above the pleurae. The *Lichas* aff. *verrucosa* Eichwald from the Hoare Edge Grit (Pocock *et al.* 1938, p. 255) appears to be a *Metopolichas*. *M. contractus* differs from it in having a much narrower cranidium. A lichid from the Costonian of the Cressage District in Shropshire (BM 46455 in the Bancroft Collection in the British Museum) may also be a *Metopolichas*. *M. contractus* is much narrower than it, has more strongly curved longitudinal furrows and larger bicomposite lobes.

Family ODONTOPLEURIDAE Burmeister 1843
Subfamily ODONTOPLEURINAE Burmeister 1843
Genus PRIMASPIS Richter and Richter 1917

? *Primaspis* sp.

Plate 116, fig. 22

Material. One pygidium, internal and external mould.

Locality. SJ 12172815, 200 yards north-north-west of Nant, 1 mile north of Llanrhaiadr-ym-Mochnant, Montgomeryshire.

Horizon. Upper Llandeilo, Calcareous Shale.

Description. *Pygidium*: outline semi-elliptical, length one-fifth of maximum breadth excluding spines. Axis tapering back almost to reach posterior border, strongly convex,

defined by very shallow axial furrows which are a little deeper opposite ring furrow and articulating furrow. Articulating furrow of uniform depth; ring furrow shallow mesially and a little deeper laterally. Two axial rings, posterior one rounded distally and falling to level of pleurae, almost twice as broad as long. Pleural region horizontal, gently raised forward to broad shallow border. Border at side and rear more marked and narrower; from border arise one major and seven minor pairs of spines; there being three pairs of minors between majors; anterior pair appears to be directed slightly downwards and outwards, next two pairs slightly outwards and backwards but horizontally, remaining pairs backwards horizontally. Major spines though not entirely preserved appear to curve slightly inwards. Spines evenly spaced throughout. Major spines connected to anterior axial ring by pleural ridges. Whole surface, except for furrows, articulating half-ring and distal ends of spines, carries tubercles in roughly symmetrical pattern.

Remarks. Since only the pygidium has been collected, it can only be tentatively placed in this genus. This species differs from the contemporary *P. whitei* Whittard in having sixteen radial spines with the fourth pair from the mid-line larger than the others; they are otherwise similar. This species differs from *P. harnagensis* (Bancroft) in having only two axial rings.

GENERAL REMARKS

The fauna consists of *Basilicus tyrannus* (Murchison), *Ogygiocarella debuchii* (Brongniart), *Bumastus powisensis* sp. nov., *Proetidella* sp., *Dimeropyge* sp., *Marrolithus inflatus maturus* Williams, *M. favus* (Salter), *M. magnificus* sp. nov., *M. lirellatus* sp. nov., *Marrolithoides* sp., *M. cf. arcuatus* Whittard, *Atractopyge sedgwicki* sp. nov., *A. williamsi* sp. nov., *Flexicalymene cambrensis* (Salter), *Metopolichas contractus* sp. nov., and ? *Primaspis* sp.

Much of this fauna is indigenous in the sense that the genera were already present in Llanvirn or earlier Llandeilo rocks in the Anglo-Welsh province. The following genera are indigenous in this sense: *Basilicus*, *Ogygiocarella*, *Marrolithus*, *Marrolithoides*, *Atractopyge*, *Flexicalymene*, *Metopolichas*, and ? *Primaspis*.

Basilicus tyrannus is an abundant fossil in the shelly facies of the Llandeilo along almost the whole outcrop from Pembroke to Shelve except at Builth. The occurrence of *Ogygiocarella debuchii* is similar, but includes Builth; it is rare in the sandier beds such as occur in the Berwyns. *Marrolithus* and *Marrolithoides* are also common, the former more so, along the main outcrop except at Builth. Some species, e.g. *M. favus*, are widespread while others are still only known from restricted areas. The resemblance of *M. lirellatus* to *M. bureaui* (Oehlert), the only marrolithid known at present from Brittany, is noteworthy. *Atractopyge* is present in the Middle Meadowtown Beds of Llandeilo age in Shelve and also the Llandeilo of Carmarthenshire, though there the exact horizon is not known. *Flexicalymene* is widespread along the outcrop except at Builth where *Platycalymene* occurs. *Metopolichas* first appears in this country in the Upper Llanvirn of Llandeilo and is also present in the Llandeilo of Shelve; it is rare, however, and continues to be so in the Caradoc of Shropshire. ? *Primaspis* is doubtfully indigenous, a single specimen only being collected and uncertainly referred to the genus. Odontopleurids are rare in the Anglo-Welsh province at this time, a single specimen having been obtained by Williams at Llandeilo, but two species of *Primaspis* and one of

Diacanthaspis are recorded by Whittard (1961, pp. 199–205) from the Llandeilo of Shelve. *Primaspis* also occurs in the Upper Llandeilo of Bohemia (Whittington 1956, p. 186).

The origin of the *Proetidella* is uncertain, little being known of Ordovician proetids. Williams found a proetid at Llandeilo but it has not been described, and there seem to be no other records from the Llanvirn–Llandeilo rocks of Britain to date.

The two remaining genera suggest an Appalachian derivation. *Dimeropyge* occurs in approximately contemporary North American rocks, several species having been described by Whittington and Evitt (1953). *Bumastus* has not previously been recorded in Britain as early as this, but a North American origin is possible.

The trilobite fauna agrees with the brachiopod fauna already described (MacGregor 1961) in containing elements not previously known from the main Llandeilo outcrop. One reason for this seems to lie in the lithology of the Llandeilo rocks of the Berwyns, where a shelly fauna has continued to dominate in calcareous, sandy and muddy, near shore sediments. Elsewhere along the main outcrop the Upper Llandeilo rocks are fine-grained calcareous and non-calcareous shales with only a sparse shelly fauna or a predominantly graptolitic fauna. Only in the Berwyns does a true shelly fauna persist into the Upper Llandeilo. It is in this Upper Llandeilo fauna that the genera *Proetidella*, *Bumastus*, and *Dimeropyge*, so far as is known at present, make their first appearance in the Anglo-Welsh province.

REFERENCES

- BANCROFT, B. B. (ed. A. LAMONT). 1949. Upper Ordovician trilobites of zonal value in south-east Shropshire. *Proc. roy. Soc.*, Ser. B, **136**, 291–315, pl. 9–11.
- BRONGNIART, A., in BRONGNIART, A. and DESMAREST, A. G. 1822. *Histoire naturelle des crustacés fossiles, sous les rapports zoologiques et géologiques. Savoir: Les Trilobites*: 1–66, pl. 1–4. Paris.
- COOPER, B. N. 1953. Trilobites from the Lower Champlainian Formations of the Appalachian Valley. *Mem. geol. Soc. Amer.* **55**, 1–69, pl. 1–19.
- JAANUSSON, V., and STRACHAN, I. 1954. Correlation of the Scandinavian Middle Ordovician with the graptolite succession. *Geol. Fören. Stockh. För.* **76**, 684–96.
- KIELAN, Z. 1959. Upper Ordovician Trilobites from Poland and some related forms from Bohemia and Scandinavia. *Palaeont. polon.* **11**, 1–198, pl. 1–36.
- MACGREGOR, A. R. 1961. Upper Llandeilo Brachiopods from the Berwyn Hills, North Wales. *Palaeontology*, **4**, 177–209, pl. 19–23.
- MÄNNIL, R. 1958. Trilobity semejstv Cheiruridae i Encrinuridae iz Estonii (Trilobites of the families Cheiruridae and Encrinuridae from Estonia). *Tr. Inst. Geol. Akad. Nauk Est. SSR*, **3**, 165–212, pl. 1–8.
- MURCHISON, R. I. 1839. *The Silurian System*. London.
- OEHLERT, D. P. 1895. Sur les *Trinucleus* de l'ouest de la France. *Bull. Soc. géol. Fr.* **23**, 229–336, pl. 1, 2.
- POCOCK, R. W., WHITEHEAD, T. H., WEDD, C. B. and ROBERTSON, T. 1938. Shrewsbury District including the Hanwood Coalfield. Sheet 152. *Mem. Geol. Surv.* 1–297.
- SALTER, J. W. 1848. Palaeont. Appendix. *Mem. Geol. Surv.* **2**, 350, pl. 9.
- 1864–1883. Monograph of the British Trilobites from the Cambrian, Silurian and Devonian Formations. *Palaeont. Soc. London*, 1–224, pl. 1–30.
- SCHMIDT, F. 1881. Revision der Ostbaltischen Silurischen Trilobiten. Abt. 1. *Mém. Acad. Imp. des Sci. St.-Petersbourg*, Sér. 7, **30**, 1–237, pl. 1–16.
- SHIRLEY, J. 1931. A Redescription of the known British Ordovician species of 'Calymene' (s.l.). *Mem. Manchr. lit. phil. Soc.* **75**, 1–35, pl. 1, 2.
- 1936. Some British Trilobites of the family Calymenidae. *Quart. J. Geol. Soc. London*, **92**, 384–422, pl. 29–31.

- SINCLAIR, G. W. 1946. The Ordovician trilobite *Dimeropyge*. *Amer. J. Sci.* **244**, 854-60, pl. 1.
- TRIPP, R. P. 1957. The classification and evolution of the superfamily Lichacea (Trilobita). *Geol. Mag.* **94**, 104-22.
- TROEDSSON, G. T. 1929. On the Middle and Upper Ordovician faunas of northern Greenland. *Medd. Grönland*, **72**, 1-198, pl. 1-56.
- WHITTARD, W. F. 1931. The geology of the Ordovician and Valentian rocks of the Shelve Country, Shropshire. *Proc. Geol. Ass.* **42**, 322-39, pl. 10, 11.
- 1955—. The Ordovician Trilobites of the Shelve Inlier, west Shropshire. *Palaeont. Soc. London.*
- WHITTINGTON, H. B. 1956. Silicified Middle Ordovician Trilobites: the Odontopleuridae. *Bull. Mus. Comp. Zool. Harv.* **114**, 155-288, pl. 1-24.
- and EVITT, W. R. 1954. Silicified Middle Ordovician Trilobites. *Mem. geol. Soc. Amer.* **59**, 1-137, pl. 1-33.
- and WILLIAMS, A. 1955. The fauna of the Derfel Limestone of the Arenig district, North Wales. *Phil. Trans. roy. Soc., Ser. B*, **238**, 397-430, pl. 38-40.
- WYATT-EDGELL, H. 1866. On a species of *Lichas* and other forms from the Llandilo Flags. *Geol. Mag.* **3**, 160-3.

A. ROY MACGREGOR
Department of Geology,
The University,
St. Andrews, Fife

Manuscript received 31 January 1962

EARLY PERMIAN FUSULINIDS FROM MACUSANI, SOUTHERN PERU

by CHARLES A. ROSS

ABSTRACT. *Triticites patulus* Dunbar and Newell and *Schwagerina adamsi* sp. nov. from the early Wolfcampian (Permian) part of the Copacabana Group near Macusani, southern Peru, show morphological features that add new data concerning the evolution of the genera *Schwagerina* and *Pseudoschwagerina* from lineages arising within the genus *Triticites* near the close of the Pennsylvanian.

ONE of the greatest diversification of species within the family Fusulinidae took place in the latest part of the Pennsylvanian and the earliest part of the Permian. The two species described here are from the southern part of Peru and represent part of this diverse fusulinid fauna. *Triticites patulus* Dunbar and Newell is a member of one of the lineages within the genus *Triticites* that evolved during this time and *Schwagerina adamsi* sp. nov. is an early species of the genus *Schwagerina* which became abundant and widespread during the Wolfcampian and early part of the Leonardian Epochs of the Permian. The two species occur in a single block of light-grey limestone (biomicrosparite) from a bed of the Copacabana Group at the summit of the highest hill, 1 kilometre north-west of Macusani, Carabaya Province, Department of Puno, in southern Peru (text-fig. 1). The material was collected by Dr. A. J. Charig in June 1959.

