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THE PALAEOONTOLOGICAL ASSOCIATION

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Cover: The acritarch *Umbellasperidium saharicum* Jardine *et al.* 1972 from the Tournaisian Bedford Shale of Ohio, U.S.A., $\times 1000$. I.G.S. specimen number MPK 3152 deposited in the micropalaeontological collection of the Institute of Geological Sciences, Leeds. Photograph by S. G. Molyneux. This group of fossils was unknown when the Association was founded, twenty-five years ago.

RAPID EVOLUTION IN ECHINOIDS

by PORTER M. KIER

ABSTRACT. The evolution of the irregular echinoid and of the sand dollar occurred in a very short time. The first irregular echinoid appears abruptly in the Early Jurassic (Sinemurian); and by the Toarcian, only ten million years later, irregular echinoids possess all the features necessary to permit them to live buried in the sediment. The first clypeasteroid appears in the Paleocene. By the middle Eocene its very specialized descendants, the sand dollars, have a worldwide distribution. This rapid evolution and diversification seem to result from a sudden adaptive breakthrough. The presence of so few intermediates indicates the evolutionary steps must have been large.

Two of the most significant events in the evolution of the echinoids are the development of the irregular echinoid and the subsequent appearance of the sand dollar. Both of these events were believed to have occurred over a long period of time (Durham 1966, p. U289) but new evidence suggests otherwise. The irregular echinoid was assumed to have evolved during the Triassic and perhaps during the latter part of the Paleozoic. However, study of the Triassic faunas indicates that no irregulars were present then and that the great changes from the regular to the irregular echinoid occurred during the early part of the Early Jurassic. Likewise, it was believed (Durham 1966, p. U290) that the clypeasteroids arose during the Late Cretaceous and Paleocene. New evidence suggests that the first clypeasteroid actually appeared in the Paleocene, and that the great evolution to the sand dollar occurred during the early Eocene.

EVOLUTION OF THE IRREGULAR ECHINOID

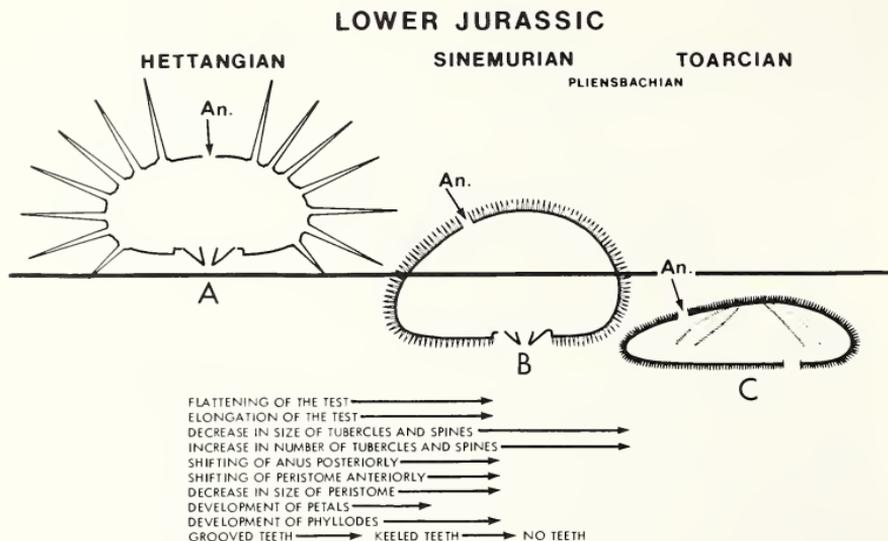
The first irregular echinoid, *Plesiechinus hawkinsi* Jesionek-Szymańska (text-fig. 1B), occurs in the Early Jurassic (Sinemurian). This echinoid, a pygasterid, differs from all other echinoids of the same age or older in having an asymmetrical test with small tuberculation, short and numerous spines, differentiated pores with the adapical pores larger than the adoral ones, posteriorly eccentric periproct, and presumably keeled teeth (although the lantern was not found with any specimens of this species, Melville (1961) found keeled teeth in a *Pygaster*).

One might assume that the great changes necessary to derive this irregular echinoid from a regular form would have taken a very long time. Many workers believe that these changes occurred during the Triassic or possibly in the Paleozoic. They attributed the lack of intermediates found during the Triassic to the poor fossil record of that period. However, that does not appear to be the case. Although it is true that few echinoids are known from the Triassic, particularly from the Early and Middle Triassic, a prolific echinoid fauna occurs in the Late Triassic St. Cassian beds of Italy. These beds (Kier 1977b) have been painstakingly searched by Rinaldo Zardini who has found many complete tests and thousands of fragments. I have searched through all this material and have failed to find any keeled teeth or any test fragments with the fine tuberculation of an irregular echinoid. As shown by Kier (1977a), irregular echinoids are much more likely to be preserved than regular echinoids. Had they been living during St. Cassian time, they should have been preserved as fossils. Furthermore, no irregular echinoids or any form resembling them have been found in the lowermost Jurassic (Hettangian).

I am convinced that this change from a regular echinoid to *Plesiechinus hawkinsi* must have occurred extremely quickly during the latter part of the Hettangian or early Sinemurian. Evolution then continued at a rapid rate, because by the Toarcian, still within the Early Jurassic, the cassiduloid *Galeropygus dumortieri* (Paris) (text-fig. 1C) has appeared with all the features of an irregular

echinoid. It is more advanced than *P. hawkinsi* in having a more flattened and elongate test, a more eccentric periproct, larger adapical pores forming incipient petals, and smaller, more numerous, tubercles and spines. Its peristome is smaller, elongate, and eccentric anteriorly. There are no gills. The most profound differences are the lack of a lantern and lantern supports and the presence of well-developed phylloides.

Presumably, one of the reasons for this rapid evolution was that these changes enabled echinoids to occupy a habitat not available to them before. They were now able to burrow (Smith 1978) into the sediment and extract the organic material contained within. Simpson (1944, 1953), and later Stanley (1979), proposed that a higher taxon arises rapidly through the occurrence of a sudden adaptive breakthrough. During the Triassic all echinoids apparently lived on the surface of the sea floor and could not burrow into the sediment. They all had jaws and grooved teeth which were used (presumably like modern regular echinoids) to tear off and chew organic material which was then passed into the gut. The small amount of faecal discharge could be easily carried away by water currents. Most modern irregular echinoids lacking teeth feed differently. They burrow (text-fig. 1)



TEXT-FIG. 1. Evolution of the irregular echinoid showing the changes that enabled the echinoid to live buried in the substrate. A, an Hettangian regular echinoid such as *Diademopsis*; B, the earliest known irregular, *Plesiechinus hawkinsi* Jesionek-Szymańska; C, a cassiduloid, *Galeropygus*.

EXPLANATION OF PLATE I

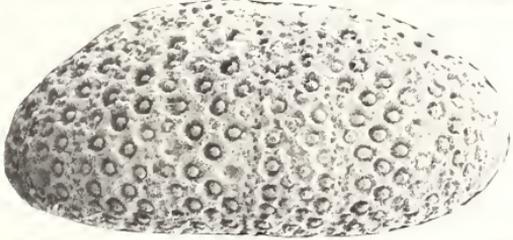
Figs. 1-5. *Togocyamus seefriedi* (Oppenheim). Paleocene, Ekekoro Formation, Ekekoro quarry, 55 km north-west of Lagos, Nigeria. 1, accessory pore on dorsal side of USNM 312503 just beyond petal I. The large pores on the lower right side are at the end of petal I, $\times 74$. 2, enlarged view of accessory pore in USNM 312504 showing large neural pore, $\times 500$. 3, side view of USNM 312505, $\times 19$. 4, top view of USNM 312503, $\times 13$. 5, bottom view of USNM 312504, $\times 15$.



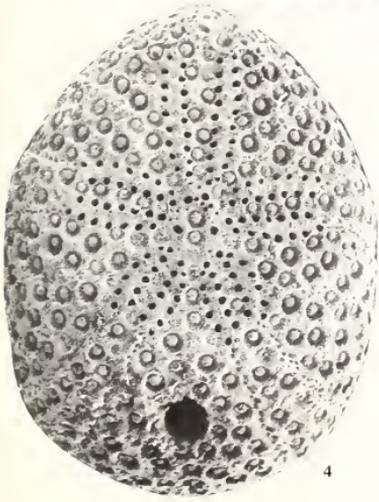
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into the sediment, collect large amounts of sediment with their tube-feet, and pass it through the gut while extracting the organic material. The sediment is then expelled through the anus (periproct). Most of the differences between an irregular and regular echinoid relate to these differences in mode of feeding.

The posterior migration of the periproct made it possible for the irregular echinoid to leave this large volume of discharged sediment in its trail rather than over its dorsal surface. At the same time that the periproct migrated, most irregular echinoids increased the oxygen-gathering capability of their dorsal tube-feet by greatly broadening them. The result was the formation of the 'petals' so typical of most irregulars. Specialized tube-feet were also produced around the mouth. They were larger, more numerous, and were used to collect sediment that was then passed to the mouth.

EVOLUTION OF THE CLYPEASTEROID ECHINOID

The first clypeasteroid echinoid, *Togocyamus* (Pl. 1, figs. 1-5), appears in Paleocene strata. By the middle Eocene the highly specialized sand dollar had evolved. Until now it was believed that these developments required a long time from the Cretaceous through the Eocene. New evidence indicates that the change was much more rapid. In fact the change from a cassiduloid ancestor to a clypeasteroid probably occurred within the Paleocene; and the change from a primitive clypeasteroid to a sand dollar occurred during the early Eocene.

The earlier 'Cretaceous' origin of the clypeasteroids was based on the supposed occurrences of three species of clypeasteroids in the Late Cretaceous. These occurrences are probably erroneous. One of the three species is too poorly preserved to be identified, and the stratigraphic data with the other two are inadequate. Extensive collecting has been done in the Late Cretaceous beds where these two species supposedly were found and neither Meijer (1965) nor Ernst (1972) have found any clypeasteroids. Ernst, in the course of his study, examined over 15000 echinoids from the Late Cretaceous.

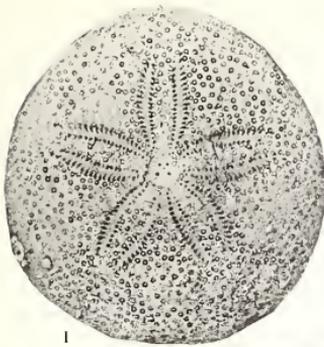
The chronologically later origin of the clypeasteroids is supported by their absence from the Paleocene of the Western Hemisphere. An exhaustive search by Kier through washings of the Paleocene Vincentown, Aquia, and Clayton Formations (from which eighteen echinoid species are known) revealed no fragments that could be identified as clypeasteroid, although echinoid fragments are very common. It is noteworthy that the small fibularids, like those found in the Paleocene of Africa, were absent but normally would be expected in this material. They usually live buried in this type of sediment and are small enough to have their tests preserved intact in these sands.

The earliest confirmed clypeasteroid, *Togocyamus*, occurs in the Paleocene of West Africa. It differs so markedly from all previous echinoids that there is disagreement as to its origin. Some workers consider the clypeasteroids to be derived from a holactypoid, but Phelan (1977, p. 419) makes a strong case for their derivation from a juvenile stage of a cassiduloid. Its evolution must have been extremely rapid and probably occurred within the Paleocene. The Late Cretaceous echinoid record is not only extensive but very well studied (Ernst 1972) and no intermediates have been found there. Current information indicates that the subsequent diversification and radiation of the clypeasteroids from a fibularid to a sand dollar occurred very abruptly (text-fig. 2) in the early part of the middle Eocene. Only two species, both fibularids, are known in the Paleocene: *Togocyamus*

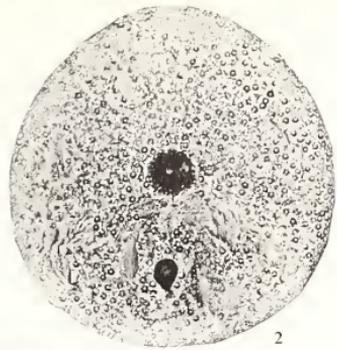
EXPLANATION OF PLATE 2

Figs. 1-3. *Sismondia logotheti* Fraas. Early Eocene, from Siout (= Assiout), Egypt. 1, 2, 3, top, bottom, side views of topotype B22908, Muséum National d'Histoire Naturelle, Paris, $\times 5$.

Figs. 4-6. *Periarchus lyelli* (Conrad). Middle Eocene, Castle Hayne Formation, from North Carolina Lime Company pit, adjacent to Tuckahoe Church, 3.8 miles (6.1 km) west of Comfort, Jones County, North Carolina. 4, 5, 6, side, top, bottom views of USNM 312506, $\times 1$.



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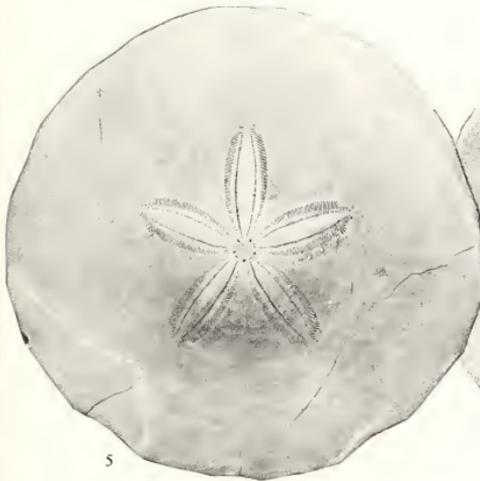
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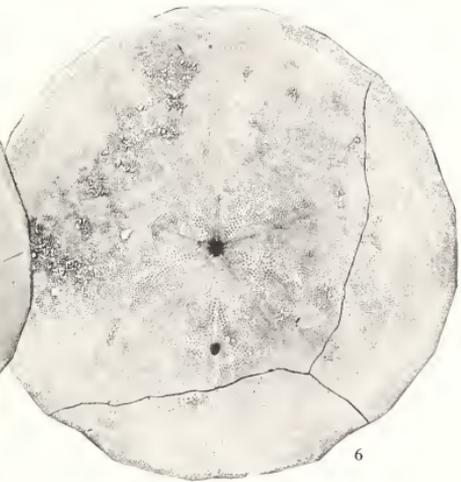
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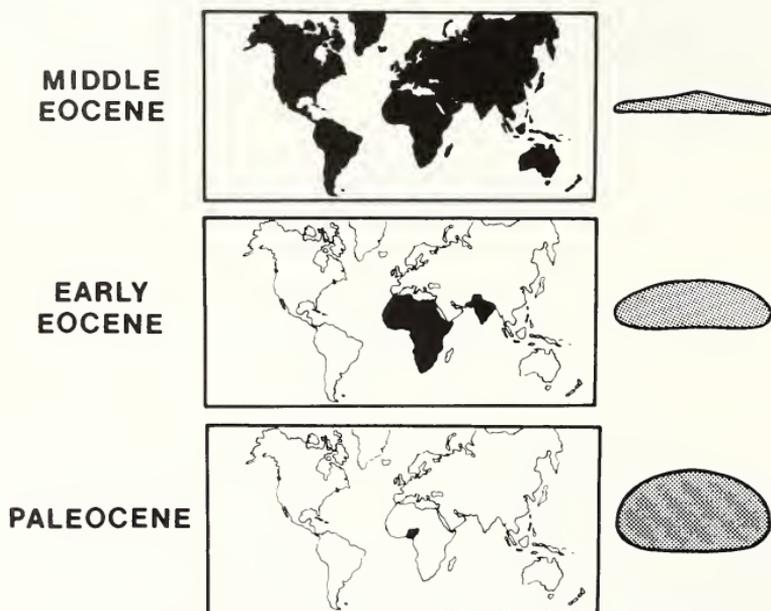
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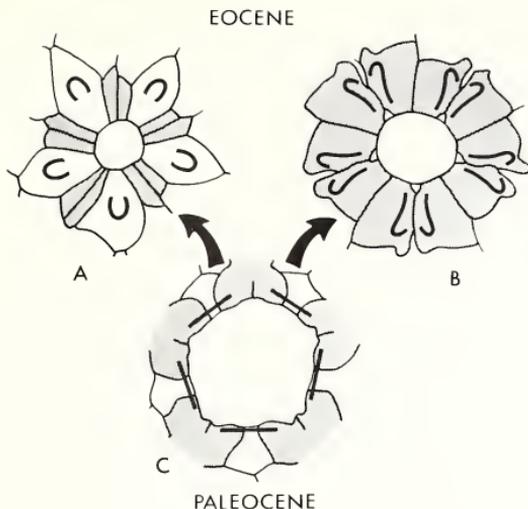
seefriedi (Oppenheim) and *T. alloiteaui* Roman and Gorodiski. During the early Eocene the clypeasteroids (text-fig. 2) were confined to Africa and India and consist of six species of fibularids and two species of *Sismondia*, the most primitive member of the laganids. By the end of the middle Eocene, the clypeasteroids had worldwide distribution with over 62 species representing 20 genera and 4 families.

In summary, the first clypeasteroid appeared in the Paleocene, and by the middle Eocene its far more complex and specialized descendants were present all around the world.



TEXT-FIG. 2. Evolution and radiation of the clypeasteroid echinoid. The Paleocene clypeasteroids are confined to West Africa and are a small, high species with incipient petals. In the early Eocene they are more flattened, have more-developed petals, and occur in Africa and India. By the middle Eocene they are fully developed sand dollars and are present all around the world.

The Cretaceous origin of the clypeasteroids was suggested by previous workers not only because of the supposed occurrence of Cretaceous species, but also because it was believed that the Palaeocene fibularids were not primitive enough to be ancestral to all later clypeasteroids. New information is now available on *Togocyamus*. It is more primitive than previously thought and could be close to the ancestral stock of all clypeasteroids. Although it has been assumed that its lantern supports were like those found in later fibularids with each support composed of a single interambulacral plate, the supports in *T. seefriedi* (Oppenheim) are both interambulacral and ambulacral in origin. Each support (text-fig. 3c) is formed by the extension of the primordial interambulacral plate and the adjacent half-ambulacral plates. This discovery is important for it has been suggested (Philip 1965, p. 58; Kier 1970, p. 105) that the clypeasteroids could be divided into two orders on the basis of the character of the lantern supports. The suborder Clypeasterina includes all those clypeasteroids



TEXT-FIG. 3. The lantern supports in the clypeasteroids. C, the oldest clypeasteroid, the Paleocene *Togocyamus seefriedi* (Oppenheim) has lantern supports (indicated by a solid line) composed of ambulacral (shaded) and interambulacral plates; A, B, Eocene clypeasteroids have lantern supports composed of interambulacral plates as in the suborder Scutellina (A) or ambulacral plates as in Clypeasterina (B).

having ambulacral lantern supports (text-fig. 3B); in the suborder Scutellina the supports are interambulacral (text-fig. 3A). The presence of supports, both interambulacral and ambulacral in origin, in the oldest known and most primitive clypeasteroid adds weight to the supposition that *Togocyamus* is close to the ancestral stock of both suborders. By simply reducing the size of the ambulacral extensions and increasing the size of the interambulacral ones, supports could be produced that are typical of later species of the fibularids and the rest of the Scutellina. Conversely, the reduction in the size of the interambulacral and increase in the ambulacral extensions would produce the typical Clypeasterina supports that first appear in the late Eocene.