Triticites patulus was described by Dunbar and Newell (1946) and Roberts (*in* Newell, Chronic, and Roberts 1953) from the Copacabana Group in southern Peru and western Bolivia. In its internal features *T. patulus* shows a striking divergence from the larger species of late Pennsylvanian and early Permian *Triticites* in having high chambers in which the lower half of the septa are strongly folded and the upper half are nearly planar, and in having true chomata in the first two or three volutions which gradually pass into pseudochomata and into other secondary deposits in later volutions. In most features *T. patulus* bridges the morphological gaps between the genus *Triticites* and early species of *Pseudoschwagerina* such as *P. beedei* Dunbar and Skinner (1937).

Schwagerina adamsi sp. nov. belongs to an early lineage of species of *Schwagerina* that are small in size, including *S. campa* Thompson (1954), *S. turki* (Skinner) (1931), *S. jewetti* Thompson (1954), and *S. emaciata* (Beede) (1916). It has low, inconspicuous chomata in its early volutions which pass into pseudochomata that thicken the base of the septa near the tunnel in later volutions. The pseudochomata pass into secondary deposits which fill the septal folds adjacent to the tunnel in the later volutions.

The evolution of the genus *Pseudoschwagerina* has been discussed in its broader aspects by Ross (1962). The species of *Pseudoschwagerina* that are found in Peru and Bolivia are part of the early history of the genus and their probable phylogenetic

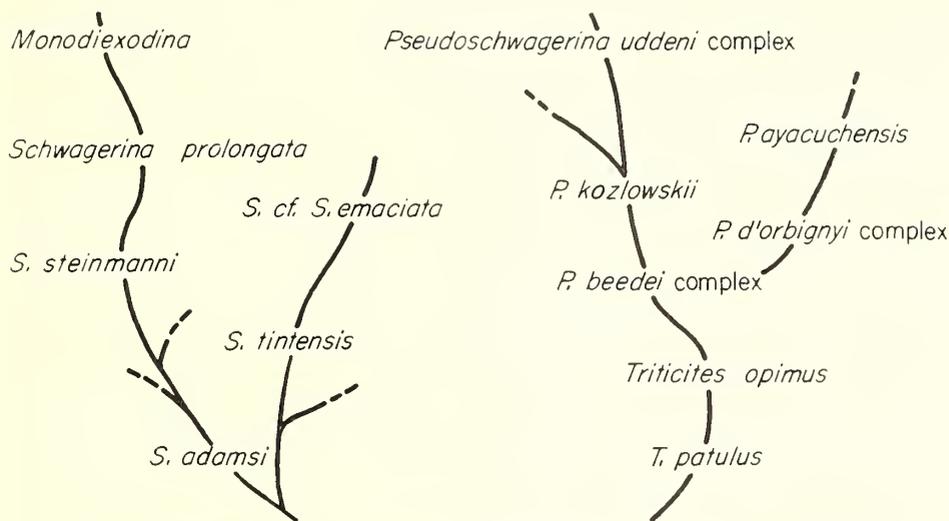
relations are indicated in text-fig. 2. *Triticites patulus* is apparently ancestral to *T. opimus* Dunbar and Newell, which has inflated chambers and strong septal folds in its outer volutions. Most of the morphological features of *T. opimus* would suggest its assignment to the genus *Pseudoschwagerina*; however, the species has low chomata extending into the outer volutions, a diagnostic feature of *Triticites*.



TEXT-FIG. 1. Map of the southern part of Peru showing the location of Macusani.

The *Pseudoschwagerina beebey* complex apparently evolved from *T. opimus*; it retained the strong chomata in the juvenarium, but lost the chomata in the inflated volutions. *P. kozlowskii* Dunbar and Newell is typical of this complex in having the upper part of the septa nearly planar and the lower part folded into narrow projections that have a semicircular cross-section. The *P. uddeni* complex appears to have evolved from the *P. beebey* complex by greatly increasing the height of its inflated chambers to give the test a subglobose shape. In the *P. d'orbigny* complex further reduction of the chomata even in the juvenarium suggests that it was an offshoot from the *P. beebey* complex (text-fig. 2). Because the members of the *P. d'orbigny* complex retain strong septal folds throughout their volutions, as in *Triticites opimus*, this complex probably arose shortly after the differentiation of the *P. beebey* complex. *P. ayacuchensis* Roberts is an advanced species in the *P. d'orbigny* complex, in which there is a particularly sharp change from the juvenarium into the inflated volutions.

Schwagerina adamsi is apparently an early representative of a lineage in which the tests gradually became more elongate and evolved to form such species as *S. steinmanni* Dunbar and Newell and *S. prolongata* (Berry). *S. prolongata* is a transitional species connecting this lineage with *Monodiexodina*, which has well-developed cuniculi (openings at the points of contact of the septal folds of adjacent septa). Another related lineage consists of *S. tintensis* Roberts and *Schwagerina* cf. *S. emaciata* (Beede) (text-fig. 2).



TEXT-FIG. 2. Phylogeny of two lineages of early Permian fusulinids from southern Peru and Bolivia.

The stratigraphic ranges of many of these species apparently overlap and text-fig. 2 shows only their inferred phylogenetic relations. The stages of evolution of the two species, *Triticites patulus* and *Schwagerina adamsi*, and the reported association of *T. patulus* with *Pseudoschwagerina* elsewhere in the region by Dunbar and Newell (1946, pp. 400-1) and Newell, Chronic, and Roberts (1953, p. 24) suggest that this rock sample from near Macusani is from strata equivalent in age to the early Wolfcampian Neal Ranch Formation in the Glass Mountains, Texas (Ross 1959).

Acknowledgements. It is a pleasure to thank Dr. Charles G. Adams, British Museum (Natural History), who located and kindly loaned the collection for this study. I am also indebted to Dr. June Phillips Ross, Illinois State Geological Survey, for helpful discussions and suggestions on some of the philosophical problems during the preparation of this paper.

Repositories. The illustrated material and most of the rock sample are housed in the British Museum (Natural History). Additional thin sections and a part of the rock sample are deposited in the U.S. National Museum.

SYSTEMATIC DESCRIPTIONS

Genus TRITICITES Girty 1904

Triticites patulus Dunbar and Skinner

Plate 119, figs. 11-17

1946 *Triticites patulus*; Dunbar and Newell, p. 478, pl. 10, figs. 1-10.1933 *Fusulina peruana* Berry [non Meyer], p. 269, pl. 22, figs. 4, 8, 9, 12.

Description. This species has thickly fusiform tests with bluntly rounded poles that reach 6 to 6.5 mm. in length and 2.5 mm. in diameter in five to six volutions. The proloculi are 0.15 to 0.25 mm. in diameter and the first $1\frac{1}{2}$ volutions are low and thickly fusiform. Succeeding volutions increase markedly in height and length maintaining the general thickly fusiform shape of the test. The chambers are high and are loosely coiled about the axis (Pl. 119, figs. 11, 14, 15).

The wall is composed of a tectum and keriotheca clearly displaying alveoli (Pl. 119, fig. 15). It thins gradually from the midplane of the test to the poles. The septa are thin and are strongly folded only along their lower half, the upper half being nearly planar (Pl. 119, figs. 11-15). Chomata are conspicuous in the first two volutions and pseudo-chomata and secondary filling of the septal folds adjacent to the tunnel are common in the succeeding volutions (Pl. 119, figs. 15, 17).

Remarks. The rapid expansion of the chambers, the thick secondary deposits adjacent to the tunnel forming the pseudo-chomata, and the mode of septal folding separate *Triticites patulus* from most other species of this genus. The lineage of *Triticites* including *T. meeki* (Möller) and *T. ventricosus* (Meek and Hayden) have more elongate tests with much less strongly folded septa and lower chambers. *T. californicus* Thompson and Hazzard has heavier and more persistent chomata throughout its subglobose test.

Occurrence. Dunbar and Newell (1946) found *Triticites patulus* in many of their collections from Bolivia and Peru in the Lake Titicaca region, where it is commonly associated with *Pseudoschwagerina* and *Schwagerina*. The specimens illustrated here are from the Copacabana Group, bed at top of hill, 1 kilometre north-west of Macusani, Peru.

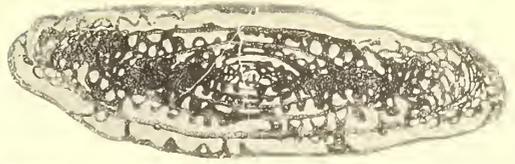
EXPLANATION OF PLATE 119

Figs. 1-10, *Schwagerina adamsi* sp. nov., Copacabana Group, 1 kilometre north-west of Macusani, Peru. 1, 2, Axial sections of holotype, $\times 10$ and $\times 20$, B.M.(N.H.) P42647. 3, 4, 5, 8, Axial sections, B.M.(N.H.) P42648, P42649, P42650, and P42651, $\times 10$. 6, 9, Sagittal sections, B.M.(N.H.) P42652, P42653, $\times 10$. 7, 10, Tangential sections showing nearly planar septa in the upper part of the chambers and closely folded septa in the lower part, B.M.(N.H.) P42660, P42661, $\times 10$.

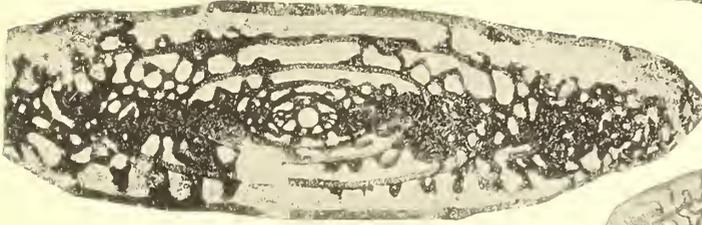
Figs. 11-17, *Triticites patulus* Dunbar and Skinner, Copacabana Group, 1 kilometre north-west of Macusani, Peru. 11, Axial section, B.M.(N.H.) P42654, $\times 10$. 12, 13, Tangential sections showing the thick secondary deposits on the septa near the tunnel that form chomata and pseudo-chomata, B.M.(N.H.) P42655, P42656, $\times 10$. 14, 15, Axial sections showing dense infilling of the septal loops near the tunnel to form chomata and pseudo-chomata, B.M.(N.H.) P42657, $\times 10$ and $\times 20$. 16, Axial section of an aberrant specimen, B.M.(N.H.) P42658, $\times 10$. 17, Sagittal section showing marked variation in the chomata and pseudo-chomata, B.M.(N.H.) P42659, $\times 10$.