A second discovery in *Togocyamus* is that its accessory pores are few in number and are restricted to the border of the ambulacra (Pl. 1, fig. 1). As pointed out by Durham (1966, p. U451), accessory pores are an exclusive feature of the clypeasteroids, occurring in all species. The fact that they are less well developed in this species than in any other is further evidence of the primitiveness of this form.

In the light of the primitive features of *Togocyamus*, we can now postulate the evolutionary history of the earliest clypeasteroids:

1. The Paleocene *Togocyamus* (Pl. 1, figs. 3-5) has a small, high test with its periproct in a primitive dorsal position, slightly developed petals with simple nonconjugate pores, a very erect lantern with supports of interambulacral and ambulacral origin. Its few accessory pores are confined to the borders of the ambulacra. It has no food grooves and has a large peristome.

2. By the early Eocene, *Sismondia* (Pl. 2, figs. 1-3) has a larger, more flattened test, a lower lantern, interambulacral lantern supports, and a ventral periproct. The petals are better developed with conjugate pores; the accessory pores are far more numerous.

3. The middle Eocene *Protoscutella* and *Periarchus* (Pl. 2, figs. 4–6) are typical sand dollars having a large, very flattened test, food grooves, very wide and low lantern, and a very small peristome. Accessory pores are spread all over the ambulacra, and the test is strongly reinforced by calcareous supports that are pierced by many canals for the water vascular system serving these pores. The adoral plate arrangement is now distinctive; there are far fewer and larger plates than in earlier clypeasteroids. As pointed out by Durham (1966, p. U450), these changes in the adoral plates result from the flattening of the test. In flattened species the number of plates on the adoral surface is determined at an early ontogenetic stage and thereafter growth is only by enlargement of the plates.

The morphological changes that produced the sand dollar are specializations that enabled the echinoid to live more efficiently in sand (Seilacher 1979). The flattened test made it easier for the echinoid to burrow. The accessory tube-feet were used to pass sand over the top of the test and to convey food to the food grooves. The better-developed petals increased the respiratory capability of the petaloid tube-feet by increasing their area. The internal supports strengthened the test, enabling the sand dollar to live in environments of higher energy. The change from the erect lantern and large peristome in the primitive fibularid to the low lantern with horizontal teeth and small peristome in the sand dollar reflects a change in eating habits. According to Märkel (1974, 1978; Märkel, Gorny, and Abraham 1977) and Nichols (1959), the fibularid uses its lantern to scrape organic material from sand grains. This feeding method puts little stress on the teeth. The sand dollar, however, uses the teeth for grinding and chewing. The great stress can be withstood because the teeth are horizontal, and the stress is transmitted to the long axis of the teeth. The larger peristome in the fibularid permits the teeth to extend further out of the test to grasp food; in the sand dollar the sand is passed to the teeth within the test.

If it is true, as suggested herein, that the clypeasteroids originated in the Paleocene then all these changes necessary to derive a sand dollar from a cassiduloid ancestor occurred within 20 million years. Certainly there can be little question that the evolution from a fibularid to a typical sand dollar occurred between the beginning of the early Eocene and the latter part of the middle Eocene, a period of less than 10 million years.

CONCLUSIONS

The sudden appearance of the first irregular and the first clypeasteroid echinoids and their rapid diversification indicate a rate of evolution much faster than previously supposed. The mechanisms producing these great changes are uncertain, but the evolutionary steps must have been large. If each speciation event produced only small morphological change, than a multitude of transitional species would have resulted. The fossil record of the irregular echinoids is excellent (Kier 1977a). Even if this rapid evolution occurred in peripherally isolated populations, somewhere in the world we should have found more of these transitional species. I believe the absence of a large number of transitional species is explained not because they have not been preserved as fossils, but because they never existed. This conclusion supports Stanley's (1979, p. 212) statement that 'rates of evolution are highest early in adaptive radiation, when degree of divergence per speciation event is high . . . '.

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THE PALAEOBIOLOGY OF THE CRETACEOUS IRREGULAR ECHINOIDS *INFULASTER* AND *HAGENOWIA*

by ANDREW S. GALE and ANDREW B. SMITH

ABSTRACT. The taxonomy of the infaunal holasteroids *Infulaster* and *Hagenowia* is revised in the light of new material from the Senonian Chalk of southern England. Investigation of the plating structure in *Hagenowia* permits a more precise definition of its species, and a better understanding of the evolution of the rostrum. The majority of structural modifications in the *Infulaster-Hagenowia* lineage were caused directly, or indirectly, by apical elongation and size reduction. A detailed study of test and ambulacral pore morphology, tuberculation, and spines, taken in comparison with living echinoids, allows reconstruction of the life habits of *Infulaster* and *Hagenowia*. The evolutionary changes are related to the adoption of a specialized method of feeding and an attempt to avoid predation.

THE echinoid genus *Hagenowia*, in which the apical part of the test is drawn out to form a rostrum, is the most bizarre of a wide range of holasteroids which inhabited the Upper Cretaceous Chalk Sea of north-west Europe. The ancestry of this genus was traced by Wright and Wright (1949) to *Infulaster*, and the evolutionary story further discussed and elaborated by Ernst and Schulz (1971).

The Upper Chalk in England falls into two distinct faunal provinces, the boundary of which ran approximately east-west through north Norfolk (Peake and Hancock 1961; Reid 1976; Rawson *et al.* 1978). *Infulaster* and *Hagenowia* have been regarded as characteristic members of the northern province fauna (where they occur commonly) and recorded hitherto only as occasional rarities in the south. *Hagenowia* is the most common fossil in one interval of the Yorkshire Upper Chalk and has been used there as a local zonal index in place of *Micraster coranguinum* (Rowe 1904; Wright and Wright 1942).

Collecting during recent years from the Senonian Chalk of south-east England has yielded abundant material of both genera and shows that they occur frequently at certain stratigraphical levels in at least part of the southern province. This material has provided much new information (particularly concerning the rostrum of *Hagenowia*) which has allowed a reappraisal of the taxonomy and phylogeny of *Infulaster* and *Hagenowia*.

Irregular echinoid lineages in the Chalk have provided a number of classical evolutionary stories, of which the best known is in *Micraster* (Rowe 1899). Progressive morphological changes in *Micraster* were interpreted by Nichols (1959) as adaptations to an increasing depth of burial. A similar explanation has been advanced for the *Infulaster-Hagenowia* story (Nichols 1959; Ernst and Schulz 1971). Our work suggests that changes in this lineage, particularly the development and modification of the rostrum, are related to the adoption of a specialized method of feeding, and avoidance of predation.

METHODS OF STUDY

Although the surface details of *Infulaster* and *Hagenowia* from southern England are often well preserved, the tests are invariably distorted by compactional crushing. For this reason, biometrical studies on the material have not been attempted.

In a detailed study of the rostrum of *H. elongata* (Nielsen) Schmid (1972) used a special technique to elucidate the plating structure. This took advantage of the naturally separate reflectivity of

individual plates, accentuated by gold coating. This method proved to be effective on *H. blackmorei* Wright and Wright, but unsuccessful on earlier members of the genus. To work out the plating arrangements of these, naturally weathered rostra were stained with black ink to pick out the sutures. Surface details of the echinoids, particularly tubercles and pores, were studied with the scanning electron microscope

Abbreviations used for museum collections are as follows: BMNH—British Museum (Natural History); IGS—Institute of Geological Sciences, London; MMH—Mineralogical-Geological Museum, Copenhagen.

STRATIGRAPHY

In this paper the usage of stages and zones within the Upper Chalk of England have been adopted from Rawson *et al.* (1978). Text-fig. 1 gives a generalized succession of all but the lowest Senonian in east Kent, and is based on the cliff sections between Dover and Kingsdown, and on the Isle of Thanet. The section is abstracted from detailed measurements made by one of us (A. S. G.) and gives only selected marker horizons, to which records of species are related.

Details of the distribution of *Infulaster* and *Hagenowia* in north-west Germany are taken from Ernst and Schulz (1971, 1974). In connection with this, it is important to note that the Turonian-Coniacian boundary in Germany is taken at a different level from that generally used in England, where the *Holaster planus*-*Micraster cortestudinarium* zonal junction is taken as the stage boundary (Rawson *et al.* 1978). The base of the Coniacian in the German sense probably falls within the basal few metres of the *coranguinum* Zone at Dover, on the basis of evidence from *Inoceramus* faunas.

SYSTEMATIC PALAEOLOGY

Order HOLASTEROIDA Durham and Melville, 1957

Family HOLASTERIDAE Pictet, 1857

Genus INFULASTER Desor, 1858

Type Species. *Cardiaster hagenowi* d'Orbigny 1853 (= *Spatangus excentricus* Woodward 1833; see Wright and Wright 1949, p. 455).

Diagnosis. Small to medium-sized holasterids, proportionately narrow and tall, with apex positioned anteriorly. Anterior ambulacrum set in a sulcus which runs from the apex to the transversely rounded peristome on the adoral surface. Paired ambulacra flush with test, non-petaloid. Apical system uninterrupted, elongated, with four genital pores. Periproct situated at summit of steep posterior truncation. Plastron metasternal, weakly keeled. Marginal fasciole present.

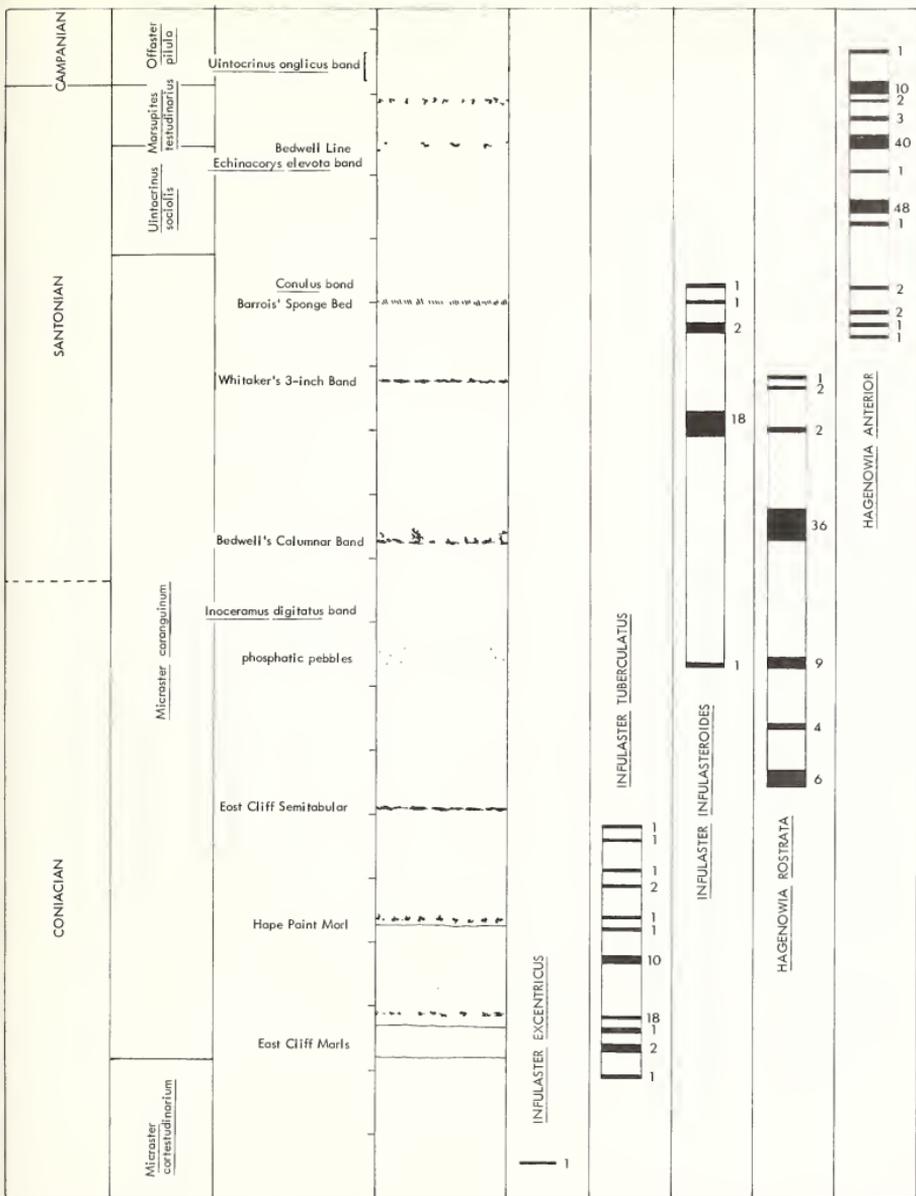
Remarks. The diagnosis given above essentially follows the description of *Infulaster* given by Wright and Wright (1949), with some elaboration.

Wright and Wright (1949) regarded *I. excentricus* as the only valid species of *Infulaster*, and placed *I. krausei* Desor, *I. borcharidi* Desor, *I. hagenowi* (d'Orbigny), and *I. tuberculatus* Valette in synonymy with it. *I. tuberculatus* is here considered to be a separate species, and its descendant, *Hagenowia infulasteroides* Wright and Wright is transferred to *Infulaster*. This species displays a number of features previously thought to be exclusive to *Hagenowia*, notably interruption of the pastron and elongation of the dorsolateral plate columns. *Infulaster* thus differs from *Hagenowia* only in its uninterrupted apical system and lack of a rostrum.

Infulaster excentricus (Woodward, 1833)

Text-fig. 2 (1)

Remarks. Large forms of *Infulaster* occur commonly in the Middle and Upper Turonian of the northern province in England (north Norfolk, Lincolnshire, Yorkshire) and in the eastern extension of the province in north-west Germany (Ernst and Schulz 1971), Poland (Nietsch 1921) and the Caucasus (Moskveena 1959). For these, the name *I. excentricus* is used provisionally, and it is not intended in this paper to revise and redescribe this material, which may include more than one species.



TEXT-FIG. 1. Generalized succession in the Senonian Chalk (lowest beds omitted) of the Kent coast, with selected marker bands only, showing the distribution of species of *Infulaster* and *Hagenowia*. Scale on left of column in 5 m intervals. Flints solid black.

Only one specimen of *I. excentricus* is known from southern England, from the Coniacian *M. cortestudinarium* Zone at Dover, 3·2 m below the Lower East Cliff Marl (text-fig. 2 (1); BMNH E76832, A. S. Gale Coll.)

Infulaster tuberculatus Valette, 1913

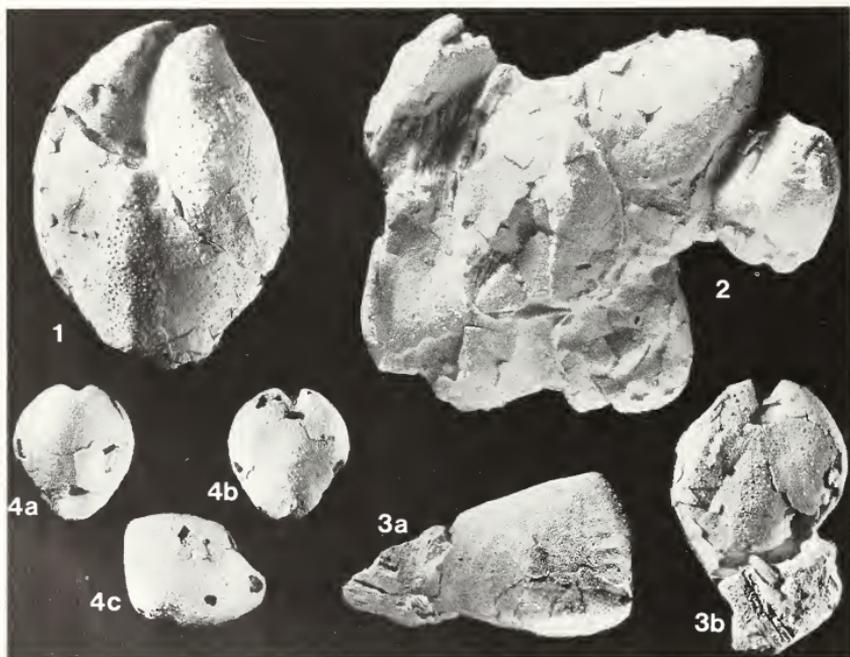
Plate 4, figs. 2, 11; Plate 5, fig. 3; Plate 6, fig. 5; text-fig. 2 (2-4)

1913 *Infulaster tuberculatus* Valette, p. 5, fig. 1.

p. 1949 *Infulaster excentricus* (Woodward) Wright and Wright, p. 456.

Holotype. Valette's solitary specimen came from the Coniacian zone H, of Rosoy near Sens, France. The specimen is presumably with Valette's collection, now in the University of Dijon.

Diagnosis. Small *Infulaster* in which the test is short and proportionally tall. The apex may be acutely angled. Plastron uninterrupted by ambulacra I, V.



TEXT-FIG. 2. *Infulaster* spp. from east Kent: 1, *Infulaster excentricus* (Woodward), oral view, from 3·2 m below summit of *Micraster cortestudinarium* Zone, East Cliff, Dover. BMNH E76832 A. S. Gale Coll. 2-4, *I. tuberculatus* Valette. 2, group of specimens from basal *M. coranguinum* Zone, 0·8 m above Upper East Cliff Marl, cliffs north-east of St. Margaret's Bay, near Dover, Kent. BMNH E76833, A. S. Gale Coll. 3a, b, oral and lateral views of individual without stratigraphical location, east of Dover, Kent. BMNH E10300 Cockburn Coll. 4a-c, dorsal, oral, and lateral views of specimen from 0·5 m below Lower East Cliff Marl, top of *M. cortestudinarium* Zone, East Cliff, Dover, Kent. BMNH E76834, A. S. Gale Coll. All specimens $\times 2$. Coated in ammonium chloride.