1



3



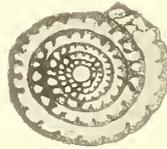
2



4



5



6



7



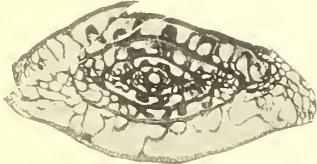
8



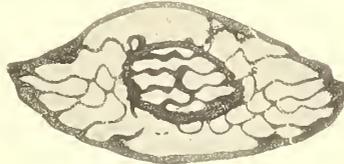
9



10



11



12



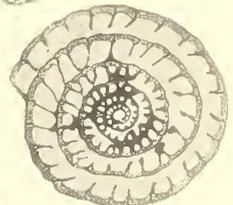
13



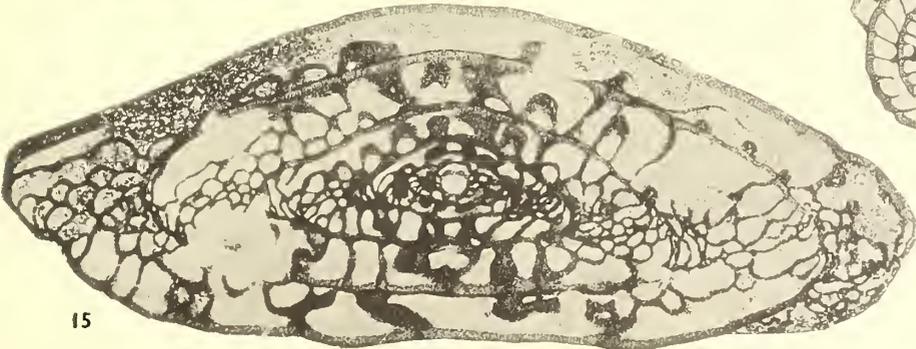
14



16



17



15

Measurements of *Triticites patulus* B.M.(N.H.) specimens

	Volution	P42654	P42657	P42659	
Radius vector (mm.)	0	0.08	0.09	0.09	
	1	0.17	0.15	0.20	
	2	0.30	0.25	0.35	
	3	0.55	0.40	0.55	
	4	0.85	0.75	0.80	
	5	..	1.10	1.20	
Half-length (mm.)	1	0.30	0.30	No. of septa { 12	
	2	0.70	0.55		16
	3	1.20	0.90		21
	4	1.60	1.50		27
	5	..	2.50		22
	Form ratio	1	1.8		2.0
	2	2.3	2.2		
	3	2.1	2.2		
	4	1.9	2.0		
	5	..	2.3		
Wall thickness (mm.)	0	0.02	0.02		
	1	0.03	0.02		
	2	0.03	0.03		
	3	0.04	0.03		
	4	0.06	0.06		
	5	..	0.08		
Tunnel angle (°)	1	20	25		
	2	20	25		
	3	15	25		
	4	20	35		
	5		

Genus *Schwagerina* Möller 1877 (emend. Dunbar and Skinner 1936)*Schwagerina adamsi* sp. nov.

Plate 119, figs. 1-10

Description. This species has small, elongate fusiform tests of 5 to $5\frac{1}{2}$ volutions that reach 5.5 to 6.5 mm. in length and 1.5 to 2.0 mm. in diameter. The proloculi are about 0.10 to 0.20 mm. in diameter and the first volution is subglobose in outline. Succeeding volutions rapidly increase in length along the axis of coiling, giving the test a progressively elongated shape (Pl. 119, fig. 2).

The wall is formed of a tectum and a thick keriotheca clearly displaying alveoli (Pl. 119, fig. 2). The thickness of the wall gradually increases from 0.01 mm. in the proloculus to 0.07 mm. in the fifth volution. The septa are folded into regularly spaced septal folds that reach nearly to the top of the chambers (Pl. 119, figs. 1-5, 7, 10).

Chomata are small and inconspicuous in the first one to two volutions and grade into pseudochomata in later volutions. Secondary deposits commonly fill the septal folds

adjacent to the tunnel (Pl. 119, fig. 2). Axial deposits heavily coat the septa in the polar regions of the volutions.

Measurements of *Schwagerina adamsi* B.M.(N.H.) specimens

	Volution	P42647	P42648	P42650	P42649	P42653
Radius vector (mm.)	0	0.07	?	0.12	0.07	0.07
	1	0.20	0.15	0.20	0.15	0.15
	2	0.25	0.25	0.25	0.25	0.25
	3	0.40	0.35	0.40	0.35	0.35
	4	0.55	0.50	0.60	0.50	0.50
	5	0.80	0.70	0.85	0.70	0.70
	6	..	1.00	..	1.00	..
Half-length (mm.)	1	0.30	0.15	0.25	0.20	No. of septa { 9 18 23 25 23 ..
	2	0.55	0.55	0.55	0.35	
	3	0.90	0.80	0.90	0.70	
	4	1.80	1.55	1.60	1.30	
	5	2.90	2.50	2.70	2.20	
	6	..	3.40	..	3.00	
	6	..	3.40	..	3.00	
Form ratio	1	1.5	1.0	1.2	1.3	
	2	2.2	2.2	2.2	1.4	
	3	2.2	2.3	2.2	2.0	
	4	3.3	3.1	2.7	2.6	
	5	3.6	3.6	3.2	3.1	
	6	..	3.4	..	3.0	
	Wall thickness (mm.)	0	0.01	?	0.01	0.01
1		0.02	0.02	0.02	0.01	
2		0.02	0.03	0.03	0.02	
3		0.03	0.04	0.04	0.03	
4		0.04	0.06	0.06	0.03	
5		0.08	0.08	0.07	0.05	
6		..	0.10	..	0.08	
Tunnel angle (°)	1	20	35	25	25	
	2	35	40	30	25	
	3	50	35	30	25	
	4	50	40	30	30	
	5	50	..	40	35	
	6	
	6	

Remarks. *Schwagerina adamsi* is similar to a number of species of *Schwagerina* having a small size and rudimentary or inconspicuous chomata in their early volutions. *S. campa* Thompson (1954) lacks prominent secondary deposits; *S. jewetti* Thompson (1954) has higher septal folds that have steeper sides and it has higher chambers; *S. emaciata* (Beede) (1916) has more pointed poles and irregularly folded septa; and *S. turki* (Skinner) (1931) is larger and has irregularly folded septa. *Dunbarinella mantarogensis* Roberts is less slender and *S. steinmanni* Dunbar and Newell is much larger and lacks the prominent secondary deposits.

This species is named after Dr. C. G. Adams, Department of Zoology, British Museum (Natural History).

Occurrence. Copacabana Group, bed at top of hill, 1 kilometre north-west of Macusani, Peru. Holotype B.M.(N.H.) P42647, shown in Pl. 119, figs. 1, 2.

REFERENCES

- BEEDE, J. W. 1916. New species of fossils from the Pennsylvanian and Permian rocks of Kansas and Oklahoma. *Indiana Univ. Studies*, **3**, 5-15.
- BERRY, WILLARD. 1933. *Fusulina* from Peru and Bolivia. *Pan Am. Geologist*, **59**, 269-72.
- DUNBAR, C. O., and NEWELL, N. D. 1946. Marine early Permian of the central Andes and its fusuline faunas. *Am. J. Sci.* **244**, 377-402, 457-91.
- and SKINNER, J. W. 1936. *Schwagerina* versus *Pseudoschwagerina* and *Paraschwagerina*. *J. Paleont.* **10**, 83-91.
- — 1937. The geology of Texas, pt. 2, Permian Fusulinidae of Texas. *Texas Univ. Bull.* **3701**, 517-825.
- GIRTY, G. H. 1904. *Triticites*, a new genus of Carboniferous Foraminifera. *Am. J. Sci.* (4), **17**, 234-40.
- MÖLLER, V. VON. 1877. Ueber Fusulinen und ähnlichen Foraminiferen-Formen des Russischen Kohlenkalks. *Neues Jb. f. Min. und Pal., Jahrb.* 1877, 138-46.
- NEWELL, N. D., CHRONIC, JOHN, and ROBERTS, T. G. 1953. Upper Paleozoic of Peru. *Geol. Soc. Am. Mem.* **58**, 1-276.
- ROSS, C. A. 1959. The Wolfcamp Series (Permian) and new species of fusulinids, Glass Mountains, Texas. *J. Wash. Acad. Sci.* **49**, 299-316.
- 1962. Evolution and dispersal of the Permian fusulinid genera *Pseudoschwagerina* and *Paraschwagerina*. *Evolution*, **16**, 3, 306-15.
- SKINNER, J. W. 1931. New Permo-Pennsylvanian Fusulinidae from northern Oklahoma. *J. Paleont.* **5**, 16-22.
- THOMPSON, M. L. 1954. American Wolfcampian Fusulinids. *Kansas Univ. Paleont. Contr.*, Protozoa art. 5, 1-226.
- WHEELER, H. E., and HAZZARD, J. C. 1946. Permian Fusulinids of California. *Geol. Soc. Am. Mem.* **17**, 1-77.

CHARLES A. ROSS
State Geological Survey Division,
Urbana, Illinois,
U.S.A.

Manuscript received 6 February 1962

THE PALAEOONTOLOGICAL ASSOCIATION

Extracts from the Annual Report of the Council for 1961–2

MEMBERSHIP. On 31 December 1961 there were 961 members (518 Ordinary, 39 Student, and 404 Institutional), a net increase of 101 members.

FINANCE. Differential subscription rates operated for the first time in 1961. The income from subscriptions has risen by about £1,250, and in addition income from sales has more than doubled; interest from investments has shown a modest increase. General donations have continued at the same generous level as in 1960, but there has been a fall of nearly £1,000 in special donations (two large donations were received in respect of specific papers published in Volume 3).

Estimates for 1962 suggest that income for that year will exceed £6,200. This should allow the absorption of the increase in printing costs already imposed, and also cater for the expansion of *Palaeontology* planned by Council. However, this is only possible on account of the generosity of the firms which have been supporting the Association with donations.

PALAEOONTOLOGY. Four parts of Volume 4 (for 1961) were published during 1961–2. They contained 44 papers.

MEETINGS. Three meetings took place during 1961–2, and two others regrettably had to be postponed. The Association is grateful to the Council of the Geological Society of London; Prof. B. C. King (Bedford College, London); and Prof. W. F. Whittard (University of Bristol) for generously granting facilities for meetings, and to the Local Secretaries for their efficient services.

- a. The Fourth Annual General Meeting was held in the Rooms of the Geological Society of London, Burlington House, W. 1, on Wednesday, 8 March 1961, at 5.0 p.m. The Annual Report of the Council for 1960–1 was adopted, and the Council for 1961–2 elected. Prof. T. M. Harris delivered the Fourth Annual Address on 'The Fossil Cycads'.
- b. A Demonstration Meeting was held in the Department of Geology, Bedford College, Regent's Park, London, N.W. 1, on Saturday, 6 May 1961, at 2.30 p.m. There were 10 exhibits and 45 persons attended.
- c. A Discussion Meeting was held in the Department of Geology, The University, Bristol 8, on Friday/Saturday, 15/16 December 1961. The subject was 'Mesozoic Palaeontology'. About 70 persons attended. Eight papers were read during two sessions, and there were 16 exhibits. A Palaeontological Association Dinner was held in the Senior Common Room at 8.0 p.m. on 15 December. Dr. D. T. Donovan and Dr. R. J. G. Savage were the Local Secretaries.

COUNCIL. The following were elected members of the Council of the Association for 1961–2 at the Annual General Meeting on 8 March 1961: *President*: Professor O. M. B. Bulman, F.R.S.; *Vice-Presidents*: Professor T. N. George, Professor W. F. Whittard, F.R.S.; *Treasurer*: Professor P. C. Sylvester-Bradley; *Assistant Treasurer*: Dr. T. D. Ford; *Secretary*: Dr. Gwyn Thomas; *Assistant Secretary*: Dr. C. H. Holland; *Editors*: Dr. W. H. C. Ramsbottom, Mr. N. F. Hughes, Dr. W. S. McKerrow; *Other members*: Dr. D. V. Ager, Dr. F. T. Banner, Dr. A. J. Charig, Dr. L. R. Cox, F.R.S., Dr. R. H. Cummings, Dr. R. Goldring, Dr. J. C. Harper, Professor F. Hodson, Dr. M. R. House, Dr. R. G. S. Hudson, F.R.S., Dr. J. W. Neale, Dr. Dorothy H. Rayner, Mr. J. D. D. Smith, Dr. C. D. Waterston.

BALANCE SHEET AND ACCOUNTS FOR
THE YEAR ENDING 31 DECEMBER 1961

BALANCE SHEET		£	s.	d.	£	s.	d.
<i>Liabilities</i>							
Publications Reserve Account:							
Balance as per Annexed Account					4,886	8	2
Amounts Received in Advance:							
Subscriptions for 1962		167	17	6			
Special donation towards cost of <i>Palaeontology</i> , Vol. 5		8	16	1			
					176	13	7
Provision for cost of publication of <i>Palaeontology</i> , Vol. 4 as per Income and Expenditure Account		4,383	12	4			
Less Expenditure incurred to 31 December 1961		2,247	4	7			
					2,136	7	9
Sundry Creditors					118	5	1
					£7,317	14	7
<i>Assets</i>							
Investments at Cost—5% Defence Bonds					3,000	0	0
Sundry Debtors:							
Authors for reprints		439	1	9			
Donations (promised, not yet received)		50	0	0			
Subscriptions unpaid 1961		179	1	10			
					668	3	7
Cash at Bank—Deposit Account		2,031	6	3			
Current Account		1,618	4	9			
					3,649	11	0
					£7,317	14	7

Report of the Auditors to the Members of the Palaeontological Association. We have examined the above Balance Sheet and annexed Income and Expenditure Account which in our opinion give respectively a true and fair view of the state of the Association's affairs as at 31 December 1961 and of its income and expenditure for the year ended on that date.

BAKER BROS. HALFORD & CO.
Chartered Accountants.

INCOME AND EXPENDITURE ACCOUNT

<i>Expenditure</i>	£	s.	d.	£	s.	d.
To Provision for cost of publication of <i>Palaeontology</i> , Vol. 4, Part 1	883	12	4			
Part 2	1,200	0	0			
Part 3	1,100	0	0			
Part 4	1,200	0	0			
	4,383	12	4			
Less Excess provision for Vol. 3 not required		36	12	8		
				4,346	19	8
Administrative Expenses:						
Postage and stationery	156	5	8			
Insurance	3	2	6			
Audit fee	5	5	0			
Miscellaneous	28	12	10			
Cost of distribution of publications	42	14	9			
				236	0	9
Excess of Income over Expenditure for the year transferred to Publications Reserve Account				2,105	2	9
				£6,688	3	2
<i>Income</i>						
By Subscriptions for 1961				3,764	5	0
Subscriptions for previous years				112	3	7
Sales of publications				1,349	13	2
Interest received—5% Defence Bonds	154	2	2			
Bank Deposit Account	79	7	3			
				233	9	5
Special Donations				103	12	0
General Donations:						
Attock Oil Co. Ltd.	50	0	0			
British Petroleum Co. Ltd.	250	0	0			
Burmah Oil Co. Ltd.	100	0	0			
Iraq Petroleum Co. Ltd.	300	0	0			
Kuwait Oil Co. Ltd.	200	0	0			
Texaco	175	0	0			
Ultramar Co. Ltd.	50	0	0			
				1,125	0	0
				£6,688	3	2

PUBLICATIONS RESERVE ACCOUNT

Balance per Balance Sheet 4,886	8	2
	£4,886	8	2
Balance 31 December 1960 2,781	5	5
Transfer of Excess of Income over Expenditure for the year 2,105	2	9
	£4,886	8	2

INDEX

Pages 1 to 148 are contained in Part 1; pages 149 to 354 are in Part 2; 355 to 618 in Part 3; and 619 to 826 in Part 4. Figures in **Bold Type** indicate plate numbers.

A

- Acanthodii, class, 25.
Acanthoptychoceras, 529; *spiniatocostatum*, 530, **74**, **75**, **76**.
Acanthotriletes, 590; *mirus*, 590, **81**; *multisetus*, 590, **80**.
Acrolepis addamsi, 17.
Actinopteria persulcata, 370, 403, **58**.
 Adams, C. G. Calcareous adherent Foraminifera from the British Jurassic and Cretaceous and the French Eocene, 149.
Aegocrioceras bicarinatum, 129, **19**; *varicostatum*, 129.
Agassisiceras illatum, 102, **15**; *personatum*, 102.
Alatisporites tessellatus, 654, **95**.
 Algae: Dalradian, from Islay, 268, **39**.
Amaltheus clevelandicus, 112; *depressus*, 113; *exaciatius*, 113; *nodulosus*, 113; *reticularis*, 113; *subnodosus*, 113; *vittatus*, 113.
Anauroceras conjunctivum, 113, **16**; *ferrugineum*, 114; *lenticulare*, 114.
 Ammonites. See Cephalopoda.
Amyelon, 213; *bovius*, 216, **33**; *equivius*, 219, **33**; *radicans*, 214.
Anaphragma, 205; *shucknellensis*, 205, **31**.
Anapiculatisporites, 587; *concinuus*, 587, **80**; *serratus*, 589, **80**.
 Ancyloceratidae, 529.
Ancyrospora, 175; *A. (Triletes) ancyrea*, 176, 182; *ancyrea* var. *ancyrea*, 177, **25**; *ancyrea* var. *brevispinosa*, 179, **25**; *ancyrea* var. *spinobaculata*, 180, **26**, **27**; *grandispinosa*, 175, **27**; *longispina*, 181, **26**.
Androgynoceras arcigerens, 112, **16**; *heterogenes*, 112; *maculatum*, 112.
Anomia, 5; *desioi*, 5.
Anthracoeras, 361, 375, 376; *glabrum*, 372; *paucilobum*, 386, 395; *tenispirale*, 375, 376, 394, **57**, **58**, **59**; fauna, 375, 422.
Anthraconaia fabaformis, 308, **47**; aff. *fabaformis*, 308, **47**; *fugax*, 331, **47**; aff. *fugax*, 331, **47**; cf. *fugax*, 331, **47**; sp., 331, **47**.
Anulatisporites anulatus, 617, **87**; *canaliculatus*, 619, **88**; *labiatus*, 249, 618, **37**, **87**; *orbiculatus*, 619, **88**.
Apiculatisporis uacerrus, 589, **81**.
Apodoceras aculeatum, 108; *decussatum*, 109, **16**; *hamiltoni*, 109; *hastatum*, 109; *marshallani*, 109, **15**; *mutatum*, 109; *sinuatum*, 109; *spicatum*, 109; *subtriangulare*, 110.
Archaeocidaris urii, 364, 376.
Archaeofenestella, 542; *rigidula*, 543, **77**; *rigidula polynodosa*, 544.
Arietoceras geometricum, 119, **18**; *nitescens*, 119.
Arietites radiatus, 101.
Arnioceras acuticarinatum, 103; *senicostatum*, 103; *vetustum*, 103, **15**; *youngi*, 103.

- Arthropoda. See Crustacea, Eurypterids, Trilobites.
 Atactotoechid Bryozoa, 733.
Atactotoechus, 734; *chazyensis*, 734, **107**, **108**; *kayi*, 737, **106**, **107**.
Atractopyge sedgwicki, 805, **117**; *williamsi*, 806, **117**, **118**.

B

- Baird, D. A haplolepid fish fauna in the early Pennsylvanian of Nova Scotia, 22.
Baltisphaeridium debilispinum, 777, **112**; *ehrenbergi*, 486, **70**; *parvispinum*, 488; *pilosum*, 482, **70**; *polytrichum*, 487, **70**; *stimuliferum*, 488, **70**; *tribuliferum*, 487, **70**; sp., 490, **70**.
 Barnard, P. D. W. Revision of the genus *Auyelon* Williamson, 213.
 Barnard, T. Polymorphinidae from the Upper Cretaceous of England, 712.
Basilicus tyrannus, 791, **116**.
Batostonia, 206; sp., 206, **31**.
Batostonella, 201; *hemiseptensis*, 201, **29**; *hexauesapora*, 202, **29**.
Beaniceras luridum, 111.
 Belgium: Namurian correlations, 427.
Bicuspina, 741; *multicostellata*, **109**; *spiriferoides*, **109**, **110**.
Bifericeras integricostatum, 106; *vitreum*, 106.
 Bivalvia. See Lamellibranchs.
Boualcitoceras? antiquatum, 101.
 Boucot, A. J. The Eospiriferidae, 682.
 Brachiopoda: ecology and Lower Greensand palaeogeography, 253; Eospiriferidae, 682; Triplesiaacea, 740.
Brachymimulus, 741.
 British Honduras: Permian foraminifera, 297.
 Bryozoa: Chazyan, 727; Ludlovian from Ludlow district, 195; Ordovician, 52; Wenlockian fenestrate, 540.
Bullopore, 153; *globulata*, 158; *globulata* var. *minima*, 158, **24**; *laevis*, 158, **23**, **24**; *rostrata*, 157, **24**; *rostrata* var. *irregularis*, 157, **24**; *tuberculata*, 159, **24**.
Bunastus powisensis, 793, **116**.
Bythopora, 202; *parallela*, 202, **30**.

C

- Calanospora*, 579; *microrugosa*, 579, **79**.
Calanotrypa, 206; *millichopensis*, 207, **31**.
Calathlops trisperma, 235, **34**, **35**.
Calcitonella, 156.
Calliphylloceras fabricatum, 98.
Caloceras belcheri, 99; *convolutum*, 100.