Remarks. Small *Infulaster* with lengths of 10–20 mm are common in the Lower *coranguinum* Zone of east Kent. These are almost invariably crushed and fragmentary, but the few well-preserved individuals show close similarities in shape with Valette's figures of *I. tuberculatus*. The species differs from *I. excentricus* in having a proportionally shorter test with a steep posterior slope in addition to the consistent difference in size. Many individuals are slightly inflated just posterior to the apex. Specimens from the higher part of the range of the species at Dover, although distorted, have acutely angled apices, and can only be distinguished from *I. infulasteroides* (Wright and Wright) by their uninterrupted plastrons.

Occurrence. At Dover the species occurs in the highest 1.5 m of the *M. cortestudinarium* Zone, and the basal 18 m of the *M. coranguinum* Zone (text-fig. 1). The species is most common just beneath a band of large flints about 1 m above the upper East Cliff Marl, where clusters of individuals are found. The type specimen came from the Coniacian H of Rosoy, a level equivalent to approximately the lower half of the *coranguinum* Zone.

Infulaster infulasteroides (Wright and Wright 1949)

Plate 4, fig. 2

1949 *Hagenowia infulasteroides* Wright and Wright, p. 470, figs. 17, 18.

1971 *Hagenowia infulasteroides* Wright and Wright; Ernst and Schulz, p. 138, pl. 13, figs. 1–4; text-fig. 6.

Types. The holotype is a flint steinkern from the Haldon Gravel of Devon (Wright and Wright 1949, fig. 17; BMNH E8403). A paratype, similarly preserved, comes from flint gravel at Lulworth, Dorset (BMNH E1709). Both were probably derived originally from the upper part of the *coranguinum* Zone. A second paratype, a crushed, incomplete test from the *coranguinum* Zone of the North Foreland, near Broadstairs, Kent (BMNH E33886, Rowe Coll.) almost certainly came from a level 2–4 m below Whitaker's 3-inch band, the only horizon at which the species is common in east Kent.

Diagnosis. Test with acutely angled apex. Plates of interambulacra 1 and 4 on sides of test elongated. Plastron interrupted by ambulacra I and V.

Remarks. This species is transferred from *Hagenowia* to *Infulaster* on account of its undivided apical system, and the absence of a rostrum. The general morphology and variation is well illustrated by Ernst and Schulz (1971).

Occurrence. In east Kent *I. infulasteroides* ranges from 10 m below Bedwell's Columnar Band, up to the base of the *Uintacrinus* Zone (text-fig. 1). It is only common 2–4 m below Whitaker's 3-inch band, where it occurs in clusters. *I. infulasteroides* is also known from the upper *coranguinum* Zone of Berkshire, Hampshire, Sussex and the Isle of Wight, and the *Uintacrinus* Zone of Hampshire. Ernst and Schulz (1971) record this species from the Middle Santonian of Lagerdorf.

Genus HAGENOWIA Duncan, 1889

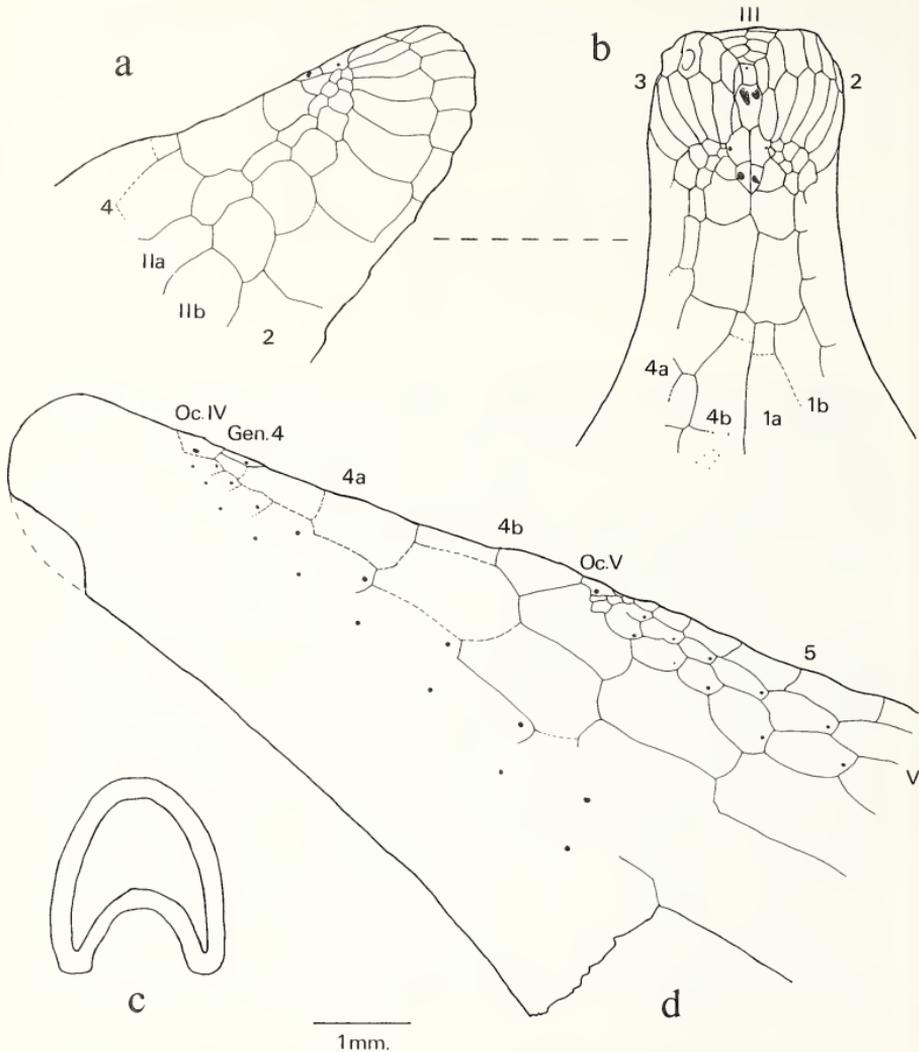
(= *Martinosigra* Nielsen, 1942)

Type species. *Cardiaster rostratus* Forbes 1852 by original designation.

Diagnosis. Small holasterids in which the apical part of the test is elongated antero-dorsally to form a tapering rostrum. Narrow, well-defined sulcus runs from apex of rostrum to circular peristome. Apical system disjunct, with two posterior oculars at base of rostrum separated from remainder of system (which is on rostral tip) by interambulacra 1 and 4. Two or four genital pores.

Longitudinally oval periproct is positioned at the summit of the posterior truncation. Plastron metasternal, keeled. Marginal fasciole.

Remarks. The diagnosis of *Hagenowia* is amended from that of Wright and Wright (1949), to exclude *I. infulasteroides* from the genus. The most important diagnostic feature of *Hagenowia* is



TEXT-FIG. 3. Plating structure and cross-sectional shape of the rostrum in *Hagenowia rostrata* (Forbes): *a* and *b*, dorsal and lateral views of a small individual from 1 m above Bedwell's Columnar Band, East Cliff, Dover. BMNH E76835, A. S. Gale Coll. *c*, cross-section of the rostrum, taken at the 3rd plate of interambulacral row 1*b*. Specimen from 1.5 m above Bedwell's Columnar Band, Ramsgate. BMNH E76836, A. S. Gale Coll. *d*, lateral view of specimen from 2 m above the East Cliff Semitabular, East Cliff, Dover. BMNH E76837, A. S. Gale Coll.

the separation of the apical system. Interruption of the plastron by ambulacra I and V is seen in all *Hagenowia* and is also present in *I. infulasteroides*.

Hagenowia rostrata (Forbes, 1852)

Plate 3, figs. 1-5; Plate 4, fig. 3; Plate 5, figs. 1, 2, 5; text-figs. 3, 4

1852 *Cardiaster rostratus* Forbes, p. 3, pl. 10, figs. 19-24.

1858 *Infulaster rostratus* (Forbes); Desor, p. 348.

1881 *Infulaster rostratus* (Forbes); Wright, p. 307, pl. 70, figs. 2, 3.

1889 *Hagenowia rostrata* (Forbes); Duncan, p. 210.

1942 *Martinosigra rostrata* (Forbes); Nielsen, p. 163.

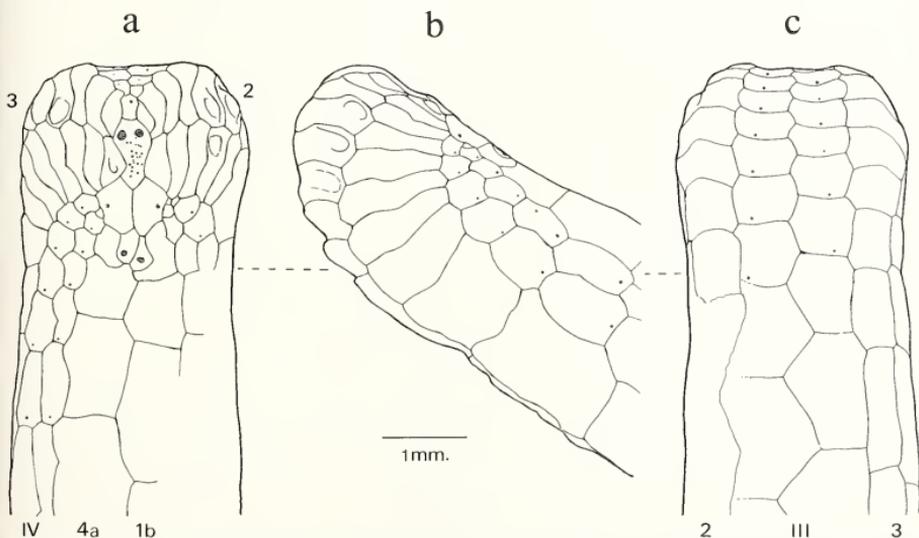
1949 *Hagenowia rostrata* (Forbes); Wright and Wright, p. 462, figs. 7, 8, 11, 12, non 9, 10.

1971 *Hagenowia rostrata* (Forbes); Ernst and Schulz, p. 138, pl. 13, fig. 5; pl. 14, fig. 1; text-fig. 7.

Lectotype. A specimen figured by Forbes (1852, pl. 10, figs 19-21; IGS 38656) was taken as lectotype by Wright and Wright (1949). This came from the 'Chalk with Flints of Bostal Heath, near Plumstead' (Forbes 1852, p. 3), in south-east London, presumably from the upper part of the *coranguinum* Zone.

Diagnosis. Rostrum short, sharply tapering; plates of ambulacral rows IIa, IVb contiguous, not reduced; posterior side of rostrum broad, evenly rounded; sulcus deep; subanal protruberance double, asymmetrical.

Remarks. The plating arrangements of the rostrum is completely known only in this species of *Hagenowia* (text-figs. 3, 4). Oculars I and V are small, and positioned at the base of the rostrum. Together with ambulacra I and V, and interambulacrum 5, they are separated from the rest of the apical system along the dorsal margin of the rostrum by interambulacra 1 and 4 (text-fig. 3). The



TEXT-FIG. 4. Plating structure of the rostrum tip in *Hagenowia rostrata* (Forbes): a-c, Dorsal, lateral, and frontal views of large specimen from 3 m below Whitaker's 3-inch band, North Foreland, near Broadstairs, Kent. BMNH E76838, A. S. Gale Coll.

first two plates of interambulacral rows 1a and 4b meet along the dorsal margin of the rostrum above oculars I and V. The second plates are often slightly swollen in lateral profile and form a distinct, low protuberance at the base of the rostrum (e.g. Pl. 3, fig. 2b). 1a and 4b are occluded from the rostrum above this level by two or three plates of the outer rows, 1b and 4a.

Variations in test shape of *H. rostrata* is shown by a group of specimens from the upper *coranguinum* Zone of the Kent coast (Pl. 3, figs. 1-5). Low, depressed forms with relatively high anterior angles (Pl. 3, fig. 1) intergrade continuously through to tall individuals with steep sides and more upright rostra (Pl. 3, fig. 2). No stratigraphical separation of these forms is known to occur. Small individuals of *H. rostrata* have shorter, less well demarcated rostra (Pl. 3, fig. 4).

Ernst and Schulz (1971, p. 138, text-fig. 7, fig. 1) recorded a stratigraphically low 'early form' of *H. rostrata* from the (? Lower) Coniacian of Lagerdorf, north-west Germany. This has a short posterior slope, a short rostrum, and a flat profile to the base. A single specimen (Pl. 3, fig. 5) from the lowest horizon at which *Hagenowia* occurs at Dover, some 2 m above the East Cliff Semitabular flint (text-fig. 1) compares quite well in lateral profile with the figured Lagerdorf individual. The Dover specimen differs from other English examples of *H. rostrata* in having a broad, relatively shallow sulcus without narrow margins. In anterior profile, the sides of the test do not inflect sharply as the body passes into the rostrum.

Occurrence. On the Kent coast (text-fig. 1) *H. rostrata* is found in a succession of discrete bands in the *coranguinum* Zone, from the East Cliff Semitabular to Whitaker's 3-inch band. It occurs in the same zone throughout its outcrop in southern England, although precise details of horizon are seldom recorded. In northern France a solitary example was found 3 m below the equivalent of Whitaker's 3-inch band at Coquelles, near Calais (A. S. G. Coll.). In Yorkshire, Rowe (1904) used *H. rostrata* as a local index for the *M. coranguinum* Zone, which was subsequently formalized by Wright and Wright (1942). Recent study has shown that the species of *Hagenowia* common in the flintless chalk of the Yorkshire coast below the entry of *Uintacrinus* is, in fact, *H. anterior*. The only true *H. rostrata* we have seen from Yorkshire are from the flinty chalk with *Inoceramus involutus* of Little Weighton (Wrights' Coll.). In north-west Germany *H. rostrata* occurs in the Coniacian Chalk at Lagerdorf (Ernst and Schulz 1971, text-fig. 5; 1974, text-fig. 4a).

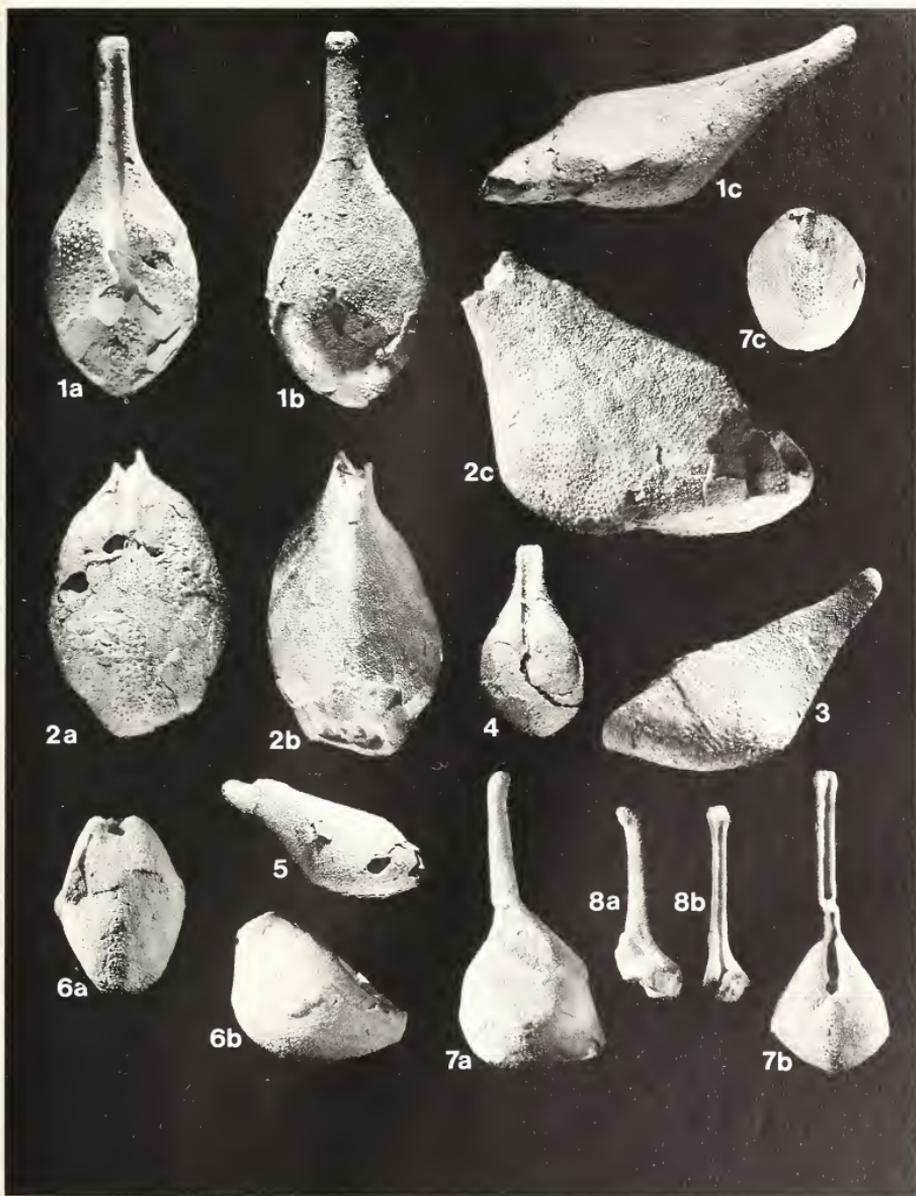
EXPLANATION OF PLATE 3

Figs. 1-5. *Hagenowia rostrata* (Forbes). *Micraster coranguinum* Zone, Kent coast. 1a-c, oral, dorsal, and lateral views of depressed specimen from 3 m beneath Whitaker's 3-inch band, North Foreland near Broadstairs. BMNH E76838, A. S. Gale Coll. 2a, b, oral and lateral views of high individual, with more vertical rostrum, retaining radioles on the base from 2 m above Bedwell's Columnar Band, same locality. BMNH E76848, A. S. Gale Coll. 3, lateral view of specimen, same horizon and locality. BMNH E76849, A. S. Gale Coll. 4, small individual with short rostrum, 1 m above Bedwell's Columnar Band, East Cliff, Dover. BMNH E76835, A. S. Gale Coll. 5, lateral view of specimen with poorly demarcated rostrum. 2 m above East Cliff Semitabular, East Cliff, Dover. BMNH E76850, A. S. Gale Coll.

Fig. 6a, b. *H. anterior* Ernst and Schulz. Oral and lateral views of body. The rostrum has broken off, and its base is bored. *Uintacrinus* Zone, Harding's Whiting Pits, Devizes Road, Salisbury Wilts. BMNH E35788, Blackmore Coll.

Figs. 7, 8. *H. blackmorei* Wright and Wright. 7a-c, lateral, frontal, and oral views of the holotype (body only). The rostrum belongs to *H. anterior* and has been artificially attached. Lower Campanian, probably lower *G. quadrata* Zone, West Harnham, near Salisbury, Wilts. BMNH E33916, Blackmore Coll. 8a, b, lateral and frontal views of rostrum from *Hagenowia* horizon, lower *G. quadrata* Zone, pit no. 3 of Gaster (1924), North Lancing, near Worthing, Sussex. I.G.S. no. Zm 2907.