- Camptonotriletes velatus*, 640, 645, 93, 96.
 Canada: Nova Scotia fish fauna, 22.
Caneyella membranacea, 367, 370, 397, 60; *membranacea horizontalis*, 398, 61.
Cannosphaeropsis caulleryi, 482, 70.
Carbonicola, 310; *extenuata*, 310, 48; aff. *extenuata*, 312, 48; *extima*, 310, 327, 48; *crispa*, 318; cf. *limax*, 325, 48; *pontifex*, 324, 329, 48; aff. *pontifex*, 325, 48; *proxima*, 322; aff. *proxima*, 323, 48; *sp.*, 325, 48.
 Carboniferous: dispersed spores, 247; fructifications from Scotland, 225; microfloras from Spitsbergen, 550, 619; micro-organisms and syngenetic pyrite, 444, 451; Namurian palaeontology, Co. Leitrim, Eire, 355; non-marine lamellibranchs, 307; Nova Scotia fish fauna, 22; plant roots from Scotland, 213; spores from Spitsbergen, 679; South African fish, 9.
Cardioceras chalcidonicum, 126; (*Scarburgiceras scarbugeuse*, 126; (*Maltouiceras*) *maltonense*, 127.
Carixia, 156; *langi*, 160.
Carolia, 5; *libyca*, 5.
Catacoeloceras crassum, 118; *crossbeyi*, 119; *foveatum*, 119; *puteolum*, 119.
Cenoceras, 96; *annulare*, 96, 13; *astacoides*, 96, 13; *heterogeneum*, 96, 13; *undulatum*, 96.
 Cephalopoda: Barremian, from Bulgaria, 527; Berriasian, Speeton Clay, 272; Kimmeridgian, from Scotland, 765; Namurian, from Eire, 355; Toarcian hildoceratid, 86; Yorkshire types, 93.
Ceratiocaris papilio, cuticle, 7, 8.
Chaenocardiola, 404; *bisati*, 367, 372, 406, 61; *footii*, 369, 371, 372, 376, 404, 56, 62; cf. *haliotoidea*, 376, 406, 61.
Chaetosphaerites, 573; *pollenisimilis*, 573, 78.
 Chaloner, W. G. A *Sporangiostrabus* with *Deusosporites* microspores, 73, 10, 11.
Chanoussetta funifera, 125; *lenticularis*, 125.
Cidarites mouiliferus, 786, 115.
Cincturaspores, *auritus*, 251, 37.
Cirratiradites, 644; *elegans*, 251, 644, 38, 92; *solaris*, 644, 92.
Cliftonia, 741; *oxoplecioides*, 761, 109.
Climacograptus alterius, 521, 72; *tamariscoides*, 513, 71; *taughshaniensis linearis*, 514, 72.
Coelodoceras retusum, 108; *sociale*, 108; *validum*, 108.
Coleolus namurcensis, 364.
Couvolutispora clavata, 593; *crassa*, 594, 81; *harlandii*, 593, 81; *labiata*, 595, 82; *tuberculata*, 592, 81; *usitata*, 595, 82; *vermiformis*, 593, 82.
Coroniceras validum, 101, 14.
Cosmosporites, nomenclatural note, 192.
 Cox, L. R. Tertiary Bivalvia from Libya, 1.
Craspedites, 277.
 Craspeditidae, 276.
Craveuceras, 388; *cowlingense*, 371; fauna, 371, 416; cf. *gairnense*, 372, 388, 56; *holmesii*, 375, 376, 395; fauna, 376, 422; *leiou*, 367, 369, 55; zone, 366, 367, 413; *malhamense*, 370; zone, 366, 370, 415; *subplicatum*, 373, 375, 389, 57; fauna, 373.
Cravenoceratoides, 390; cf. *bisati*, 373, 392, 56; fauna, 373, 420; subzone, 366; *edaleise*, 373, 392, 56, 57; fauna, 373, 420; *lirifer*, 392; *uitidus*, 376, 390, 52; subzone, 366, 421; zone, 366; *nititoides*, 376, 391, 57; fauna, 376, 423; subzone, 366; *stellarum*, subzone, 366.
 Cretaceous: ammonites from Bulgaria, 527; ammonites from the Speeton Clay, 272; brachiopod ecology and Lower Greensand palaeogeography, 253; foraminifera from Britain, 149, 712; Yorkshire type ammonites and nautiloids, 93.
Crioceratites beaui, 129, 19.
Cristatisporites, 637; *echinatus*, 637, 680, 91, 96.
 Crustacea, ceratiocaridid, 30.
 Cryptostomata, order, 55.
Ctenopteris elegans, 20, 143.
 Currey, J. D. The histology of the bone of a prosauropod dinosaur, 238.
 Cuticle, crustacean, 30.
Cycloceras purvesi, 369.
Cyclograusporites, 585; *flexuosus*, 585, 79; *lasius*, 585, 79.
Cymbites arctus, 104; *denuyi*, 104.
Cyrtia, 701; *exporrecta*, 102, 104; *sp.*, 102.
 Czechoslovakia: Namurian correlations, 426.

D

- Dactylioceras andersoni*, 115; *annuliferum*, 115; *athleticum*, 115; *crassibundum*, 115, 16; *crassifactum*, 115, 16; *crassiusculosum*, 115; *crassiusculum*, 116; *crassulosum*, 116; *crassulum*, 116; *delicatum*, 116; *gracile*, 116; *semicelatum*, 116; *tenuicostatum*, 116; *vernus*, 116.
 Dalradian: calcareous algae from Islay, 268, 39.
 Dean, W. T. The Ordovician trilobite genus *Tiresias* McCoy, 1846, 340.
Defossiceras defossus, 103.
Dekayella, 199; *ranosa*, 200; *whitcliffensis*, 200, 29.
Deusosporites, 79, 83, 620; *aculeatus*, 631, 88; *bialatus*, 621, 88; *deutatus*, 622, 88; *diatretus*, 623, 88; *duplicatus*, 626, 89; *rarispinosus*, 630, 89; *sphaerotriangularis*, 250, 37; *spitsbergeusis*, 627, 89; *striatiferus*, 627, 88; *subrenatus*, 623, 88; *variabilis*, 625, 88; *variomarginatus*, 629, 89; *sp.*, 631, 88.
Deshayesites fissicostatus, 132.
 Dettmann, Mary E., and Playford, G. Sections of some spores from the Lower Carboniferous of Spitsbergen, 679. See also Hughes, N. F.
 Devonian: Eospiriferidae, 682; and see Old Red Sandstone.
Diatomozouotriletes, 646; *hughesii*, 648, 93; *rarus*, 649, 93; *saetosus*, 647, 93; *trilinearis*, 649, 93.
Dictyopyxis areolata, 494, 70.
Dictyotriletes caperatus, 596, 83.
Diueropyge sp., 796, 118.
Diurophoceras, 361, 375; cf. *D. looneyi*, 373.
 Dimorphoceratidae, 393.
 Dinoflagellates: Upper Jurassic, Yorkshire, 478.
 Dinosaurs: histology of bone of prosauropod, 238, 36.
 Diplograptidae, 500.
Distoloceras curvioidum, 131; *hystrix*, 132, 19.

Donovan, D. T. New information on the Toarcian ammonite genus *Pseudohillia* Maubeuge 1949, 86, 12.

Downie, C. See Wall, D.
Dumbarella elegans, 364, 372, 376; *sp.*, 365.
Dwyka shales: fish, 9.

E

Eagar, R. M. C. New Upper Carboniferous non-marine lamellibranchs, 307.

Echinoids: *Cidarites moniliferus* Goldfuss and the status of *Eucidaris*, 785.

Echioceras aureoleum, 106; *cereum*, 106; *exortum*, 106.

Edestus (*Edestodus*) *sp.*, 376, 409, 62.

Eleganticeras elegantulum, 120; *ovatum*, 120; *rugulatum*, 120, 17; *simile*, 120, 18.

Elonichthys, 17; *whaitsi*, 17.

Eucrinurus deomenos, 473, 67, 68; *macrourus*, 469, 65, 66, 67, 68; *moe*, 474; *multisegmentatus*, 474; *omniensis*, 471, 65, 67; *ornatus*, 475; *punctatus*, 460, 461, 65, 66, 67, 68; *stubblefieldi*, 471, 65, 67, 68; *tuberculatus*, 467, 65, 66, 67, 58; *variolaris*, 474, 65; *sp.*, 473, 65.

Endosporites, 651; *micromanifestus*, 652, 93.

Eocene: Bivalvia, 1; micro-organisms and syngenetic pyrite, 455.

Eoderoceras anguiforme, 107; *armiger*, 107; *diversum*, 107, 15; *miles*, 107; *owenense*, 107.

Eoleptoceras, 532; *E. (Tzankoviceras)*, 533; *assimilis*, 533, 73, 74; *tzankovi*, 533, 75; *E. (Wrightites)*, 534; *parvulum*, 535, 75; *parvulum kraptschenensis*, 535, 75; *wrighti*, 535, 75.

Eospirifer, 685; *radiatus*, 97.

Eospiriferidae, 682.

Eoverbeekina aff. *E. americana*, 303, 46.

Eparietites denotatus, 103; *impedens*, 103; *tenellus*, 104.

Eridotrypa, 203; *unbonensis*, 203, 30.

Escharopoid group, Bryozoa, 55.

Estonia: *Encrinurus punctatus*, Silurian, 460.

Euagassisceras transformatum, 102; *resupinatum*, 102.

Euaspidoceras acuticostatum, 128; *silhouense*, 128.

Euchondria aff. *levicula*, 376, 399, 58.

Euchondriidae, 399.

Eucidaris, 785.

Eumorphoceras, 377; age, Lower (E₁), 366; age, Upper (E₂), 366; *angustum*, 369, 370, 380; *bisulcatum*, 372, 384; fauna, 371; zone, 366; *bisulcatum erinense*, 372, 382, 384, 53, 54; *bisulcatum ferrimontanum*, 372, 383, 385, 52, 53, 54; *bisulcatum grassingtonense*, 371, 372, 381, 384, 52; *bisulcatum leirrinense*, 373, 375, 385, 53, 54, 55; fauna, 375; *bisulcatum varicata*, 372, 386; *medusa*, 367, 369, 378; *medusa stenosum*, 367; *pseudobilingue*, 369, 370, 379, 51; zone, 366, 369, 414; *pseudobilingue A*, 367, 378, 51, 53; *pseudobilingue C*, 370, 380, 52; *pseudocoronula*, 367, 377, 51; *rostratum*, 376, 387, 55; *rota*, 367, 378.

Euphenax, 3; *variolosa*, 3.

Eurypterid, *Pagea*, 137.

F

Favositella, 196; *interpuncta*, 197, 28.

Fenestella pseudosubantiqua, 544, 77; *pseudosubantiqua catrionae*, 545.

Fish: Carboniferous from Nova Scotia, 22; Namurian *Edestus*, 409; Palaeozoic from South Africa, 9; Triassic *Saurichthys*, 344.

Fistulipora, 197; *crassa*, 197; *strawi*, 198, 28; *umbrosa*, 199, 28.

Flexicalymene cambrensis, 808, 117.

Foraminifera: calcareous adherent, 149; Cretaceous Polymorphinidae, 712; Permian from British Honduras, 297; Permian from Peru, 817; with pyrite infillings, 447.

Foveosporites, 600; *insculptus*, 601, 85.

France: Eocene foraminifera, 149, 151.

Frechiella subcarinata, 123.

Fructifications: Lower Carboniferous of Scotland, 225.

G

Gardiner, B. G. *Namaichthys schroederi* Gürich and other Palaeozoic fishes from South Africa, 9, 6.

Gagaticeras gagateum, 106; *neglectum*, 106.

Gemellaroceras tubellum, 111.

Germany: Namurian correlations, 424.

Gleviceras lens, 105, 15.

Globulina, 715; *lacrima*, 715; *lacrima subsphaerica*, 715.

Glyptograptus elegans, 519, 72; *enodis*, 515, 71, 72; *enodis enodis*, 517, 71, 72; *enodis latus*, 518, 71; *incertus*, 518, 72; *serratus*, 524, 72; *tamariscus*, 501, 71, 72; *tamariscus acutus*, 511, 71; *tamariscus angulatus*, 510, 71; *tamariscus distans*, 507, 71; *tamariscus linearis*, 506, 72; *tamariscus tamariscus*, 504, 71; *tamariscus varians*, 509, 71; *G. sp. cf. G. tamariscus fastigans*, 512, 71.

Goliathiceras ammonoides, 126; (*Goliathites*) *capax*, 126.

Goniatites cf. *falcatus*, 364; *granosus*, 364; *striatus*, 362, 365.

Gonyaulax eisenacki, 482, 69; *eumorpha*, 481, 69; *nealei*, 480, 69; *nuciformis*, 482, 69; *paliuros*, 481, 69.

Grauatiasporites, 583; *planusculus*, 583, 79.

Graptolites: monograptids from Illinois, 59; Silurian diplograptids from Britain, 498.

Griffith, J. The Triassic fish *Saurichthys krambergeri* Schlosser, 344.

Grossouvria (Klematosphinctes) vernoni, 127.

Gutulina senicostata, 719; *sororia*, 721; *irigoulula*, 721.

Gyracanthus sp., 25.

H

Hackman, B. D., and Knill, J. L. Calcareous algae from the Dalradian of Islay, 268.

Haplolepid fish fauna, 22.

Haplolepis (Parahaplolepis) aff. *anglica*, 22; cf. *corrugata*, 29.

Harpoceras exaratum, 119; *mulgravium*, 119; *multifoliatum*, 120, 17; *signifer*, 120.