All specimens $\times 2$. Coated with ammonium chloride.



GALE and SMITH, Cretaceous irregular echinoids

Hagenowia anterior Ernst and Schulz, 1971

Plate 3, fig. 6; Plate 4, figs. 5, 10, 12; Plate 5, figs. 6, 8; Plate 6, figs. 2, 6, 8; text-fig. 5

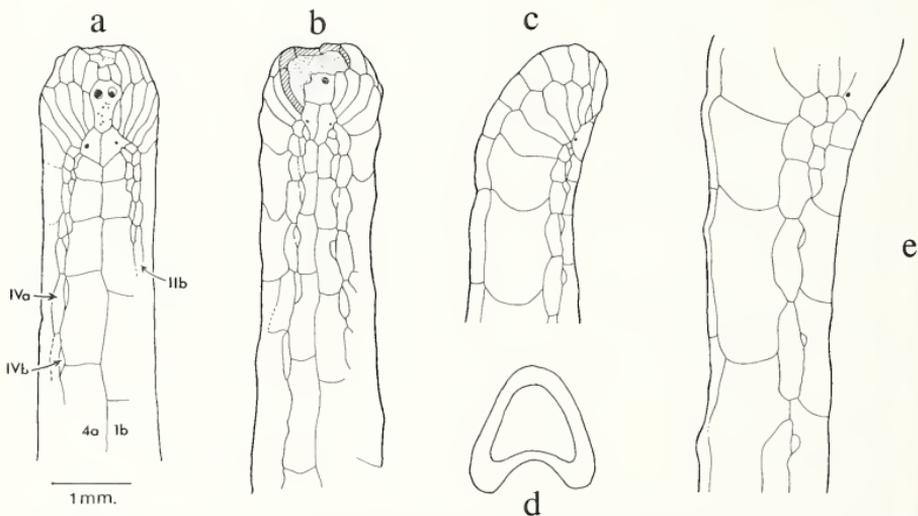
1949 *Hagenowia rostrata* (Forbes); Wright and Wright, p. 462, figs. 9, 13.

1971 *Hagenowia blackmorei* Wright and Wright, *anterior* Ernst and Schulz, p. 140, pl. 13, fig. 6; pl. 14, figs. 2, 3; text-fig. 8.

Types. The holotype is from the Middle Santonian *rogalae-westfalica* Zone of Lagerdorf, north-west Germany (Ernst and Schulz 1971, text-fig. 8, fig. 1; pl. 14, figs. 2, 3). The paratypes are from the same horizon and locality.

Diagnosis. Rostrum long and slender, cross-section triangular, posterior side evenly rounded; individual plates of ambulacral rows IIa, IVb small, separated by interambulacral rows 1a, 4b and ambulacral rows IIb, IVa in the rostrum; subanal protruberance single, narrow.

Remarks. The plating arrangement of all but the basal rostrum is known in this species (text-fig. 5). Individual plate rows are proportionately longer and narrower than in *H. rostrata*. At least six plates of interambulacral rows 1a, 4b meet along the dorsal margin of the rostrum (text-fig. 5b); these are variable in width. Plates of ambulacral rows IIa and IVb are small, and although the first few are usually in contact with each other, most are separated by 1a and 4b, and IIb, IVa (text-fig. 5A-C, E). The size and shape of these occluded plates is variable. In some individuals (e.g. text-fig. 5f) plates of IIa and IVb are locally separated by interambulacra 1a, 4b and 2a, 3b. Genitals 1 and 4 are absent.



TEXT-FIG. 5. Plating structure and cross-sectional shape of the rostrum in *Hagenowia anterior* Ernst and Schulz: a, dorsal view of rostrum from 5 m above Whitaker's 3-inch band, Kingsgate, Kent. BMNH E76839, A. S. Gale Coll. b, dorsal view of rostrum from basal 1 m. of *Marsupites* Zone, Minnis Bay, Kent. BMNH E76840, A. S. Gale Coll. c, lateral view of rostrum tip, mid *Uintacrinus* Zone, near Margate, Kent. BMNH E76841, A. S. Gale Coll. d, cross-section of rostrum, taken at 2nd/3rd plate of interambulacral row 1b, mid *Uintacrinus* Zone, near Margate. e, lateral view of rostrum, base of *Uintacrinus anglicus* band, Foreness Point, near Margate. BMNH E76842, A. S. Gale Coll.

Some variation in the attitude of the rostrum occurs in *M. anterior*, although the body shape is quite consistent. Lateral furrows on the sides of the test, just anterior to the periproct (Ernst and Schulz 1971, text-fig. 8, figs. 2, 3) are sometimes present. *H. anterior* is raised to specific rank on account of significant differences in rostral structure and body shape from *H. blackmorei*.

Occurrence. In east Kent the species first appears at 3.5 m above Whitaker's 3-inch band in the *coranguinum* Zone and ranges up into the *Uintacrinus anglicus* band in the lower *Offaster pilula* Zone (text-fig. 1). Levels of abundance occur in the mid *U. socialis* Zone and in the basal *Marsupites* Zone. Scattered records of this species exist from Dorset, Wiltshire, Hampshire, and the Isle of Wight (*Uintacrinus* Zone). In Yorkshire *H. anterior* occurs commonly in the flintless upper part of the *coranguinum* Zone and ranges up into the lower Campanian *I. lingua* Zone. At Lagerdorf the species ranges from the mid *rogalae-westfalica* Zone to the *Marsupites* Zone, with one doubtful earlier record from the *coranguinum-westfalica* zone (Ernst and Schulz 1971, 1974).

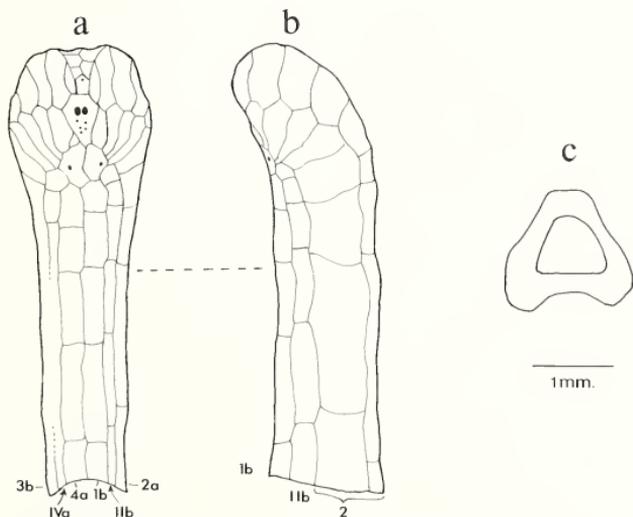
Hagenowia blackmorei Wright and Wright, 1949

Plate 3, figs. 7, 8; Plate 4, fig. 6; Plate 6, figs. 4, 7, 9; text-fig. 6

1949 *Hagenowia blackmorei* Wright and Wright, pp. 467-70, figs. 14-16.

1971 *Hagenowia blackmorei blackmorei* Wright and Wright; Ernst and Schulz, p. 140, text-fig. 2.

Types. The specimen chosen as holotype by Wright and Wright (1949, fig. 14) is from the Lower Campanian Chalk of East Harnham, near Salisbury, Wiltshire (BMNH E33916, Blackmore Coll.), probably from the *G. quadrata* Zone. However, as pointed out by C. J. Wood (*in* Ernst and Schulz 1971), the body and rostrum belong to two specimens of separate species, and have been artificially joined. The body belongs to the species



TEXT-FIG. 6. Plating structure and cross-sectional shape of the rostrum in *Hagenowia blackmorei* Wright and Wright: a, b, dorsal and lateral views of rostrum, based on specimen from 10 m. above *planoconvexa* bed, *G. quadrata* Zone, cliffs west of Newhaven, Sussex. BMNH E76843, A. S. Gale Coll. c, cross-section of rostrum 3 mm below tip, same horizon and locality.

characteristic of the lower *quadrata* Zone of southern England, and possesses the features of *H. blackmorei* as described by Wright and Wright. The rostrum is from an individual of *H. anterior* from the Santonian. The body alone is therefore selected as lectotype. The paratype is an internal and external mould in flint from the Haldon Gravel, Devon (Wright and Wright 1949, figs. 14, 15; BMNH E8404, Vicary Coll.).

Diagnosis. Rostrum slender, upright, well demarcated from body, equilaterally triangular in cross-section; interambulacral rows 1a, 4b form narrow dorsal ridge on rostrum, surface of ambulacral rows IIb, IVa slightly inset; sulcus shallow, with a gently concave floor; IIa, IVb not present in rostrum; body squarish in lateral profile, anterior part of base vertically below peristome; subanal protuberance single, small; posterior slope steep; fasciole noticeably oblique.

Remarks. The structure of the rostrum in this species (text-fig. 6) is similar to that in *H. elongata* (Nielsen) (Schmid 1972) but individual plates are less elongated and broader than in the Maastrichtian species. The dorsal ridge on the rostrum is broader and less sharply defined than in *H. elongata*, and genitals 2, 3 are not usually separated from oculars II, IV in *H. blackmorei*, as is invariably so in *H. elongata*. The latter species has only two, vertically situated, madreporic pores, whereas the number and arrangement of these is variable in *H. blackmorei*.

A few *Hagenowia* rostra are known from the Upper Campanian *Belemnitella mucronata* Zone of southern England (Wright and Wright 1949). These show affinities with both *H. blackmorei* and *H. elongata*, but lack the specialized madreporic pores of the latter and are referred to *H. cf. blackmorei*.

Occurrence. *H. blackmorei* appears to be restricted to the lower part of the *G. quadrata* Zone in southern England. Gaster (1924) used the term *Hagenowia* horizon for this level in Sussex. Collecting from the cliffs west of Newhaven in Sussex suggests that the species occurs only within the 12 m of chalk above the marl pair (*planoconvexa* bed) taken by Brydone (1914) as the base of the *G. quadrata* Zone. The species is only abundant in the interval from 9–11 m above this bed, where approximately fifty specimens have been found. Blackmore's material from East Harnham lacks detailed stratigraphical location, but probably came from the correlative horizon.

Hagenowia elongata (Nielsen, 1942)

Plate 4, figs. 4, 7–9; Plate 5, figs. 7, 9; Plate 6, figs. 1, 3, 10

1942 *Martinosigra elongata* Nielsen, p. 163, fig. 2.

1949 *Hagenowia rostrata* (Forbes); Wright and Wright, p. 462.

1950 *Hagenowia elongata* (Nielsen); Mortensen, p. 97, fig. 100.

1971 *Hagenowia elongata* (Nielsen); Schmid, in Ernst and Schulz, p. 141, text-fig. 2, cl.

1972 *Hagenowia elongata* (Nielsen); Schmid, p. 179, pls. 1–4; text-figs. 1, 2.

Diagnosis. Plate rows in rostrum very long and narrow; genitals 2 and 3 separated from oculars II and IV by interambulacral rows 2a, 3b; madreporite with only two, vertically situated, pores; sulcus shallow, flat.

Remarks. Now that the rostral structures of preceding species of *Hagenowia* are known, it is necessary to modify the interpretation of this species from Schmid (1972). Instead of representing both plate rows of ambulacra II and IV, the four rows of plates on the dorsal side of the rostrum are IIb, IVa (outer rows) and 1b, 4a (inner rows). There is little else to add to Schmid's excellent description of the species. The outline of a body stated to belong to this species was shown by Ernst and Seibertz (1977, text-fig. 6), but this new material awaits detailed description and figuring.

Occurrence. Upper Lower Maastrichtian, Zone of *Belemnella occidentalis*, Denmark and north-west Germany.

PHYLOGENY

Wright and Wright (1949) suggested that *I. infulasteroides* arose from the 'small *I. excentricus*' of the *costestudinarium* Zone (here *I. tuberculatus*) and subsequently gave rise to *H. rostrata*. They regarded *H. blackmorei* as a short-lived offshoot from *H. rostrata*, which itself survived into the Upper Campanian. Ernst and Schulz (1971, p. 141, text-fig. 2) modified this story only slightly, by placing the origin of *H. rostrata* near the point at which an *infulasteroides* lineage diverged from the main *Infulaster* stock. They retained separate *rostrata* and *blackmorei* lineages throughout the Santonian and Campanian. More recently, Ernst and Seibertz (1977, p. 563, text-fig. 6) showed the *H. rostrata* lineage as terminating within the Middle Santonian.

It is suggested here that only two lineages are recognizable in this group of echinoids.

1. *Infulaster* lineage: *I. excentricus* (*sensu lato*)—*I. tuberculatus*—*I. infulasteroides*
2. *Hagenowia* lineage: *H. rostrata*—*H. anterior*—*H. blackmorei*—*H. elongata*.

Since *Hagenowia* appeared before *I. tuberculatus* gave rise to *I. infulasteroides*, it is likely that the origins of this genus lay in the former species, probably during the mid-Coniacian. In this case, *I. infulasteroides* parallels rather than antecedes *Hagenowia* in the development of an acutely angled apex and an interrupted plastron.

Although the over-all changes in each of the lineages are progressive, individual species are in general well demarcated from both ancestor and descendant. No two species in either lineage are known definitely to overlap in stratigraphical order.

EVOLUTIONARY TRENDS

1. *Size*. In the *Infulaster* lineage there is a dramatic decrease in size from *I. excentricus*, which is characteristically between 40 and 50 mm in length, to *I. tuberculatus* (15–25 mm). With this change, the test became proportionately shorter and deeper. In late *I. tuberculatus* and in *I. infulasteroides* the apex of the test became more acutely angled resulting from an increase in the length of plate rows on the sides of the test.

2. *Rostrum*. In *Hagenowia* the apical system is separated into two parts to form a trivium and bivium. This was a direct consequence of the considerable elongation of the apical region.

In the earliest species, *H. rostrata*, oculars I and V are separated from genitals 1 and 4 by interambulacral rows 1 and 4 along the dorsal side of the rostrum. Plate rows 1a and 4b are occluded from the distal rostrum by rows 1b and 4a, which meet along the dorsal mid-line. Rostral plates are elongated, the sulcus is deep, and the body cavity within the rostrum is large. In profile, the rostral tip is only slightly enlarged.

In *H. anterior* the rostrum is better demarcated from the body and is relatively narrow. Plate rows are proportionally narrower and more plates per row are present in the rostrum. Plates of ambulacral rows IIa and IVb are typically diminutive while genitals 1 and 4 have been lost. In comparison with *H. rostrata*, the rostrum of *H. anterior* is more equilaterally triangular in cross-section and the rims of the sulcus, formed by interambulacral rows 2b and 3a, are distinctly thickened. The walls of the rostrum are also proportionally thicker and the body cavity smaller. The sulcus is significantly shallower.

The trend towards increasing slenderness and sharper demarcation of the rostrum is continued in *H. blackmorei*. Ambulacral rows IIa and IVb are lost completely from the part of the rostrum where the plating arrangement is known. Rostral plates are more elongate than in previous species. In cross-section, the rostrum is triangular and thickened at each corner while the body cavity is further reduced. Ambulacral plate rows IIa and IVb are slightly depressed. The sulcus is shallower than in *H. anterior* and its rims are parallel. The tip of the rostrum is broader than the shaft and the rostrum is more or less vertical in attitude.

Rostral development is most pronounced in *H. elongata*. Rostral plates are narrower and more elongate than in any of its predecessors. Interambulacral plate rows 2a and 3b always separate

genitals 2 and 3 from oculars II and IV. Only two vertically placed madreporic pores are present.

Summarizing these trends, there is a progressive increase in the slenderness and clearer demarcation of the rostrum. This is achieved through elongation and narrowing of plate rows, increasing the number of plates in each row present, and loss of plate rows. The rostrum adopts a more vertical attitude and is strengthened by the development of buttresses and by thickening of the walls. The body cavity within the rostrum is progressively reduced and genitals 1 and 4 are lost during evolution.

3. *Body*. The body of *H. rostrata* differs little from that of the ancestral *Infulaster*. During the evolution of *Hagenowia* there were five important changes to the structure of the body. Firstly, the plastron became interrupted in *I. infulasteroides* and in all species of *Hagenowia*. Secondly, the base became progressively more convex. Thirdly, the peristome moved from a basal to an anterior position with a vertical attitude. Fourthly, the posterior slope became more vertical and the fasciole more oblique. Finally there was a change from a double, asymmetrical sub-anal protruberance in *H. rostrata* to a single centrally placed protruberance in later species.

4. *Pore morphology*. The more important changes in pore morphology during the evolution of *Infulaster* and *Hagenowia* include the progressive loss of phyllode and dorso-lateral pores and the increasing differentiation of pores at the rostral tip. Three distinct regions of pores are recognizable and will be dealt with separately. Pore terminology is taken from Smith (1980a).

(a) *Phyllode pores*. In *Infulaster*, phyllode pores are relatively large isopores, rounded in outline, with an axially positioned neural canal in an adoral position. They are 300–350 μm in length in *I. excentricus* but only 180–250 μm in length in later species. Thirty such pores lie around the peristome in *I. excentricus* but only 20 to 22 are present in *I. tuberculatus* and *I. infulasteroides*. Similar phyllode pores are found in *H. rostrata* and *H. anterior*. *H. rostrata* has between 14 and 18 such pores while *H. anterior* has slightly fewer (the exact number cannot be ascertained in any of the specimens examined). *H. blackmorei* has only two small, circular unipores lacking any periporal ornament. These lie on either side of the anterior sulcus immediately above the peristome. There is no sign of pores in lateral and posterior ambulacra adjacent to the peristome.

(b) *Latero-dorsal pores*. In *Infulaster*, isopores of the posterior columns of ambulacra II and IV are twice as long as other latero-dorsal pores. These elongate isopores have no obvious neural

EXPLANATION OF PLATE 4

Bottom of micrograph adoral unless otherwise stated.

Fig. 1. *Infulaster infulasteroides*: latero-dorsal partitioned isopore from interambulacrum 5. BMNH E76851.

Fig. 2. *I. tuberculatus*: partitioned isopore with axially positioned neural canal near the apex of ambulacrum III. BMNH E76852.

Fig. 3. *Hagenowia rostrata*: partitioned isopore with axially positioned neural canal near the apex of ambulacrum III. BMNH E7684.

Fig. 4. *H. elongata*: simple unipore of ambulacrum III within the rostral sulcus. MM 12820.

Fig. 5. *H. anterior*: unipore with broad periporal area in ambulacrum III at the rostral head. Adoral to the right. BMNH E76844.

Fig. 6. *H. blackmorei*: unipore with broad periporal area in ambulacrum III at the rostral head. BMNH E76846.

Fig. 7. *H. elongata*: unipore in ambulacrum III at the rostral head.

Fig. 8. *H. elongata*: tuberculation on the lateral face of the rostrum. Apex to the left, dorsal ridge at top.

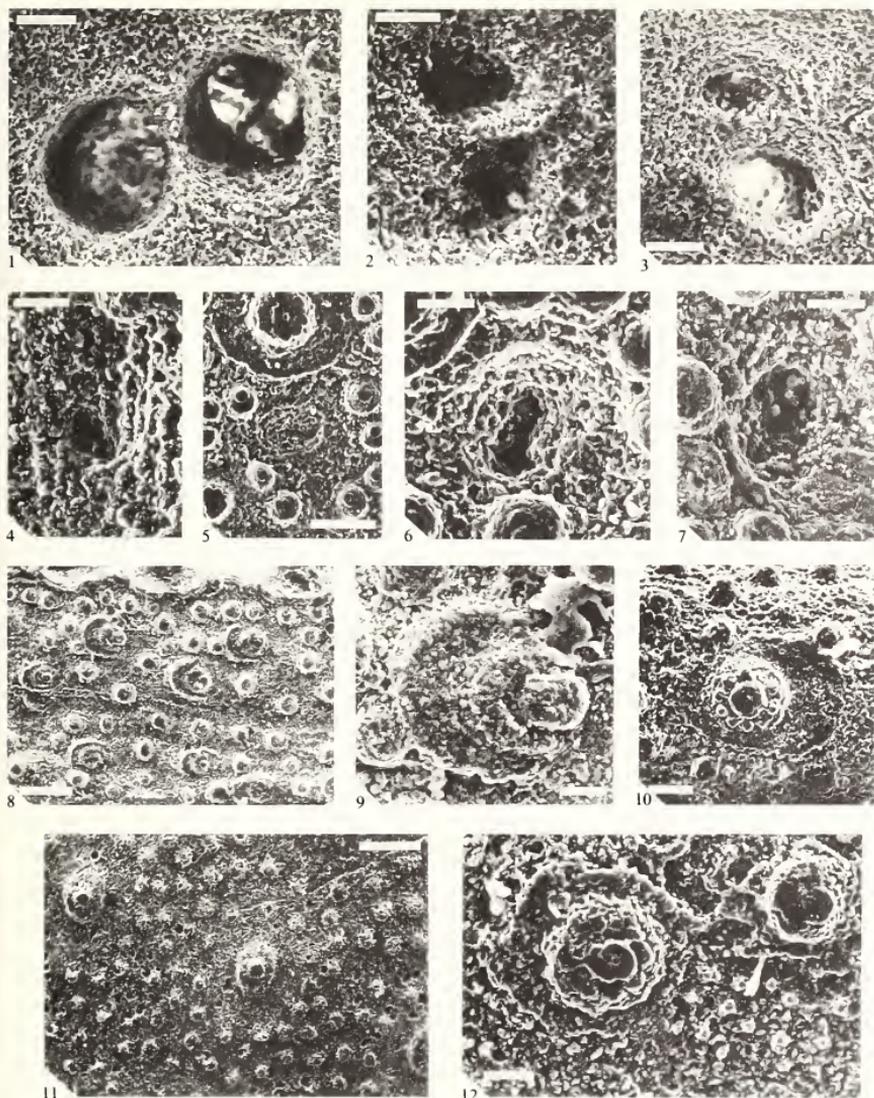
Fig. 9. *H. elongata*: enlargement of fig. 8 showing one tubercle.

Fig. 10. *H. anterior*: dorsal tubercle on rostrum showing enlarged areole and radially symmetrical crenulation.

Fig. 11. *I. tuberculatus*: latero-dorsal tubercles.

Fig. 12. *H. anterior*: latero-dorsal tubercles at the base of the rostrum.

Scale bar in figs. 1–4, 6, 7, 9, 12 = 100 μm ; figs. 5, 8, 10, 11 = 200 μm .

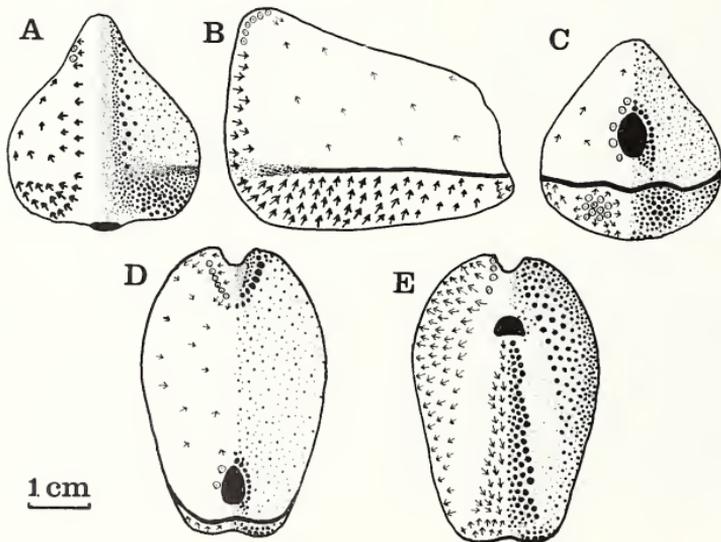


GALE and SMITH, Cretaceous irregular echinoids

canal and the interporal partition is more or less flush with the test surface and may be very broad. Other dorso-lateral pores are partitioned isopores with a small, laterally positioned neural canal (Pl. 4, fig. 1). All isopores are widely spaced and have no recognizable attachment area. Pores of *I. excentricus* are approximately twice the size of pores in later species.

Latero-dorsal pores vary tremendously in specimens of *H. rostrata*. In some of the larger specimens there are isopores, arranged as in *Infulaster*. One of these has elongate isopores of ambulacra IIb and IVa which are even larger than those in *I. excentricus*. The majority of specimens lack such elongate isopores and have small partitioned isopores in all columns. In other specimens, all latero-dorsal pores are reduced to unipores. Finally, one specimen has unipores in ambulacral columns IIb and IVa and small partitioned isopores in columns IIa and IVb. In *H. anterior* there are no pores in rostral plates of ambulacra II and IV but there are between three and five partitioned isopores in each column on the body above the fasciole. There are no latero-dorsal pores in *H. blackmorei*.

(c) *Ambulacrum III pores*. Pores in the frontal sulcus are similar in size and shape in the three species of *Infulaster* and in *H. rostrata*. These are partitioned isopores with axially aligned neural canals (Pl. 4, figs. 2, 3). Pores near the apex are identical with those within the sulcus. In later species of *Hagenowia*, pores in the sulcus are smaller than those at the apex. The 12 to 14 most adapical pores in *H. anterior* and *H. blackmorei* are unipores, circular in outline, and with a narrow central pore surrounded by a clear periporal area (Pl. 4 figs. 5, 6). Unipores in the sulcus are smaller with a reduced periporal area. In the apical unipores of *H. elongata*, the central pore is much larger and most of the periporal area is lost (Pl. 4, fig. 7). Unipores in the sulcus are minute and lack periporal ornament (Pl. 4, fig. 4).



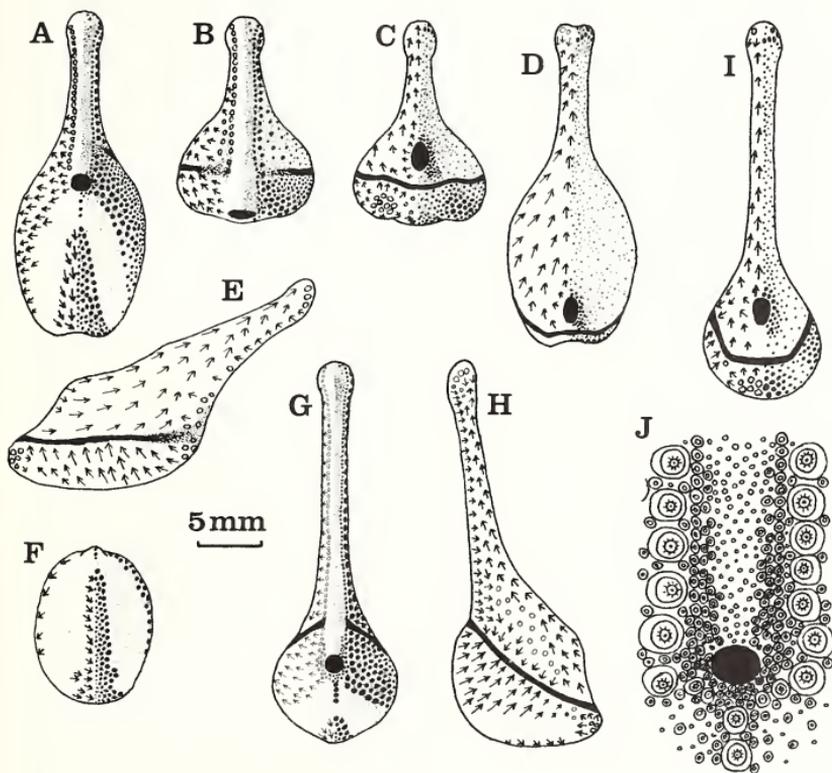
TEXT-FIG. 7. Tubercle arrangement in *Infulaster excentricus*. A—anterior: B—lateral: C—posterior: D—aboral: E—oral. Arrows on the left-hand side of diagrams show the direction of arcole enlargement. Circles indicate radially symmetrical tubercles. Stippling on the right-hand side of diagrams indicates the size and arrangement of tubercles. The marginal fasciole appears as a black band.

5. *Tubercle arrangement.* Although some marked changes occur in the detailed arrangement of tubercles during the evolution of *Hagenowia*, all functionally distinct groups of tubercles were already developed in *I. excentricus*. The more important changes are outlined below.

(i) There is a slight reduction in the area of plastron tubercles in later species of *Hagenowia*. This is accompanied by a corresponding increase in the tubercle-free ambulacral zones on either side of the plastron. The plastron is extremely narrow in *H. blackmorei* (text-fig. 8F).

(ii) There is a relative increase in the area of ventro-lateral tubercles, which are best developed in *H. blackmorei*. This is a consequence of the increasing obliquity of the fasciole (which, in turn, arose from the progressive shift of the peristome).

(iii) Tubercles in the sub-anal region are radially arranged around two points in *Infulaster* and *H. rostrata* (text-figs. 7, 8). In *H. anterior* and *H. blackmorei*, sub-anal tubercles are radially arranged around a single point (text-fig. 8i).



TEXT-FIG. 8. Tubercle arrangement in *Hagenowia*. A-E, *H. rostrata*: A—oral; B—anterior; C—posterior; D—aboral; E—lateral. F-I, *H. blackmorei*: F—oral; G—anterior; H—lateral; I—posterior; J—arrangement at the base of the sulcus and surrounding the peristome. For explanation see text-fig. 7.

(iv) Latero-dorsal tubercles in *Infulaster* have an areole which is radially symmetrical or only weakly enlarged adapical (Pl. 4, fig. 11). In *Hagenowia* the areole becomes increasingly enlarged in an adapical direction, whilst crenulation is enlarged on the opposite side (Pl. 4, figs. 8-10, 12; text-fig. 8). Latero-dorsal tubercles are least dense immediately above the marginal fasciole and become progressively denser towards the dorsal ridge. Tubercle density over the dorsal surface increases progressively during evolution. There are between 1 and 3 tubercles per mm² in *I. excentricus* and *I. tuberculatus* and this increases to 4 or 5 tubercles per mm² in *I. infulasteroides*. A similar tubercle density is found laterally at the base of the rostrum in species of *Hagenowia*. On the rostrum itself, tubercle density increases to 8 to 10 tubercles per mm² in *H. blackmorei* and as much as 15 tubercles per mm² in *H. elongata* where there are four closely packed rows of tubercles.

(v) The parts of interambulacra 2 and 3 which form the outer zone of lateral walls of the anterior sulcus have relatively small and radially symmetrical tubercles (Pl. 5, figs. 3-9). There are three rather irregular rows of these tubercles above the marginal fasciole in *I. tuberculatus* and *I. infulasteroides* the interambulacral zones are narrower and there is only a single rather irregular row of tubercles marginal to the sulcus (Pl. 5, fig. 3). In *H. rostrata* these tubercles are linearly arranged along the sulcus lip and each is separated from its neighbours by a single row of miliaries (Pl. 5, fig. 5). A similar arrangement is found in later species of *Hagenowia* though without the intervening miliaries (Pl. 6, figs. 1-4).

(vi) Tubercle density progressively increases on the lateral and posterior edges of the peristome in *Hagenowia*. They are best developed in *H. blackmorei* where they form a dense U-shaped band at the base of the sulcus (text-fig. 8).

EXPLANATION OF PLATE 5

Bottom of micrograph adoral unless otherwise stated.

Fig. 1. *Hagenowia rostrata*: ventral view of rostrum apex with ambulacrum III on the right. The large interambulacral tubercles at the apex face outwards and their spines obviously did not converge. BMNH E76845.

Fig. 2. *H. rostrata*: dorsal view of rostrum apex. The large interambulacral tubercles form a collar around the frontal sulcus. BMNH E76845.

Fig. 3. *Infulaster tuberculatus*: ambulacrum III towards the apex. Large apical interambulacral tubercles set perpendicular to the anterior ambulacrum can be seen in the top left corner. Smaller interambulacral tubercles, adjacent to ambulacrum III, are irregularly arranged and their spines would not have formed a protective arch above the ambulacrum. BMNH E76852.

Fig. 4. *I. tuberculatus*: enlargement of fig. 3 showing the relatively dense arrangement of variably sized tubercles in ambulacrum III.

Fig. 5. *H. rostrata*: stereo view of the rostral sulcus slightly below the apex. Ambulacrum III is deeply sunken and has denser and more uniformly sized tuberculation than *I. tuberculatus*. Interambulacral tubercles bordering the sulcus are arranged in two rather irregular rows, an inner row of small tubercles, that would have supported spines forming a protective arch, and an outer row of more laterally facing tubercles for excavating spines. BMNH E76845.

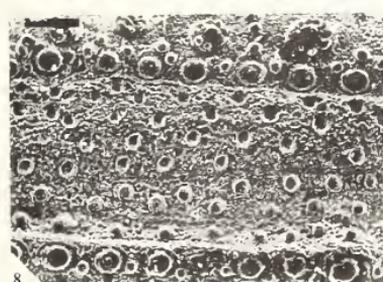
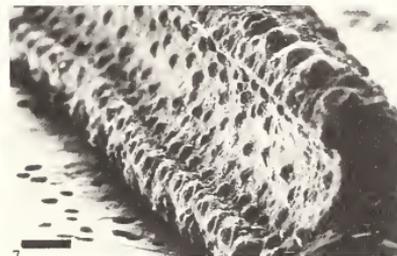
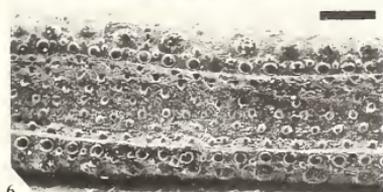
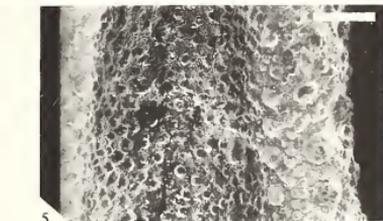
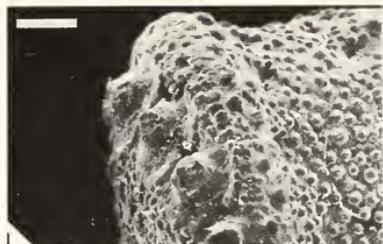
Fig. 6. *H. anterior*: ventral view of rostral sulcus about mid-length, apex to the right. Ambulacrum III is moderately sunken and rather sparsely covered in uniformly sized miliary tubercles. There are two well-defined rows of tubercles on the adjacent interambulacra, an inner row of small tubercles for spines of the protective arch and an outer row of larger, laterally facing tubercles for excavating spines. BMNH E76844.

Fig. 7. *H. elongata*: oblique ventral view of rostral sulcus, apex to right. Ambulacrum III is only slightly sunken and the two rows of adjacent interambulacral tubercles are well developed and set at different angles to the sulcus. MM 12820.

Fig. 8. *H. anterior*: enlargement of fig. 6.

Fig. 9. *H. elongata*: as fig. 7 but viewed perpendicular to the sulcus.

Scale bar in figs. 4, 7-9 = 200 μ m; figs. 1-3, 5, 6 = 400 μ m.



(vii) The large tubercles of the anterior interambulacra found on either side of the frontal sulcus are arranged in two rather irregular rows with interspersed miliaries in species of *Infulaster*. With the development of the rostrum in *Hagenowia*, the areas of interambulacra which face towards the anterior are reduced and there is only a single row of these large tubercles on either side. Tubercles are rather irregularly arranged in *H. rostrata* but in later species they abut to form a well-defined row (Pl. 5, figs. 5-9; Pl. 6, figs. 1, 2).

(viii) The size and density of the miliaries which cover the floor and walls of the frontal sulcus vary amongst species (Table 1). Miliaries are largest in *I. infulasteroides* and *H. rostrata* and become progressively smaller in later species. Miliary density does not vary along the length of the sulcus in *I. excentricus* and *I. tuberculatus*, but in *I. infulasteroides* and in *Hagenowia* the miliaries are denser at the top of the sulcus, where they may reach densities equivalent to that found in the lateral fasciole (120 to 140 miliaries per mm²). There is a corresponding increase in the density of miliaries lying outside the sulcus near the head of the rostrum. This results in the development of a rather diffuse band of miliary tubercles that fades towards the dorsal surface of the rostrum.

TABLE 1. Size and density of miliary tubercles in ambulacrum III

Species	Adapical miliaries		Median miliaries	
	Size (μm)	Mean density (mm ⁻²)	Size (μm)	Mean density (mm ⁻²)
<i>Infulaster excentricus</i>	50-60	35	50-60	35
<i>I. tuberculatus</i>	60-70	50-55	50	50-55
<i>I. infulasteroides</i>	50-75	80	80-100	50-60
<i>Hagenowia rostrata</i>	60-75	75	80-90	40-50
<i>H. anterior</i>	50	100	60-70	60-70
<i>H. blackmorei</i>	40-50	130	50-60	70
<i>H. elongata</i>	40-50	140	50-60	60

FUNCTIONAL MORPHOLOGY

Size and Shape

1. *Size*. The marked reduction in the size of *Infulaster* in the early Coniacian could have had several possible advantages. A reduction in size increases the surface area to volume ratio. This eases the animal's respiratory demands by increasing the percentage of oxygen that can be obtained by direct diffusion. By reaching sexual maturity at an earlier stage, smaller species can have a shorter generation time. This could have arisen with the development of stable and highly suitable conditions, which would favour those species able to reproduce and multiply more rapidly. The reduction in size may also have been brought about by predatory pressures. Small animals with apical elongation would be much less obvious from the surface, when buried, than larger, semi-infaunal species.