Harpoceratoides alternatus, 120.
Haugia beani, 123; *obliquata*, 124; *phillipsi*, 124.
Havlicekia, 693; *sp.*, 103.
Hemibaculites saharievae, 536, 73.
Hildaites levisoni, 123.
Hildoceras hildense, 123.
Holcodiscus caseyi, 537, 76.
Hoploceroceras phillipsi, 130, 18.
Howarth, M. K. The Yorkshire type ammonites and nautiloids of Young and Bird, Phillips, and Martin Simpson, 93, 13-19.
Hughes, N. F., Dettmann, Mary E., and Playford, G. Sections of some Carboniferous dispersed spores, 247.
Hyperderoceras mamillatum, 108, 15; *nativum*, 108.
Hystrichosphaera furcata, 486.
Hystrichospheres: Permian, 770; Upper Jurassic, 478.
Hystrichosporites, 591; *corystus*, 173, 25; *sp.*, 591, 80.

I

Indoplacuna, 6.
Ireland: Namurian correlations, 410; Namurian palaeontology, Co. Leitrim, 355; Upper Carboniferous non-marine lamellibranchs, 307.

J

Janius, 698; *insignis*, 104, cf. *nobilis*, 101; *schmidti*, 101, *sp.*, 103.
Jordanopora, 730; *heroensis*, 732, 105, 106.
Jurassic: cidarids, 785; foraminifera, 149; Kimmeridgian ammonites, 765; Liassic micro-organisms, 445; microplankton from the Ampthill Clay, 478; Toarcian ammonite, 86; Yorkshire type ammonites and nautiloids, 93.

K

Kamptokephalites, subgenus, 124.
Kazakhoceras scaliger, 370, 372, 393, 59; *sp.*, 365, 367, 369.
Knill, J. L. See Hackman, B. D.
Knoxisporites, 633; *cinctus*, 633, 89; *hederatus*, 634, 90; *literatus*, 634, 90; *margarethae*, 249, 633, 37, 90.
Kosmoceras gemmatum, 125; (*Lobokosmoceras*) *rowlstonense*, 125.

L

Labiadensites, 632, *finbriatus*, 632, 679, 90, 96.
Lamellibranchs: Namurian from Eire, 395; Tertiary from Libya, 1; Upper Carboniferous non-marine, 307.
Laugeites, 274, 293; ? *sp.*, 275, 40, 41, 42.
Leioclena, 203; *explanatum*, 204, 30; *halloporoides*, 204, 30; *ludlovensis*, 205, 30.
Leiofusa jurassica, 780, 112.
Leiorhynchus carboniferus polypleurus, 364.
Leiosphaeridia (*Chytroesphaeridia*), 492; *chytrooides*, 493, 70; *L.* (*Leiosphaeridia*), 492; cf. *similis*, 492, 70.
Leiotriletes, 573; *curiosus*, 576, 78; *inermis*, 574, 78; *microgranulatus*, 575, 78; *ornatus*, 575, 78; *subintortus* var. *rotundatus*, 574, 78.

Leptoceratinae, 531.
Leptotrypella, 200; *leintwardinensis*, 201, 29.
Leptotrypellid Bryozoa, 195, 730.
Libya: Tertiary Bivalvia, 1.
Lingula, 361, 376; cf. *parallela*, 365.
Liparoceras heptangulare, 111.
Lobokosmoceras, subgenus, 125.
Lophotriletes coniferus, 587, 79.
Lophozonotriletes, 638; *appendices*, 639, 91; *dentatus*, 639, 91; *rarituberculatus*, 638, 91; *triangulatus*, 251, 38; *variverrucatus*, 640, 91.
Love, L. G. Further studies on micro-organisms and the presence of syngenetic pyrite, 444.
Lower Greensand: Aptian, Cretaceous; brachiopod ecology and palaeogeography, 253.
Lycospora, 635; *uber*, 636, 89.
Lyrogoniatites newsoni georgiensis, 365, 431.
Lytoceras cornucopia, 98.

M

MacGregor, A. R. Upper Llandeilo trilobites from the Berwyn Hills, North Wales, 790.
Macrocephalites (*Kamptokephalites*) *terebratus*, 124.
Macrolepura, 690; *eudora*, 99, 100; *uacrolepura*, 98, 99.
Manolov, J. R. New ammonites from the Barremian of North Bulgaria, 527.
Marrolithoides cf. *arcuatus*, 803, 116; *sp.*, 804, 116.
Marrolithus, 797; *favus*, 799, 117; *inflatus maturus*, 799, 117; *lirellatus*, 802, 116; *magnificus*, 801, 117.
Megaspores: *Sporangioctrobus*, 77.
Metopolichas contractus, 810, 118.
Metoxynoticeras complanosum, 105, 15.
Micrhystridium, 771; *fragile*, 492, 70; cf. *piveteaui*, 491; *recurvatum*, 778; *rhopalicum*, 490, 70; *stellatum*, 780, 112, 113.
Micro-berrries: syngenetic pyrite, 447, 450, 64.
Microfloras: Lower Carboniferous of Spitsbergen, 550, 619.
Micro-organisms, and syngenetic pyrite, 444, 63, 64.
Microplankton: Upper Jurassic, Yorkshire, 478.
Microreticulatisporites lunatus, 596, 82.
Microspores: Carboniferous, 247; Lower Carboniferous of Spitsbergen, 550; *Sporangioctrobus*, 73.
Middlemiss, F. A. Brachiopod ecology and Lower Greensand palaeogeography, 253.
Miller, T. G. Some Wenlockian fenestrate Bryozoa, 540.
Miocene: Bivalvia, 1.
Monestieria errata, 122.
Monilospora, 641; *dignata*, 642, 92; *triungenis*, 641, 92.
Monograptus boltemicus, 64; *butovicensis*, 69; *colonus*, 71; *dubius*, 67; cf. *M. dubius*, 69; *roemeri*, 65; *varians*, 67; *varians* var. *pumilus?*, 67.
Monotrypa, 207; *crenulata*, 208, 31; *flabellata*, 209, 32; *patera*, 209, 32.
Morocco: Namurian correlations, 432.
Mourlonia striata, 364, 376.
Murospora, 608; *aurita*, 609, 87; *conduplicata*, 613,

86; *dupla*, 614, **86**; *friendii*, 617, **87**; *intorta*, 609, **86**; *strigata*, 615, **86**; *sublobata*, 613, **86**; *tripulvinata*, 616, **86**.

N

Naiadites, 307; *hibernicus*, 355, 47; aff. *hibernicus*, 307, 47.

Nannoceratopsis pellucida, 482, **69**.

Namaiclitus, 9; *molyneuxi*, 15; *schroederi*, 9, **6**; *sculptus*, 14.

Nautilus maltonensis, 97; *reticularis*, 97; *youngi*, 97.

Neale, J. W. Ammonoidea from the Lower D Beds (Berriasian) of the Specton Clay, 272.

Nematopora, 210; *hexagona*, 210, **32**.

Neoretaporina, 547.

Netrelytron stegastum, 494, **70**.

Nikiforovaena, 697; *ferganensis*, **103**.

Nodicoeloceras crassescens, 118; *crassoides*, 118; *fomiculus*, 118; *incrassatum*, 118.

Nubecularia, 151; *lucifugia*, 151, **21**; *triloculina*, 160, **21**, **23**.

Nubeculinella, 156; *bigoti*, 162, **22**, **23**; *bigoti* var. *filiformis* 163; *tibia*, 164, **23**; *tibia* var. *bacularis*, 165, **23**; *tibia* var. *bulbifera*, 165, **23**; *sp.*, 166.

Nuculoceras nuculum subzone, zone, 366.

O

Obliquipecten costatus, 367, 401, **59**, **62**.

Ogygiocarella debucii, 792, **116**.

Osterocheras anguliferum, 112; *figulinum*, 112; *omissum*, 112.

Old Red Sandstone: spores from Scotland, 171; eurypterid from Scotland, 137.

Oligocene: *Bivalvia*, 1.

Onychitreta, 742.

Onychoplecia, 741.

Orbiculoidea nitida, 376.

Orbignyella fibrosa, 199.

Ordovician: Bryozoa, 52, 727; Llandeilo trilobites, 790; trilobite, *Tiresias*, 340; Triplesia, 740.

Osteichthyes, class, 22.

Ostrea, 1; *syrtica*, 1; *asiatica*, 2.

Ovaticeras ovatum, 121.

Owen, D. E. Ludlovian Bryozoa from the Ludlow district, 195.

Oxoplecia, 742; *multicostellata*, **109**.

Oxyntoceras altaenum, 104; *bucki*, 104; *dejectum*, 104; *flavum*, 104; *linatum*, 104; *polyophyllum*, 105; *simpsoni*, 105.

Ozawainella? *sp.*, 304, **46**.

P

Pacliytyloceras gubernator, 99; *peregrinum*, 99.

Packham, G. H. Some diplograptids from the British Lower Silurian, 498.

Pagea sturrocki, 137, 138, **20**.

Palaeolystrichophora spinosissima, 483.

Palaeoniscus, 16; *capensis*, 16.

Paracraspedites, 277; *prostenomphaloides*, 277, **43**; *stenomphaloides*, 277, **40**, **45**; *subtzikwinianus*, 278, **41**; ? *sp.*, 278, **45**.

Parahaplolepis, 22.

Pareodinia ceratophora, 483, **69**.

Peltoceras atlileta, 128.

Peltoceratoides intertextus, 128; *williamsoni*, 128.

Pennines: Namurian correlations, 413.

Perisphinctes instabilis, 127; (*Arisphinctes*) *ingens*, 127; (*Arisphinctes*) *maximus*, 127; (*Arisphinctes*) *pickeringius*, 128.

Permian: Foraminifera from British Honduras, 297; fusulinids from Peru, 817; hystrichospheres from Britain, 770.

Peronoceras andraei, 116; *attenuatum*, 117; *perarmatum*, 117; *seni-armatum*, 117; **17**; *subarmatum*, 117, **17**; *turriculatum*, 117.

Perotriletes, 174, 601; *bifurcatus*, 174, **25**; *magnus*, 602, **85**; *perinatus*, 602, **85**.

Peru: Permian fusulinids, 817.

Phaenopora, 52; *stubblefieldi*, 56, **9**.

Philip, G. M. The Jurassic echinoid *Cidarites moniliferus* Goldfuss and the status of *Euclidaris*, 785.

Phricodoceras cornutum, 108; *quadricornutum*, 108.

Phylloceras easingtonense, 97, **17**; *whitbiense*, 97.

Phyllopachyceras bontshevi, 527, **73**.

Phyllotheocotrites rigidus, 580, **79**.

Phymatoceras fabile, 123; *rude*, 123.

Pitys, 222, **33**.

Placenta, 6; *africana*, 6.

Plants: See Algae, Dinoflagellates, Fructifications, Micro-berries, Microfloras, Microplankton, Microspores, Pollen, Pteridospermeae, Roots, Spores, Stromatolites.

Platygena, 2.

Platypleuroceras aureum, 110; *ripleyi*, 110; *tenuispina*, 111.

Playford, G. Lower Carboniferous microfloras of Spitsbergen, 550, 619. See also Dettmann, Mary E., and Hughes, N. F.

Plectotreta, 742.

Pleuroceras birdi, 114; *elaboratum*, 114; *hawskerense*, 114; *regulare*, 114; *solare*, 114; *solitarium*, 114;

Pliocyrtia, 704; *petasus*, **102**, **104**.

Pluriarvalium osningtonense, 482, **69**.

Poland: Namurian correlations, 426.

Pollen: with syngenetic pyrite, 447, 450, 451, **63**.

Polymorphites rutilans, 110, **15**; *trivialis*, 110.

Polyzoa. See Bryozoa.

Porpoceras vortex, 117; *vorticellum*, 118.

Posidonia becheri, 364, 365; *corrugata*, 367, 369, 371-3, 375, 376, 395, **58**, **60**; *corrugata elongata*, 372, 373, 375, 376, 396, **60**; *corrugata gigantea*, 375, 397, **60**; *lamellosa*, 371; *trapezoedra*, 367, 369.

Posidoniella variabilis, 373, 375, 376, 402, **60**; *variabilis erecta*, 373, 375, 376, 403, **61**; cf. *vetusta*, 376.

Potoniespores, 643; *delicatus*, 643, **91**.

?*Prinaspis sp.*, 813, **116**.

Productus libaniticus, 376.

Proetidella sp., 795, **116**.

Promicroceras aureum, 107; *siphunculare*, 107.

Protopytys, 225, 226; *scotica*, 227, **34**, **35**.

Pseudamysium cf. *praetenuis*, 365, 367.

Pseudogrammoceras latescens, 123.

- Pseudollilia*, 86; *murvilleensis*, 86, **12**; *emiliana*, 90.
Pseudolioceras boubliense, 121; *compactile*, 121; *lectum*, 121; *leptophyllum*, 121, **18**; *lythense*, 122; *simplex*, 122, **18**; *subconcauum*, 122
Pseudothurmannia karakaschii, 536, 73, 74.
Psiloceras erugatum, 99, **14**.
Pteridospermeae: *Staphylotheca*, Lower Carboniferous, 232; *Calathiops*, Lower Carboniferous, 235.
Pterinopectinidae, 395.
Pterospermopsis cf. *helios*, 492, 70.
Ptilodictya gracile, 211; *lanceolata*, 212.
Punctatisporites glaber, 576, **78**; *labiatus*, 578, **78**; *parvivermiculatus*, 577, **78**; *pseudobesius*, 578, **78**; *stabilis*, 578, **79**.
Pyrite, syngenetic, and micro-organisms, 444, **63**, **64**.
Pyritella polygonalis, 444, 452, 454, **64**.
Pyritosphaera barbaria, 444, 449, 451, 454.
Pyridina cylindroides, 723.
Pyridinoides acuminata, 722.
- Q
- Quenstedtoceras crenulare*, 125; *flexicostatum*, 125.
- R
- Radialetes*, 655; *costatus*, 656, **95**.
Rasemia (Rasenoioides) lepidula, 766, **111**; *R. (Semirasemia) askepta*, 768, **111**; cf. *möschi*, 767, **111**.
Recent: micro-organisms and syngenetic pyrite, 455, 64.
Remysporites, 652; *albertensis*, 652, **94**.
Reptiles: dinosaurs, Triassic prosauropod, histology of bone, 238, **36**.
Retenticeras retentum, 105.
Reteporina, 545; *reticulata*, 545, 77.
Retialetes, 655; *radforthii*, 655, **95**.
Reticulatisporites cancellatus, 597, **82**, **83**; *peltatus*, 599, **84**; *planus*, 598, **83**; *rudis*, 597, **82**; *variolatus*, 598, **84**; *R. ? sp.*, 600, **85**.
Rhodesia: histology of prosauropod dinosaur bone, Triassic, 238, **36**.
Rhombopora, 210; *mesopora*, 210, **32**; *minima*, 211, **32**.
Richardson, J. B. Spores with bifurcate processes from the Middle Old Red Sandstone of Scotland, 171.
Rolfe, W. D. I. The cuticle of some Middle Silurian ceratiocaridid crustacea from Scotland, 30, 7, 8.
Roots: *Amyelon*, Scottish Lower Carboniferous, 213.
Ross, C. A. Early Permian fusulinids from Macusani, Southern Peru, 817; Permian foraminifera from British Honduras, 297; Silurian monograptids from Illinois, 59.
Ross, J. R. P. Chazy (Ordovician) leptotrypellid and atactotoechid Bryozoa, 727; Early species of the bryozoan genus *Phaenopora* from the Caradoc Series, Shropshire, 52, 9.
- S
- Sarjeant, W. A. S. Microplankton from the Ampt-hill Clay of Melton, South Yorkshire, 478.
Saurichthys krambergeri, 344, **50**.
Saxocera aequale, 100, **14**.
Schlotheimia redcarensis, 100; *sulcata*, 101.
Schwagerina adamsi, 821, **119**; *gruperensis*, 301, **46**; sp. A, 302, **46**.
Scotland: Dalradian calcareous algae, 268; Lower Carboniferous fructifications, 225; Lower Carboniferous plant roots, 213; Middle Old Red Sandstone spores, 171; Middle Silurian crustacea, 30; Old Red Sandstone eurypterid, 137; Silurian diplograptids, 498; Upper Jurassic ammonites, 765.
Serintodinium (?*Endoscrinium*) *dictyotum*, 482, **69**; *luridum*, 480, 486, **69**; *oxfordianum*, 485, **69**; *subvallere*, 482, **69**.
Shropshire: Caradoc Bryozoa, 52; Ludlovian Bryozoa, 195.
Silurian: crustacea, 30; diplograptids, 498; trilobite, *Encrinurus*, 460; Eospiriferidae, 682; Ludlovian Bryozoa from Ludlow, 195; monograptids, 59; brachiopods, Triplesia, 740; Wenlock Bryozoa, 540.
Simbirskites concinnus, 130, **19**; *sptonensis*, 131, **19**; *venustus*, 131, **19**.
Smith, D. L. Three fructifications from the Scottish Lower Carboniferous, 225.
South Africa: Palaeozoic fish, 9.
Spinozonotriletes, 656; *baiteatus*, 657, **95**; *uncatus*, 657, 680, **94**, **96**.
Spidiscus youngi, 132.
Spitsbergen: Carboniferous spores, 247; 679; Lower Carboniferous microfloras, 550, 619.
Sporangiostrobus, 79; *ohioensis*, 79, **10**, **11**.
Spores: dispersed microspores from Lower Carboniferous of Spitsbergen, 550; Middle Old Red Sandstone from Scotland, 171; *Protopytis scotica*, Lower Carboniferous, 230; *Staphylotheca kilpatrickensis*, Lower Carboniferous, 233; with bifurcate appendages, 171; with syngenetic pyrite, 444.
Staphylotheca, 232; *kilpatrickensis*, 233, **34**, **35**.
Stenozonotriletes, 605; *clarus*, 607, **86**; *facilis* var. *praecrassus*, 605, **86**; *inductus*, 606, **86**; *perforatus*, 607, **86**; *simplex*, 606, **86**; cf. *spetcandus*, 607, **86**; *stenozonalis*, 606, **86**.
Stephanelytron redcliffense, 495, **70**; *scarburghense*, 495, **70**.
Streptis, 742.
Striispirifer, 695; *niagarensis*, **100**; *plicatella*, **100**.
Stroboceras subsulcatus, 371, 372, 376.
Stromatolites: calcareous algae from Dalradian, Islay, 268, **39**.
Stylonurus, comparison with *Pagea*, 145.
Subcraspedites, 279; aff. *cristatus*, 282, **41**, **42**, **44**; *preplicomphalus*, 281, **42**; aff. *preplicomphalus*, 281, **42**, **45**; sp., 282, **42**, **44**; ? *spp.*, **44**.
Sudeticeras crenistriatum, 364; *newtonense*, 365.
Sulphide, environment of formation, and micro-organisms, 456.
Sweden: *Encrinurus punctatus* and allied species from Silurian, 460.
Systematophora orbifera, 490.
- T
- Taramelliceras oculatum*, 124.
Tertiary: Bivalvia from Libya, 1.

- Tetraporina*, 658; *glabra*, 659, **95**; *horologia*, 659, **95**;
incrassata, 659, **95**.
Tetrataxis sp., 305, **46**.
Tholisporites, 643; *foveolatus*, 543, **91**.
Thrinoceras lubericum, 364.
Tiresias, 341; *insculptus*, 341, **49**.
Tollia, 279, 283; cf. *payeri*, 285, **40**; *pseudotolli*, 285,
40, 41, 43, 44, 45; *stenomphala*, 287, **42**; cf. *tolmat-*
schowi, 288, **42**; *wrighti*, 284, **40, 43, 44, 45**; sp.,
288, **42**; ? sp., **44**.
Toxoceratoides obliquatus, 130, **19**.
Trachyltocyeras balteatum, 98; *fasciatum*, 99; *nitidum*,
99.
Tragophylloceras ambiguum, 98; *luuntoni*, 98; *nanum*,
98; *robinsoni*, 98.
Triassic: fish, *Saurichthys*, 344; histology of dinosaur
bone, 238; Rhaetic micro-organisms, 445.
Trilobites: *Eucrinurus*, Silurian, 460; *Tiresias*, Ordo-
vician, 340; Upper Llandeilo from North Wales,
790; *Weberides*, Namurian, 407.
Tripartites complanatus, 605, **85**; *incisotrilobus*, 604,
85.
Triplesia, 742; *anticostiensis*, **110**; *extans*, **109**; *insu-*
laris, **109**; cf. *insularis*, **110**; sp., **109**.
Triplesiidae, 741.
Tripp, R. P. The Silurian trilobite *Eucrinurus punc-*
tatus (Wahlenberg) and allied species, 460.
Triquitrites, 602; *batillatus*, 604, **85**; *trivalvis*, 602, **85**.
Triticites patulus, 820, **119**.
- U
- U.S.A.: Namurian correlations, 430; Ordovician
Bryozoa from New York, 727; Silurian mono-
graptids from Illinois, 59.
Uptouia ignota, 111; *obsoleta*, 111.
- V
- Velosporites*, 653; *echinatus*, 251, 653, **38, 94**; *micro-*
reticulatus, 654, **94**.
Vermiceras multanfractum, 101, **14**.
Verrucosporites, 586; *eximius*, 587, **80**; *gobbettii*, 586,
80.
Veryliachium, 771, 778; *europaeum*, 782, **114**; *flagelli-*
ferum, 779, **112**; *formosum*, 783, **114**; ? *irregulare*,
781, **113**; cf. *lairdi*, 782; *reductum*, 780, **112**; *rhom-*
boidium, 781, **113, 114**; sp., **114**.
Vitriwebbia, 155.
- W
- Wales: Silurian diplograptids, 498; Upper Llandeilo
trilobites, 790.
Wall, D., and Downie, C. Permian hystrichospheres
from Britain, 770.
Waltzispora, 581; *albertensis*, 582, **79**; *loboptora*, 581,
79; *sagittata*, 582, **79**.
Waterston, C. D. *Pagea sturrocki* gen. et sp. nov., a
new eurypterid from the Old Red Sandstone of
Scotland, 137.
Watsonichthys, 15; *lotzi*, 16.
Webbia, 150.
Weberides cf. *slunnerensis*, 376, 407, **62**.
Wlutyceras pingue, 121.
Wright, A. D. The morphology of the brachiopod
superfamily Triplesiacea, 740.
- X
- Xiphoceras scoresbyi*, 106.
- Y
- Yates, the late Patricia J. The palaeontology of the
Namurian rocks of Slieve Anierin, Co. Leitrim,
Eire, 355.
Yorkshire: Ammonites, 93; Amphill Clay micro-
plankton, 478.
- Z
- Ziegler, B. On some Upper Jurassic ammonites of the
genus *Rasenia* from Scotland, 765.