2. *The anterior ambulacrum*. The anterior ambulacrum provides the main, if not sole, passageway for transferring sediment orally in Recent spatangoids (Smith 1980*b*). In certain species, spines of the anterior ambulacrum are specialized for mucous string feeding (Chesher 1963; Buchanan 1966). The sunken anterior ambulacrum in *Infulaster* and *Hagenowia* must also have provided an important pathway for sediment transportation. In *Infulaster* the anterior sulcus is deep but in *Hagenowia* it shallows progressively. This is accompanied by increasing development of the protective arch of spines covering the sulcus (see later, p. 36). The reduction in the depth of the

sulcus is linked to the development of rostrum. The sulcus decreases in depth as the rostrum increases in slenderness because of the reduction in internal volume. In *Hagenowia* the frontal channel is maintained as the sulcus shallows by the development of a dense grill of spines arching across ambulacrum III.

3. *The rostrum.* The development and elongation of the rostrum permitted *Hagenowia* to live buried within the sediment while maintaining contact with surface waters (Nichols 1959; Ernst and Schulz 1971). Via the rostrum, oxygenated water could be drawn into the burrow and the surface, organic-rich layer of sediment passed to the mouth. Because of its small size, *Hagenowia* cannot be said to have burrowed deeply. The oral surface of *H. blackmorei* could only have been about 3 cm below the surface, approximately the same level as postulated for *I. excentricus*. However, the rostrum presumably made *Hagenowia* less obvious from the surface since only the rostral tip would have disturbed the surface sediment and not the whole dorsal surface (text-fig. 11). Predation may have been an important selection pressure.

The rostrum, which is oblique in *H. rostrata*, becomes progressively more vertical in later species. Simultaneously it also develops a cross-section with thicker plates and buttressing. Early *Hagenowia* presumably needed an oblique rostrum to streamline their movement through the sediment and thus minimize the stresses applied to the thin-walled rostrum. In later species, as the rostrum became more robust, it could be held in a more vertical position.

4. *The anterior movement of the peristome.* In *Infulaster* the peristome lies on the oral surface near the anterior margin (text-fig. 7) but in *H. rostrata* it lies marginally at the base of the anterior sulcus and in *H. blackmorei* it has shifted to a frontal position (Pl. 3, fig. 7b). This change is thought to reflect an increasing dependence on sediment coming down the anterior sulcus. In Recent spatangoids, phyllode tube-feet are used to collect sediment from the floor of the burrow and transfer it to the mouth (Nichols 1959; Chesher 1969; Smith 1980a). This is also likely to have been true in *Infulaster*. Particles coming down the anterior sulcus would have landed on the floor of the burrow just in front of the peristome and within reach of the tube-feet. In *H. rostrata* the mouth lies at the base of the sulcus so that tube-feet would have been able to collect and transfer particles direct from the sulcus. In *H. blackmorei* the mouth is anterior and raised well above the floor of the burrow. Peristomial tube-feet are reduced and, because of their position, could only have been involved with sediment coming down the sulcus.

5. *The plastron.* The oral surface is relatively flat in *Infulaster* but becomes more or less keeled in *Hagenowia*. An arched or keeled plastron is found in Recent spatangoids which burrow in muddy or sandy substrata. Surface-dwelling spatangoids or spatangoids that burrow shallowly in sands or gravels have a flat plastron. A keeled or arched plastron may provide a better arrangement of tubercles and spines for efficient forward thrust.

6. *Sub-anal protruberances.* *Infulaster* has two clear bulges in the sub-anal region whereas *H. anterior* and *H. blackmorei* have only a single protruberance. In *H. rostrata* there are two sub-anal protruberances which are asymmetrical. Usually the right-hand bulge is larger and more prominent than the other. Devries (1953) showed that asymmetry in the test of spatangoids relates to the way in which the gut is coiled. This probably accounts for the asymmetry of the sub-anal region in *H. rostrata*.

The change from a double to a single sub-anal protruberance is probably linked with the development of asymmetry. Each bulge bore a tuft of spines (see p. 34). Whereas the test of *I. excentricus* was broad enough to have had two distinct tufts of sub-anal spines, later species had progressively narrower bodies. Presumably, as internal volume reduced, the gut became more tightly packed and any asymmetry this gave to the test was enhanced. In *Hagenowia* this made one of the tufts of spines larger and more posterior in position. The tuft of spines on the smaller bulge would therefore have become less important and was lost in later species.

Pore morphology

1. *Latero-dorsal pores and their tube-feet.* Pore morphology suggests that specialized respiratory tube-feet were present only in species of *Infulaster* and in some large forms of *H. rostrata*. By

comparison with extant species, these tube-feet were probably rather elongate with a central, partitioned region (see Smith 1980a). Respiratory tube-feet were best developed in the posterior columns of ambulacra II and IV. Other columns either had less elongate respiratory tube-feet or had thin-walled cylindrical tube-feet. The positioning of respiratory tube-feet presumably reflects the water-circulation pattern over the aboral surface.

The unipores and partitioned isopores in *H. rostrata* would have unspecialized sensory tube-feet. In later species of *Hagenowia*, aboral tube-feet are reduced and finally lost. This, at first glance, appears to be rather a strange adaptation for an infaunal echinoid. However, holasteroids, in general, show no modifications for protecting aboral tube-feet during burial. Respiratory tube-feet can function efficiently in infaunal spatangoids because of their sunken ambulacra and the curved arch of protective spines above them. Respiratory tube-feet in clypeasteroids and cassidulids function efficiently because of their extreme elongation (Smith 1980a). In *Infulaster*, respiratory tube-feet were neither extremely elongate, nor associated with sunken ambulacra nor a protective arch of spines. The tube-feet were able to play an effective part in gaseous exchange only because much of the dorsal surface remained uncovered. In *Hagenowia*, all but the extreme tip of the rostrum was covered, thus it became impossible for the tube-feet to function efficiently and they were quickly lost.

The change in efficiency of the respiratory tube-feet may be linked with the over-all reduction in body size that occurred. As more of the dorsal surface became covered by sediment, with apical elongation, respiratory tube-feet presumably became less efficient. To compensate for this, a reduction in body size took place so that a larger proportion of the total oxygen consumed could come from direct diffusion. In *Hagenowia*, body size is further reduced with the complete loss of latero-dorsal tube feet.

2. *Pores and tube-feet of the anterior ambulacrum.* Small isopores are found along the length of the anterior ambulacrum in species of *Infulaster* and in *H. rostrata*. Their similarity with the ambital isopores in other ambulacra and the fact that they are uniform in shape and size along the whole length of the ambulacrum (excluding phyllode pores) indicates that the associated tube-feet were sensory in function and terminated in a sensory pad rather than a disc. The pores diverge little as they pass inwards, and the accompanying ampullae were probably cylindrical (Smith 1980a). These tube-feet are likely to have actively probed the sediment in front of them as well as sensing the particles passing down the sulcus.

In later species of *Hagenowia*, isopores are replaced by unipores. Those in the sulcus are extremely small and, by comparison with Recent spatangoids, are likely to have borne small, non-extensible epithelial knobs which were chemosensory in function. Apical unipores differ both in size and shape. Similar broad-rimmed unipores in Recent holasteroids and spatangoids bear relatively large and extensible, sensory tube-feet (Smith 1980a). Such tube-feet are likely to have been important chemical and tactile sense organs and no doubt would have extended out of the funnel to probe the surrounding sediment.

The increase in pore size in apical unipores of *H. elongata* suggests that the associated tube-feet were more extensible than those of previous species. A larger pore means that a larger volume of coelomic fluid can pass in and out of the tube-feet rapidly.

3. *Phyllode pores and their tube-feet.* The isopores surrounding the peristome are much larger than isopores of other non-respiratory tube-feet in both *Infulaster* and *Hagenowia*. Phyllode tube-feet of Recent spatangoids and holasteroids are penicillate and work by mucous adhesion (Smith 1980a). Their broad disc requires the support of a large diameter stem. They are therefore associated with large, oval isopores or unipores. The arrangement of a few large pores around the peristome in *Infulaster* and *Hagenowia* indicates that their tube-feet also collected sediment by means of a mucous adhesive disc. However, the disc could not have been particularly broad, judging from the size of the isopores, and may not have been penicillate.

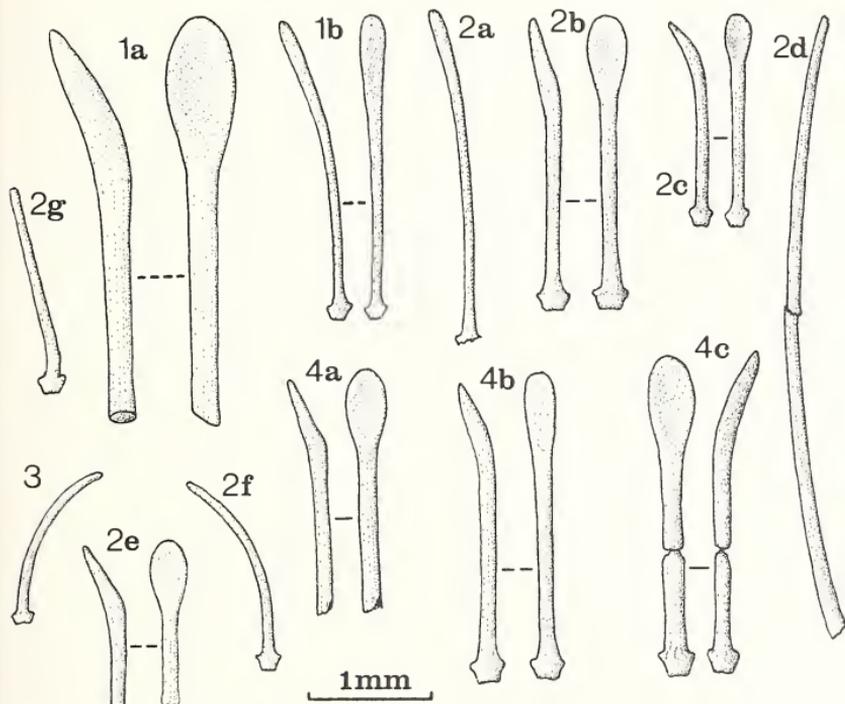
There are only two small unipores around the peristome of *H. blackmorei*. These are likely to have been associated with sensory tube-feet.

Spine morphology

A specimen of *I. infulasteroides* (BMNH E35766) and a specimen of *H. rostrata* (BMNH E76848) both retain a large number of different spines. Camera lucida drawings of these spines are given in text-fig. 9.

A large number of latero-dorsal spines lie near the dorsal ridge in the specimen of *I. infulasteroides*. These are about 1.75 mm in length and have a pronounced spatulate tip. The spatulate tip is set oblique to the straight shaft. Amongst these spatulate spines is a shaft, about 5 mm in length, with neither tip nor base preserved. The thinner, distal end tapers gently and is unspatulate. This gently curved spine almost certainly attached to one of the large interambulacral tubercles at the apex of the anterior sulcus.

Ventro-lateral spines, found below the marginal fasciole of *I. infulasteroides*, are spatulate and 2 to 2.5 mm in length. The spatulate tip is also set oblique to the shaft. On the plastron are three spatulate spines, none of which have their base preserved. Entire spines must be greater than 1.75 mm in length. On the oral surface there are two long and slender spines, one of which is broken



TEXT-FIG. 9. Spines of *Infulaster* and *Hagenowia*:

1. *I. excentricus* (BMNH E40770): a, latero-ventral spine; b, latero-dorsal spine.
2. *I. infulasteroides* (BMNH E35766): a, sub-anal spine; b, latero-ventral spine; c, latero-dorsal spine; d, apical spine; e, plastron spine; f, spine from the protective arch across the frontal sulcus; g, anterior excavatory spine.
3. *H. anterior* (BMNH E40158): spine from the protective arch across the frontal sulcus.
4. *H. rostrata* (BMNH E76848): a, latero-ventral spine; b, anal spine; c, plastron spine.

just below the milled ring, the other having no remnant of the spine base. The proximal end lies near the large tubercles of the sub-anal protruberance. Both spines are gently curved and are about 2.75 mm in length. The shaft becomes slightly broader distally, but does not appear to be spatulate.

In the anterior sulcus there are a number of non-spatulate spines. Most of those lying on the floor of the sulcus are small, slender, and strongly curved. They are about 1.5 mm in length and do not flatten distally. These are derived from the small interambulacral tubercles lining the outer margin of the sulcus, judging from the size and shape of the spine base. Stouter spines, about 1.75 mm in length, are found within the sulcus and on the adjacent interambulacra. The shaft is slightly bent a little above the milled ring, and tapers distally (the extreme tip is unfortunately not preserved). These spines are associated with the large interambulacral tubercles adjacent to the sulcus.

Plastron and latero-ventral spines of *H. rostrata* are similar to those of *I. infulasteroides*. In the specimen of *H. rostrata*, a number of stout, straight spines, up to 2.5 mm in length, are preserved within the periproct. Their tip is slightly flattened and is set slightly oblique to the shaft. These spines are probably associated with the large interambulacral tubercles which surround the periproct.

The spines in all species of *Infulaster* and *Hagenowia* are likely to be similar, judging from the similarity in tubercle structure and arrangement. The function of each group of spines is best discussed in conjunction with the structure of their tubercles. A reconstruction of the spine coverage in *I. infulasteroides* and *Hagenowia* is given in text-fig. 10. Spine posture is inferred from tubercle structure.

Tubercle structure and arrangement

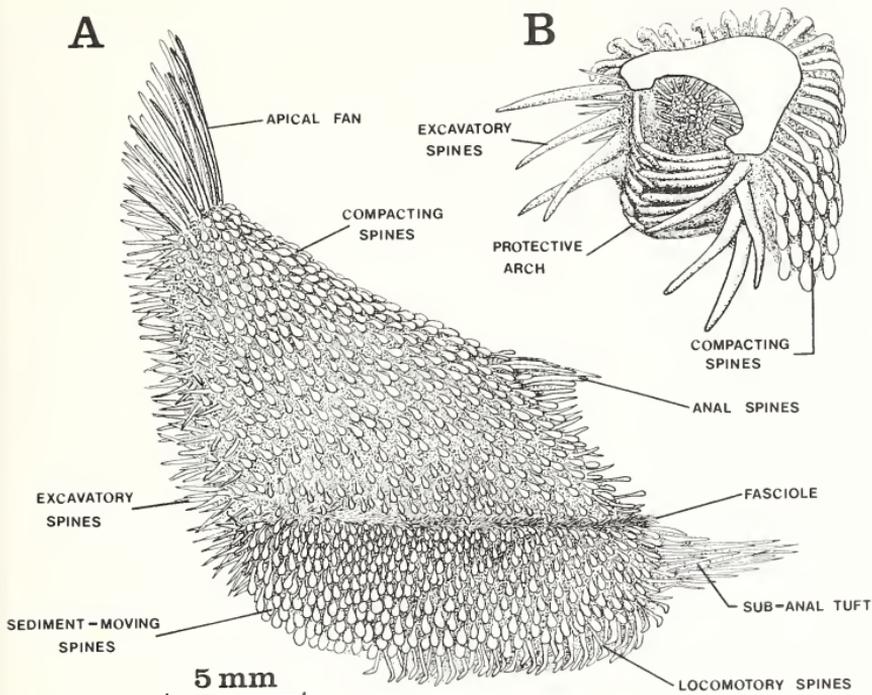
The shape and arrangement of tubercles can give information on spine posture and movement (Smith 1980*b*). There are a number of distinct areas of tubercles in *Infulaster* and *Hagenowia*, each of which bore spines with a specific function. Tubercle arrangement in *I. excentricus*, *H. rostrata*, and *H. blackmorei* is depicted in text-figs. 7 and 8. The following groups of tubercles can be distinguished.

1. *Plastron tubercles*. Plastron tubercles in both *Infulaster* and *Hagenowia* are closely spaced with only a few interspersed miliary tubercles. Largest tubercles lie laterally with smallest tubercles lying along the central ridge. Their areole is slightly enlarged on the meso-posterior side (text-figs. 7, 8) and platform crenulation is radially symmetrical. As in Recent spatangoids, the power stroke would have been towards the mid posterior, and plastron spines, with their spatulate tips, must have provided the main thrust for locomotion. However, plastron tubercles of Recent spatangoids have asymmetric crenulation and pronounced areole enlargement (Smith 1980*b*). The movement of plastron spines was probably more restricted and less effective in *Infulaster* and *Hagenowia* compared with Recent spatangoids. Radially symmetrical crenulation indicates that plastron spines were held more or less perpendicular to the test (Smith 1980*b*).

2. *Latero-ventral tubercles*. Tubercles found below the marginal fasciole in interambulacra 1-4 have their areole enlarged adambitally and towards the fasciole. Platform crenulation is either radially symmetrical or is slightly larger on the adoral side (opposite the direction of areole enlargement). These tubercles are denser on the anterior half but become more uniformly distributed in later species. They decrease in size and become more densely packed towards the fasciole.

This arrangement differs from that found in Recent spatangoids, where the areole is enlarged in a latero-posterior direction and crenulation is asymmetrical. (Smith 1980*b*). In spatangoids the associated spines lie oblique to the test and excavate sediment from beneath the animal with an oar-like action. Tubercle structure, in *Infulaster* and *Hagenowia*, indicates that, whereas oral spines were more or less perpendicular, adambital spines were inclined slightly downwards away from the fasciole. Areole enlargement suggests that spines pushed sediment outwards and upwards and were principally used in excavating and burrowing.

3. *Sub-anal tubercles*. Tubercles are radially arranged on each sub-anal bulge with large, radially symmetrical tubercles centrally, and smaller tubercles marginally (text-figs. 7 and 8). Marginal tubercles often have a slight areole enlargement on the side away from the centre. A similar tubercle



TEXT-FIG. 10. Spine posture and arrangement in *Infulaster* and *Hagenowia*. A, *Infulaster infulasteroides*, lateral view. B, *Hagenowia blackmorei*, cut-away section through the rostrum showing the anterior sulcus. The relative size of spines is based on specimen BMNH E35766, and spine posture and function is interpreted from tubercle structure.

arrangement in Recent spatangoids is associated with tufts of spines (Smith 1980b). *Infulaster* and *H. rostrata* must have had two sub-anal tufts of spines whereas later species of *Hagenowia* had only a single tuft. The upper spines of each tuft abut against the marginal fasciole. Mucus from the fasciole could easily have been transferred to the sub-anal spines. The sub-anal tuft of spines is used in constructing a tunnel, in spatangoids, with the aid of specialized tube-feet (Nichols 1959; Chesher 1968). *Infulaster* and *Hagenowia* lacked sub-anal, funnel-building tube-feet and were unlikely to have built an extensive tunnel. However, the spines alone may have been able to maintain a short sub-anal tunnel with the help of mucus from the fasciole. In spatangoids the sub-anal tunnel is used to remove water from the burrow (Chesher 1968).

4. *Anal tubercles*. Large tubercles are found around the dorsal and lateral edges of the periproct. They decrease in size away from the periproct and are most numerous dorsally and on either side immediately below the periproct. The crenulate platform is radially symmetrical. There may be slight areole enlargement on the anterior side. Beneath the periproct is a broad band of miliaries, extending to the fasciole. A similar arrangement of tubercles is found in Recent spatangoids, where a semicircle of longer spines surrounds the periproct. These maintain a space within the burrow for defaecation and prevent fouling of the aboral surface.

5. *Latero-dorsal tubercles*. Tubercles above the marginal fasciole have only a weak bilateral symmetry in *I. excentricus* and *I. tuberculatus*. This becomes much more pronounced in *Hagenowia* due to a marked enlargement of the areole on the anterior or adapical side (see text-fig. 8). Numerous miliaries occur between the tubercles. These tubercles support short, spatulate spines in *I. infulasteroides*. Similar spatulate spines, attaching to bilaterally symmetrical tubercles, are found in Recent spatangoids, where they are used for compacting the burrow walls, transporting sediment posteriorly, and moving the dorsal mucous coat (Smith 1980b). *I. excentricus* has a low aboral tubercle density but later species of *Infulaster* and *Hagenowia* have progressively denser tuberculation. The increased protection provided by a denser spine coverage is an adaptation for living infaunally. Tubercles are especially dense along the rostrum, presumably for compacting and maintaining an open passageway down into the burrow.

In *H. blackmorei*, tubercles just above the marginal fasciole have an adoral areole enlargement indicating that the spatulate tips of spines were tilted in opposite directions on either side of the fasciole, a situation common in Recent spatangoids for distributing mucus.

6. *Tubercles associated with the anterior sulcus*. There are two sets of interambulacral tubercles lying adjacent to the anterior sulcus. Firstly, there are small, radially symmetrical tubercles which form an inward-facing row along the lip of the sulcus (Pl. 4, figs. 5-9; Pl. 5, figs. 1-4). They are rather irregularly arranged in early species but become organized into a well-defined line in *Hagenowia*. The associated curved and non-spatulate spines would have formed an arched roofing to the anterior sulcus (text-fig. 10B). The increasing density and organization of these spines was partially due to the decreasing depth of the anterior sulcus and partially due to the increasing importance of the sulcus as a pathway for transporting sediment to the mouth. In *Hagenowia* the anterior shift of the peristome shows that more reliance was placed on sediment coming down the sulcus. The arch of spines would have maintained a clear frontal pathway and would have prevented sediment from the frontal wall of the burrow clogging or contaminating the stream of sediment passing down the anterior sulcus. They ensured that sediment could only enter the sulcus at the apex.

EXPLANATION OF PLATE 6

Fig. 1. *Hagenowia elongata*: large interambulacral tubercles adjacent to the rostral sulcus that support excavating spines. Crenulation is radially symmetrical but the areole is enlarged laterally away from ambulacrum III. Smaller tubercles for protective arch spines can be seen towards the bottom. MM 12820.

Fig. 2. *H. anterior*: interambulacral tubercles, as above but with intervening miliaries. BMNH E76844.

Fig. 3. *H. elongata*: row of small interambulacral tubercles immediately adjacent to the frontal sulcus (bottom of micrograph) for spines forming a protective arch to the sulcus. MM 12820.

Fig. 4. *H. elongata*: enlargement of fig. 3 showing the radially symmetrical areole and the lack of crenulation.

Fig. 5. *Infulaster tuberculatus*: large apical interambulacral tubercles, ambulacrum III to the right. These have radially symmetrical areoles and crenulation and are not tilted. Their spines must have been held pointing away from ambulacrum III. BMNH E76852.

Fig. 6. *H. anterior*: miliary tubercles near the apex of the rostral sulcus, apex to the sulcus. These are tilted adapically and laterally, away from the mid-line, suggesting that their spines had a meso-adoral power stroke. BMNH E76844.

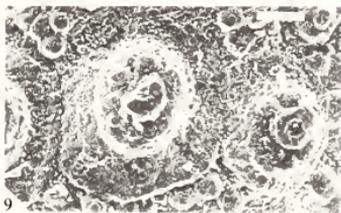
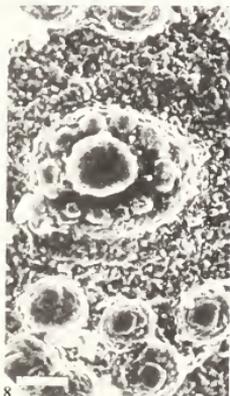
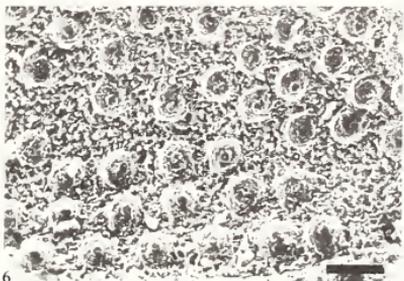
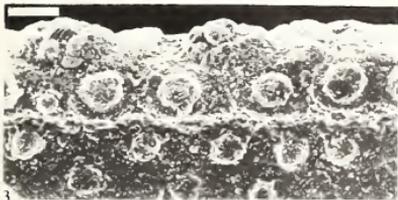
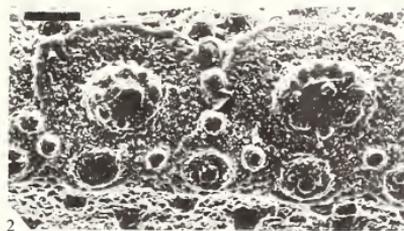
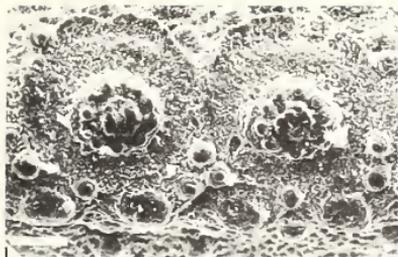
Fig. 7. *H. blackmorei*: adapical part of ambulacrum III showing dense, irregular arrangement of varying sized tubercles at the top of the sulcus. BMNH E76846.

Fig. 8. *H. anterior*: large ambulacral tubercle adjacent to an apical ambulacrum III unipore. Crenulation is slightly stronger laterally (towards the pore) and the protective spine must have been gently curved. BMNH E76844.

Fig. 9. *H. blackmorei*: large apical interambulacral tubercle with a radially symmetrical areole and slightly stronger crenulation towards ambulacrum III (top of micrograph). BMNH E76846.

Fig. 10. *H. elongata*: large apical interambulacral tubercles. The areole is slightly border to the posterior (bottom of micrograph), crenulation is radially symmetrical. MM 12820.

Scale bar in figs. 4, 8 = 40 μ m; figs. 1-3, 6, 9, 10 = 100 μ m; figs. 5, 7 = 200 μ m.



The other set of interambulacral tubercles are large and outward-facing (Pl. 5, figs. 5-9; Pl. 6, figs. 1-3). They form a single, well-defined row in *Hagenowia*. Platform crenulation is either radially symmetrical or is enlarged slightly on the side facing the sulcus. Their areole is enlarged in the opposite direction (text-fig. 8; Pl. 6, fig. 1) showing that the power stroke of the spine was directed away from the sulcus. These stout, pointed spines were probably used to loosen and excavate sediment of the anterior wall of the burrow. Recent spatangoids, such as *Echinocardium cordatum* (Pennant), have both an anterior arch of protective spines and adjacent excavating spines, and their tubercles and spines are rather similar.

The apical interambulacral tubercles and spines of *Infulaster* and *Hagenowia* are the largest they possess. There are between 16 and 20 such tubercles on the adapical plates of the anterior interambulacra. Their areoles are either radially symmetrical or are enlarged slightly to the posterior (Pl. 5, figs. 1-3; Pl. 6, figs. 5, 9, 10). Platform crenulation is more or less radially symmetrical though crenulation may be slightly enlarged on the anterior side (Pl. 6, fig. 9). Tubercles are so positioned that, were the spines to converge adapically to form a tuft, they would have to lie at a considerable angle to the tubercles and the plate surface. The structure of the tubercles, however, shows that spines were not set obliquely, forming an apical tuft, but probably formed a fan-shaped array. This fan of spines would have formed a collar to the anterior sulcus (text-fig. 10A). This arrangement is common to all species of *Infulaster* and *Hagenowia* and is also found in certain species of *Cardiaster*. As the apex is the most vulnerable part of the test in infaunal or semi-infaunal species, these apical spines may have acted as a deterrent to predators. The fan-shaped arrangement around the apical opening to the frontal sulcus suggests that apical spines were also involved in collecting sediment, either acting as a funnel or helping to cascade surface sediment into the sulcus.

Within ambulacrum III, small tubercles are interspersed with miliaries near the apex (Pl. 6, fig. 7), but in the sulcus ambulacral plates are covered almost entirely by uniformly sized miliaries (Pl. 6, fig. 6). A similar arrangement is found in *Micraster* but has not yet been reported in any Recent species (Smith, 1980b). In many Recent spatangoids, miliary tubercles of ambulacrum III bear short, straight spines with fleshy tips, usually well endowed with cilia and mucous glands. A similar type of spine was probably present in the sulcus of *Infulaster* and *Hagenowia*.

Several lines of evidence suggest that the anterior sulcus became increasingly important as a pathway for transferring sediment to the mouth. Evolutionary changes in the size and density of miliaries in the sulcus may therefore be related to an improved feeding mechanism. The progressive differentiation of a distinct band of dense miliaries at the apex of the sulcus may mark the increasing importance of ciliary currents or mucus binding for particle transportation. By concentrating miliary spines at the apex, where sediment entered the sulcus, it is possible that copious amounts of mucus could have been produced to enmesh particles loosely. The relatively few spines within the sulcus could then have transported a stream of mucus-bound sediment with relative ease. Tubercle and spine arrangement is highly distinctive in Recent, mucous string feeding spatangoids (Chesher 1963; Buchanan 1966; Smith 1980b) and very different from that in *Hagenowia*. *Hagenowia*, then, did not feed by means of a compact mucous string but may have had a much looser flow of weakly bound particles.

7. *Fascioles*. The marginal fasciole shows little change except that it becomes more sharply defined across the anterior interambulacra in later species of *Hagenowia*. The increasing obliquity of the fasciole is a direct consequence of the changing position of the peristome. The fasciole does not cross the anterior ambulacrum, as stated by Nichols (1959), but becomes more diffuse and peters out towards the sulcus.

Fascioles act as pumps, drawing oxygenated water through the burrow, and as a source of mucus. A dorsal mucous coat prevents finer particles falling between spines and clogging the burrow. Both *Infulaster* and *Hagenowia* are likely to have lived at least partially buried and the fasciole probably drew water down from the apex and over the central and posterior parts of the test.

PRESERVATION

Increased differentiation and strengthening of the rostrum in successive species of *Hagenowia* was accompanied by relative thinning of the body wall. This is reflected in the increased rarity of preservation of *Hagenowia* bodies in successively later species and the greater frequency of isolated rostra.

Bodies of *Hagenowia* are rarely bored or encrusted by the organisms which colonized much of the skeletal debris littering the chalk sea floor, and it is likely that once exhumed, the fragile tests fragmented rapidly leaving only the more durable rostra. The rostra often contain sponge crypts, and characteristic oval borings (500–1000 μm in length) with irregularly bevelled rims. Encrusters are extremely rare on *H. rostrata*, probably because they were too small to provide suitable substrata.

One preservational style occurs consistently in *Hagenowia*, in which the rostrum is lost, having broken away along plate sutures near its base (e.g. Pl. 3, fig. 2). The resulting irregular stump has, in some specimens been attacked by boring organisms (e.g. Pl. 3, figs. 6*b*, 7*a*). Such specimens frequently retain scattered spines on the sides and base of the body. Presumably these individuals remained in life orientation within the sediment after death, with the rostrum protruding above the sediment-water interface, which was stable for long enough to allow colonization by borers.

Two specimens of *Hagenowia* have repaired injury to the rostrum. In one specimen (BMNH E76849) the obliquely broken tip of the rostrum was sealed across, and new tubercles and genital pores developed. Such damage was probably the result of predation.

SELECTION PRESSURES AND MODE OF LIFE

The majority of structural changes in the *Infulaster*/*Hagenowia* lineage were caused, either directly or indirectly, by elongation of the apical region of the test, and to a lesser extent by the reduction in size. Apical elongation necessitated disruption of the apical system, plate elongation, loss of plate columns from the rostrum, and an increased slenderness of the rostrum. This increased slenderness in turn reduced the internal volume of the rostrum, which caused a decrease in depth of the sulcus, loss of two of the four gonads, and the change from extensible tube-feet with large ampullae, to small tube-feet with reduced ampullae. The slender rostrum required buttressing at the anterior and posterior margins, and an increasingly better organization of tubercles. The increase in obliquity of the fasciole was a consequence of the anterior and adapical movement of the peristome. The size reduction resulted in the change from a double to a single subanal bulge and in the interruption of the plastron.

Various features displayed by *Infulaster* and *Hagenowia* are interpreted as adaptations to an infaunal mode of life. The latero-ventral spines were specialized for excavating sediment from beneath the animal. In order for the fasciole and subanal tuft of spines to have functioned, these echinoids must have lived at least partially buried. Latero-dorsal spines modified for compacting sediment of the burrow walls are developed to immediately below the apex, as are the excavating spines and the protective arch of spines across the sulcus (text-fig. 10). This clearly implies that both *Infulaster* and *Hagenowia* lived within the sediment, with their apices at or just below the surface.

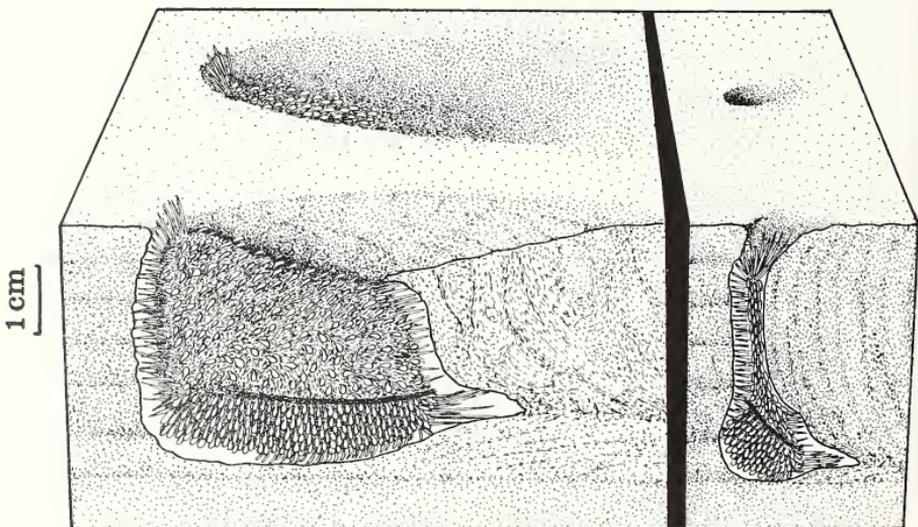
It is highly improbable that either genus could have burrowed more deeply, as funnel-building tube-feet are lacking, and the apical spines were held in a broad fan and not a tuft. Living within fine-grained sediments, they had to maintain direct contact with surface waters. This could only have been achieved by keeping the apex of the test at the surface.

I. excentricus has an almost flat dorsal surface, most of which must have remained exposed on the sea floor. Later species evolved to become less conspicuous, by apical elongation. In this way the bulk of the animal could be removed from the surface, with only a small apical part of the test visible. This apical elongation brought about the structural changes enumerated above. The loss of aboral respiratory tube-feet was probably an important factor in influencing the size reduction which occurred.

Other morphological changes accompany a change in feeding strategy. *Infulaster* used its phyllode tube-feet to pick up sediment around the mouth. Sediment coming down the frontal sulcus was not collected directly and probably formed only a small part of the animal's diet. *Hagenowia* came to rely much more heavily on sediment from the anterior sulcus and may have developed some sort of mucus binding to cope with this increased volume of sediment. Adaptations linked with this change in feeding strategy include the anterior movement of the peristome, loss of large phyllode tube-feet, and increasingly denser arch of spines across the sulcus and their extension to cover the peristome, the more extensible sensory tube-feet at the apex, and the increasing differentiation of miliaries within the sulcus.

All the morphological trends and specializations discussed are directly or indirectly concerned with adaptations for feeding or burial. The predominant pressures acting on the *Infulaster-Hagenowia* lineage were for increased efficiency in feeding and for increased protection by becoming less obvious at the surface. *I. excentricus* lived semi-infaunally with much of the dorsal surface exposed, and progressed leaving a clear furrow in its wake (text-fig. 11). In later species, as the dorsal surface became more oblique with apical elongation, less and less of the test remained exposed at the surface. In *H. blackmorei* only the very small apical head remained near the surface, the remainder of the body being fully covered (text-fig. 11). Only a small circular hole at the surface would have marked the position of this species.

It is not entirely correct to speak of an increasing depth of burial in the *Infulaster-Hagenowia* lineage, since the apex stays at the same level and the oral surface of *I. excentricus* lay at considerably greater depth than in many later species, because of the reduction in size. However, with apical elongation and the more vertical orientation of the rostrum, the oral surface was removed further from the sea floor. The most likely cause of this change is increasing predation, with selection



TEXT-FIG. 11. Mode of life of *Infulaster* and *Hagenowia*. Cut-away block sections showing the depth of burial of *Infulaster excentricus* (left-hand side) and *Hagenowia blackmorei* (right-hand side). Further back a second individual is illustrated to highlight the change in surface appearance with the development of apical elongation.

against those more obvious at the surface. Predation was a threat to *Hagenowia*, since regenerated rostra are known.

It is not clear whether the change in feeding habit resulted from a change in the nature of the sediment (e.g. the development of a surface layer richer in organic material or, conversely, an over-all reduction in organic content) or reflected a progressive adaptation to a constant sediment type. *Infulaster* and *Hagenowia* are both found in bands in apparently uniform pelagic chalk sequences. However, original subtle differences in the nature of the sediment may well have been obscured by bioturbation and diagenesis.