PRINTED IN GREAT BRITAIN
AT THE UNIVERSITY PRESS, OXFORD
BY VIVIAN RIDLER
PRINTER TO THE UNIVERSITY

THE PALAEOONTOLOGICAL ASSOCIATION

COUNCIL 1962

President

Professor T. NEVILLE GEORGE, The University, Glasgow, W. 2

Vice-Presidents

Professor O. M. B. BULMAN, Sedgwick Museum, Cambridge

Professor W. F. WHITTARD, The University, Bristol

Dr. W. H. C. RAMSBOTTOM, Geological Survey Office, Leeds

Treasurer

Professor P. C. SYLVESTER-BRADLEY, The University, Leicester

Assistant Treasurer

Dr. T. D. FORD, The University, Leicester

Secretary

Dr. C. H. HOLLAND, Department of Geology, Bedford College, London, N.W. 1

Editors

Mr. N. F. HUGHES, Sedgwick Museum, Cambridge

Dr. W. S. MCKERROW, University Museum, Oxford

Dr. GWYN THOMAS, Department of Geology, Imperial College of Science, London, S.W. 7

Other members of Council

Dr. F. T. BANNER, British Petroleum Company, Sunbury on Thames

Dr. F. M. BROADHURST, The University, Manchester

Dr. A. J. CHARIG, British Museum (Natural History), London

Dr. L. R. COX, British Museum (Natural History), London

Dr. W. T. DEAN, British Museum (Natural History), London

Dr. C. DOWNIE, The University, Sheffield

Dr. R. GOLDRING, The University, Reading

Dr. J. C. HARPER, The University, Liverpool

Dr. M. R. HOUSE, The University, Durham

Dr. J. W. NEALE, The University, Hull

Dr. R. J. G. SAVAGE, The University, Bristol

Mr. J. J. D. SMITH, Geological Survey and Museum, London

Dr. C. D. WATERSTON, Royal Scottish Museum, Edinburgh

Mr. C. W. WRIGHT, London

Overseas Representatives

Australia: Professor DOROTHY HILL, Department of Geology, University of Queensland, Brisbane

Canada: Dr. D. J. MCLAREN, Geological Survey of Canada, Department of Mines and Technical Surveys, Ottawa

India: Professor M. R. SAHNI, Department of Geology, Panjab University, Chandigarh

New Zealand: Dr. C. A. FLEMING, New Zealand Geological Survey, P.O. Box 368, Lower Hutt

West Indies and Central America: Dr. L. J. CHUBB, Geological Survey Department, Kingston, Jamaica

Eastern U.S.A.: Professor H. B. WHITTINGTON, Museum of Comparative Zoology, Harvard University, Cambridge 38, Mass.

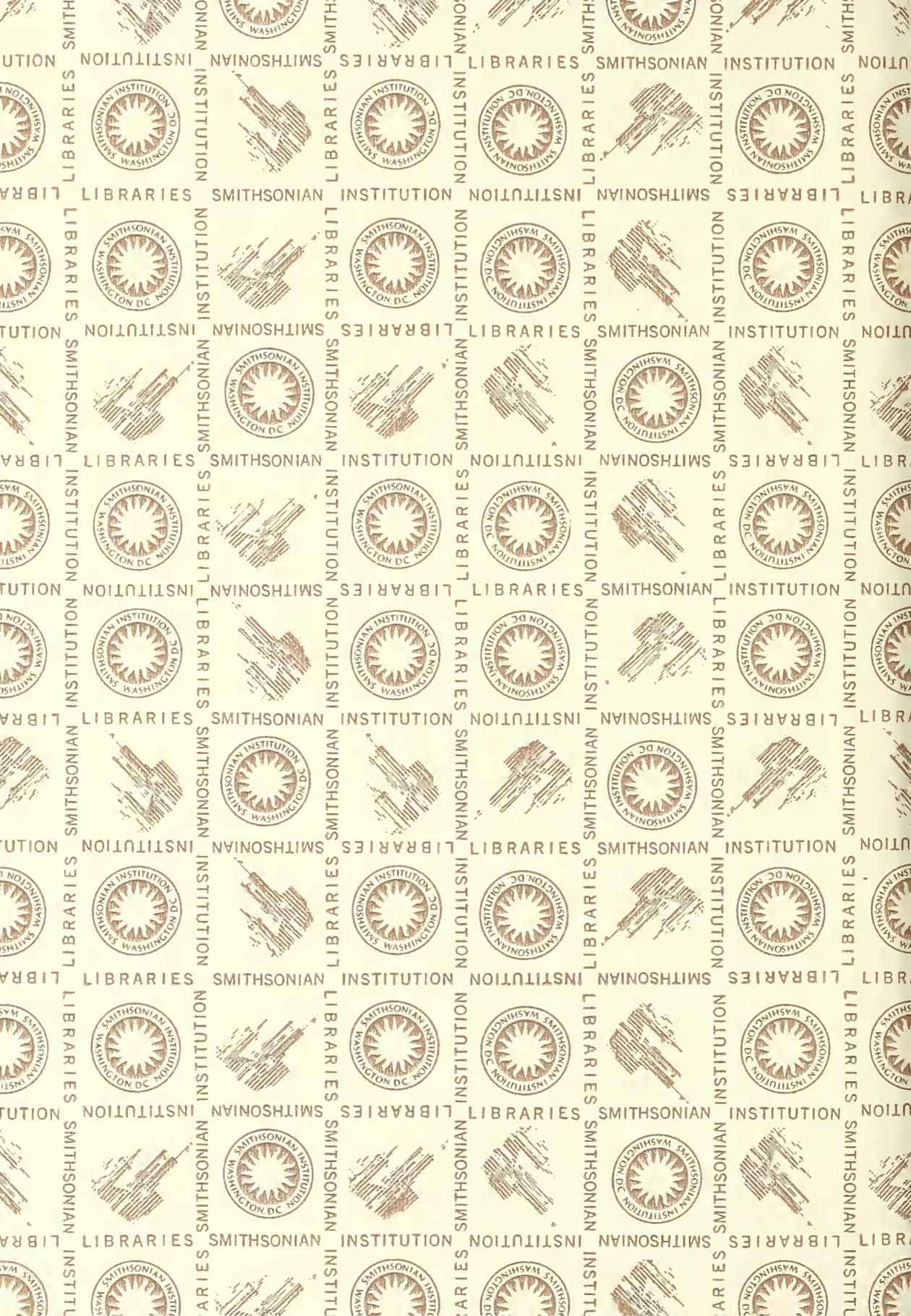
Western U.S.A.: Dr. J. WYATT DURHAM, Department of Paleontology, University of California, Berkeley 4, Calif.

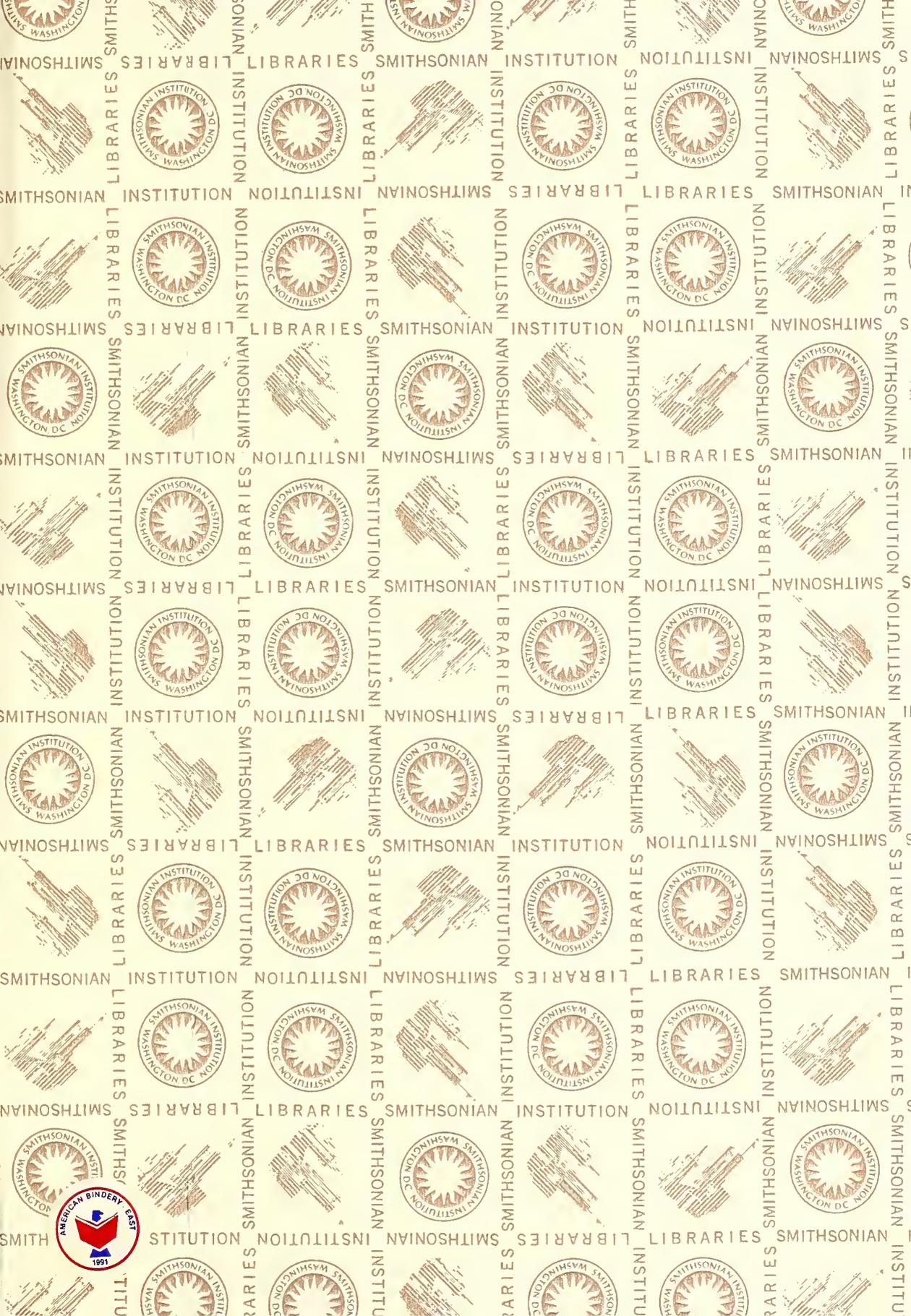
PALAEONTOLOGY

VOLUME 5 • PART 4

CONTENTS

Lower Carboniferous microfloras of Spitsbergen—Part Two. <i>By</i> G. PLAYFORD	619
Sections of some spores from the Lower Carboniferous of Spitsbergen. <i>By</i> M. E. DETTMANN and G. PLAYFORD	679
The Eospiriferidae. <i>By</i> A. J. BOUCOT	682
Polymorphinidae from the Upper Cretaceous of England. <i>By</i> T. BARNARD	712
Chazyan (Ordovician) leptotrypelliid and atactotechid bryozoa. <i>By</i> J. R. P. ROSS	727
The morphology of the brachiopod superfamily Triplesiacea. <i>By</i> A. D. WRIGHT	740
Some Upper Jurassic ammonites of the genus <i>Rasenia</i> from Scotland. <i>By</i> B. ZIEGLER	765
Permian hystrichospheres from Britain. <i>By</i> D. WALL and C. DOWNIE	770
The Jurassic echinoid <i>Cidarites moniliferus</i> Goldfuss and the status of <i>Eucidaris</i> . <i>By</i> G. M. PHILIP	785
Upper Llandeilo trilobites from the Berwyn Hills, North Wales. <i>By</i> A. R. MACGREGOR	790
Early Permian fusulinids from Macusani, southern Peru. <i>By</i> C. A. ROSS	817





SMITHSONIAN INSTITUTION LIBRARIES



3 9088 01375 6523