Hagenowia provides some indirect evidence as to the nature of the chalk sea floor. The presence of cutting and compacting spines on the rostrum implies that the sediment in which it lived was sufficiently cohesive to both require and allow such treatment. This is in accord with the suggestion made from other lines of evidence by Surlyk and Birkelund (1977) that the bottom was relatively stable, with only a superficial layer (a few millimetres thick) of easily resuspendible material.

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A REVISION OF LATE ORDOVICIAN BIVALVES FROM POMEROY, CO. TYRONE, IRELAND

by S. P. TUNNICLIFF

ABSTRACT. A history of research on Ordovician bivalves from Pomeroy is given, and their stratigraphic distribution in the Caradoc-Ashgill rocks is outlined. More than thirty taxa are described including five new species: *Praenucula dispersa*, *P. infirma*, *P. praetermissa*, *Ambonychia arundinea*, and *Cleionychia incognita*. The rostroconch *Hippocardia praeprestis* (Reed) is illustrated.

SINCE Portlock (1837, 1843) first described the faunas of the Caradoc-Ashgill rocks of the Pomeroy area of County Tyrone (text-fig. 1), some elements have been studied thoroughly, especially the trilobites and brachiopods, which have helped to show the relationship of the Pomeroy strata to the Ordovician of North America and southern Scotland (Mitchell, 1977, and others). Although molluscs are abundant in the rocks of Pomeroy, they have received scant attention in recent years. The orthoconic nautiloids were redescribed by Blake (1882) but have remained unrevised since; the gastropods have been described by Longstaff (= Donald) (1902, 1924) and Reed (1952). The bivalves were largely ignored until Reed (1952) redescribed Portlock's species and added a number of new taxa. Reed was unaware of Portlock's many duplicate specimens, including syntypes, now housed in the Ulster Museum (Tunnicliff 1980), and did not have the benefit of collections made in recent years by the Geological Survey of Northern Ireland, by Dr. W. I. Mitchell and by Mr. R. P. Tripp and others of the British Museum (Natural History). With the aid of this new material a critical re-examination of the bivalve fauna has been carried out and several new forms have been recognized.

History of Pomeroy bivalve research

Portlock (1843) mentioned or described in varying detail the following species, arranged here according to the formation from which they can now be recognized to have come.

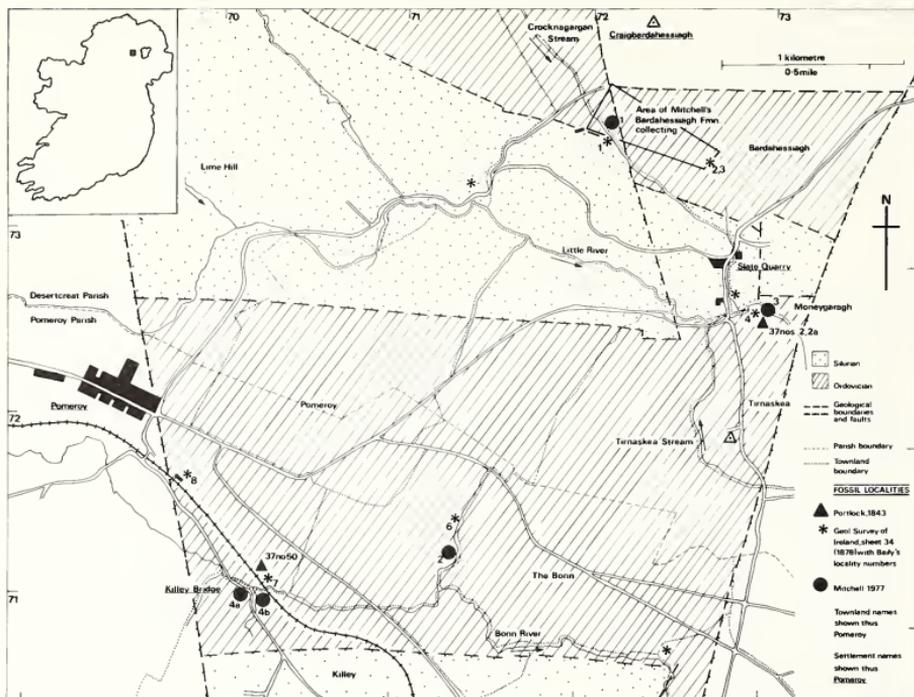
Bardaheesiagh Formation (Caradoc):

<i>Avicula obliqua</i> Murchison	<i>Modiola securiformis</i> Portlock
<i>Avicula orbicularis</i> Murchison	<i>Inoceramus priscus</i> Portlock
<i>Modiola Brycei</i> Portlock	<i>Inoceramus transversus</i> Münster
<i>Modiola expansa</i> Portlock	<i>Inoceramus trigonus</i> (Münster)
<i>Modiola Nerei</i> (Münster)	<i>Nucula radiata</i> Portlock

Killey Bridge Formation (Ashgill, Cautleyan):

<i>Inoceramus contortus</i> Portlock	<i>Arca subtruncata</i> Portlock
<i>Cypricardia simplex</i> Portlock	<i>Arca transversa</i> Portlock
<i>Arca cylindrica</i> Portlock	<i>Pectunculus ambiguus</i> Portlock
<i>Arca dissimilis</i> Portlock	<i>Pectunculus Apjohni</i> Portlock
<i>Arca Eastnori</i> (Murchison)	<i>Pectunculus semitruncatus</i> Portlock
<i>Arca obliqua</i> Portlock	<i>Nucula acuta?</i> (Sowerby) var. <i>imbricata</i> Portlock
<i>Arca regularis</i> Portlock	<i>Uncites gryphus</i> Schlotheim var.

In addition to these, Portlock had a number of specimens to which he did not refer in print but to which he fixed labels with suggested identifications and observations. Notes on how Portlock labelled his specimens are given by Tunnicliff (1980). His *Mytilus cinctus* Portlock and *Posidonomya? venusta* (Münster) are from rocks of Llandoverly age as is his *Mytilus? semi-rugatus* Portlock from Lisbellaw, Co. Fermanagh. Portlock's



TEXT-FIG. 1. The area around Pomeroy, Co. Tyrone, based on Mitchell 1977 (taken from Tunnicliff 1980), with Ireland inset to show the position of Pomeroy.

figures, although generally of natural size, often lack the detail which might be expected in modern illustrations. Many of his descriptions contain useful detail such as height and length of valves and the number of teeth visible, but others are less helpful.

Describing specimens from the collection of Sir R. Griffith, McCoy (1846) added the following species from the Bardahessyagh Formation, *Pullastra speciosa* McCoy and from the Killey Bridge Formation, *Nucula protei* Münster, *N. subacuta* McCoy, *Arca quadrata* McCoy.

In 1878 (p. 28) Baily published a list of Portlock bivalve species giving amended generic names and gave a list (p. 25) of the species collected by officers of the Geological Survey of Ireland during the survey of the 1870s.

Apart from some brief discussion by Hind (1910), Baily's was the last contribution to the study of Pomeroy Ordovician bivalves before the publication of Reed's posthumous paper in 1952. In this Reed redescribed most of Portlock's species and added the following:

Ctenodonta perangulata Reed
Ctenodonta deserta Reed
Ctenodonta cf. nitida (Ulrich)
Clidophorus occultus Reed
Vanuxemia? suspecta Reed
Modiolopsis concentrica simulans Reed
Orthodesma tyronense Reed
Conocardium praeprestis Reed

Paramodiola? sp.
Whiteavesia subexpansa Reed
Ambonychia cf. volvens Isberg
Ambonychia cf. amygdalina (Hall)
Ambonychia cf. intermedia Isberg
Clionychia subovalis Reed
Clionychia subquadrata Reed

Horizons and localities (Text-figs. 1 and 2)

The Ordovician stratigraphy of Pomeroy was discussed by Mitchell (1977, pp. 4-18). Bivalves are recorded from the following strata:

- Tirnaskea Formation (Ashgill, Hirnantian)
- Killey Bridge Formation (Ashgill, Cautleyan)
- Bardahessiagh Formation (Caradoc).

No bivalves are recognized as being from Mitchell's Junction beds.

The horizon of Portlock specimens and other material from old collections is inferred from the lithologies and from the known locality information (see Tunnicliff 1980).

The localities of many of the specimens in the old collections are uncertain, often given only as 'Pomeroy'. However, by comparison with material in the recent well-localized collections and with the small number of likely sites, it is possible to suggest localities for most specimens, usually with reference to those listed by Mitchell (1977, pp. 5-7). Portlock's localities are discussed by Tunnicliff (1980).

Stratigraphic distribution (Table 1)

The bivalve fauna of the Bardahessiagh Formation is dominated by cyrtodontids and ambonychiids, the former probably infaunal or semi-infaunal, the latter epifaunal and byssate. *Cyrtodonta?* often occurs as conjoined valves suggestive of little or no transport after death. The other infaunal genera represented in the Bardahessiagh Formation are *Praenucula*, *Deceptrix*, *Similodonta?*, and *Lyrodesma* all of which are uncommon compared with *Cyrtodonta?*. *Similodonta?* and *Lyrodesma* both occur as conjoined or closely associated valves

SERIES & Stage	Graptolite zone	Pomeroy	Girvan	Bohemia	North America
ASHGILL Hirnantian		Tirnaskea Formation	High Mains	Kosov Formation	Richmondian
Rawtheyan					
Cautleyan	<i>D. anceps</i>	Killey Bridge Formation	Drummuck Group	Králův Dvůr Formation	d5
Pusgillian	<i>D. complanatus</i>		Shalloch Formation		Maysvillian
CARADOC Onnian	<i>P. linearis</i>		Whitehouse Group		d4
Edenian					
Actonian				Bohdalec Formation	
Marshbrookian					
Woolstonian	<i>D. clingani</i>	Junction Beds	Ardwell Group		Shermanian
Longvillian		Bardahessiagh Formation			
Soudleyan	<i>C. wilsoni</i>			Zahořany F. Vínice F.	d3
Harnagian	<i>C. peltifer</i>		Balclatchie	Letná Formation	d2
Wildernessian					
Costonian	<i>N. gracilis</i>				

TEXT-FIG. 2. Approximate correlation of the Ordovician rocks of Pomeroy based on Williams *et al.* (1972), Mitchell (1977), and R. P. Tripp and J. K. Ingham (pers. comm. 1981). The approximate stratigraphic equivalents of Barrande's stages d₂, d₃, d₄, and d₅ in Bohemia are shown (based on Kříž and Pojeta 1974).

TABLE 1. The stratigraphic distribution of bivalves from the Ordovician rocks of Pomeroy, Co. Tyrone

	Bardahessiagh Formation	Killey Bridge Formation	Tirnaskea Formation
<i>Praenucula dispersa</i> sp. nov.	x		
<i>P. praetermissa</i> sp. nov.		x	
<i>P. aff. praetermissa</i> sp. nov.		x	
<i>P. infirma</i> sp. nov.		x	
<i>Deceptrix</i> sp.	x		
<i>D. apjohni</i> (Portlock)		x	
<i>D. regularis</i> (Portlock)		x	
<i>D. semitruncata</i> (Portlock)		x	
<i>D. subtruncata</i> (Portlock)		x	
<i>Similodonta?</i> sp.	x		
<i>Concavodonta imbricata</i> (Portlock)		x	
<i>Nuculites cylindricus</i> (Portlock)		x	
<i>Nuculoid</i> gen. and sp. nov.			x
<i>Cyrtodonta? expansa</i> (Portlock)	x		
<i>C.? securiformis</i> (Portlock)	x		
<i>C.? sp.</i>	x		
<i>Vanuxemia contorta</i> (Portlock)		x	
<i>Ambonychia arundinea</i> sp. nov.		x	
<i>Cleionychia transversa</i> (Portlock)	x		
<i>C. prisca</i> (Portlock)	x		
<i>C. incognita</i> sp. nov.	x		
<i>Ambonychiopsis suspecta</i> (Reed)	x		
pterineid? gen. and sp. indet.		x	
? bivalve gen. and sp. indet.	x		
<i>Modiolopsis</i> sp.		x	
<i>Corallidomus concentrica</i> (Hall and Whitfield)		x	
<i>Corallidomus? sp.</i>		x	
<i>Goniophora</i> sp.		x	
<i>Colpomya simplex</i> (Portlock)		x	
<i>Semicorallidomus? sp.</i>	x		
<i>Cycloconcha? speciosa</i> (McCoy)	x		
<i>Lyrodesma radiatum</i> (Portlock)	x		
<i>Hippocardia praepristis</i> (Reed)		?	

but, like *Cyrtodonta?*, are never suggestive of life position but rather of having been winnowed out from the substrate. Of the epifaunal ambonychiids, *Cleionychia* is best represented, and some also occur as conjoined valves. The nature of the present-day Bardahessiagh Formation exposure (Mitchell 1977, p. 5) precludes identifying the exact localities for most specimens.

In the Killey Bridge Formation the principal elements of the bivalve fauna are infaunal nuculoids, *Praenucula*, *Deceptrix*, *Concavodonta*, and *Nuculites*. These are all numerous compared with other genera, most of which are represented in the collections by only one or two specimens. Most specimens from the Killey Bridge Formation are single valves, but conjoined valves of all nuculoid genera are present. Bivalves are recorded from all the localities where the Killey Bridge Formation is represented by dark-grey calcareous mudstone (e.g. localities 1-3 of Mitchell 1977) but determinable bivalves are not known from the rottenstone and sandstone lens recorded by Mitchell (localities 4a, b of Mitchell 1977) in which brachiopods are abundant and varied.

Determinable bivalves are also almost unknown from the Tirnaskea Formation; only *Nuculoid* gen. nov. and the rostroconch *Hippocardia* (by Reed 1952) are recorded and the latter is more probably from the Killey Bridge Formation. Mitchell (1977, p. 17) compared the Tirnaskea fauna with the Hirnantian *Hirnantia* fauna.

The differences between the Bardahessiagh and Killey Bridge bivalve faunas are a reflection of their differing palaeoenvironments; the generally sandy Bardahessiagh Formation probably represents a shallow-shelf environment favouring the modes of life of cyrtodontids and ambonychiids, while the mudstones of the Killey Bridge Formation were probably the product of a more stable deeper-shelf environment. The Bardahessiagh Formation bivalve fauna has a distinctly eastern American aspect which is less obvious, but still present in the Killey Bridge Formation.

SYSTEMATIC PALAEOLOGY

In general, the classification used in the *Treatise of Invertebrate Palaeontology*, N1 and 2 (Moore 1969) is adopted. Where this is deviated from is stated in this text, and the author whose precedent is followed is given.

Measurements. In some cases tables of measurements are given in which the terms mean and median are used. Mean is used to show the sum of the items divided by the number of items; median is used to convey the mid-point between the maximum and minimum values of a group of items. All linear measurements are given in millimetres (mm), measured with a vernier caliper or under a binocular microscope with a graticule. Abbreviations used are L for length, H for height, AL for preumbonal length. In tables of measurements, the term 'angle' is used for the angle between the anterior and posterior hinge-plates in nuculoids.

Preservation. Two terms used require a note of explanation. Composite mould is used in the sense of McAlester 1962. External cast is used to describe a naturally occurring convex specimen which shows only external features but which has probably been produced in a similar manner to composite moulds.

This study is based on material in the following museums: Institute of Geological Sciences (IGS), British Museum (Natural History) (BM), Sedgwick Museum, Cambridge (SM), Ulster Museum, Belfast (UM), National Museum of Ireland, Dublin (NMI).

Class BIVALVIA Linnaeus, 1758

Subclass PALAEOXODONTA Korobkov, 1954

Order NUCULOIDEA Dall, 1889

Superfamily NUCULACEA Gray, 1824

Family PRAENUCULIDAE Pfab, 1934

Remarks. Three genera of Praenuculids are certainly recognized from Pomeroy: *Praenucula* and *Deceptrix* from the Bardahessiagh and Killey Bridge Formations and *Concavodonta* from the Killey Bridge Formation. *Concavodonta* is distinct from the other two genera (see discussion of *Concavodonta*) but *Praenucula* and *Deceptrix* are less easily distinguished at first sight. Pojeta (1971, p. 16) implied that they were synonymous ('... some authors recognize *Praenucula* Pfab as being distinct from *Deceptrix*...'). Pojeta, Kříž, and Berdan (1976) treated *Praenucula* as a subgenus of *Deceptrix*. McAlester (1969, p. 229), placed Pfab's *Praeleda* in synonymy with *Deceptrix* and both have been used for species which show the characters of *Praenucula*, for example *Praeleda ciae* (Sharpe) of Bradshaw 1970, and *Deceptrix* cf. *ciae* (Sharpe) of Babin and Robardet 1973. *Praenucula* and *Deceptrix* have remained virtually unsexed in the British Ordovician and I can find no reference to their occurrence in the British Isles, except *Praenucula* from the Arenig of Ramsey Island (Carter 1971, p. 251). Specimens from British localities which could now be placed in *Praenucula* or *Deceptrix* have usually been recorded as *Ctenodonta*, often under open nomenclature.

In the species discussed here, distinction is made between *Praenucula* and *Deceptrix* principally on the differences indicated by McAlester (1969, p. 229); that is that the posterior teeth in *Deceptrix* are smaller and more numerous than the anterior teeth, while in *Praenucula* the anterior and posterior teeth are similar in size and number. To this we may add that the umbones in *Praenucula* lie in the posterior half while in *Deceptrix* they generally lie in the anterior half. Corresponding to the greater posterior length in *Deceptrix* is the relatively greater length (equal to or longer than the anterior) of its posterior hinge-plate. In *Praenucula* the posterior hinge-plate is equal to or shorter in length than the anterior hinge-plate. In both genera the anterior hinge-plate is arched towards the body of the shell and the posterior hinge-plate is straight or gently arched away from the body of the shell. The adductor muscle scars in both genera are equal or subequal but their

relative sizes and positions differ, being larger and more ventral in *Deceptrix* (Pls. 7-9). In *Praenucula* the adductor muscle scars are close to, and may extend beyond, the ends of the hinge-plates, while in *Deceptrix* the posterior scar lies closer to the umbo, only extending as far as the end of the hinge-plate, and the anterior scar lies in the most anterior part of the shell, beyond the end of the hinge-plate.

A fourth genus, *Similodonta*, may be represented by specimens from the Bardahessiagh Formation.

Genus PRAENUCULA Pfab, 1934

Type species. By original designation of Pfab 1934, pp. 234-235, *Praenucula dispar expansa* Pfab, 1934, from the Šárka Formation (Llanvirn) of Bohemia (Havlíček and Vaněk 1966) and described and figured by McAlester (1968, p. 46, pl. 8, figs. 3-9). See discussion under Praenuculidae above.

Praenucula dispersa sp. nov.

Plate 7, figs. 1-5; text-fig. 3a

Derivation of name. From Latin *dispersus* scattered, referring to the occurrence in loose blocks.

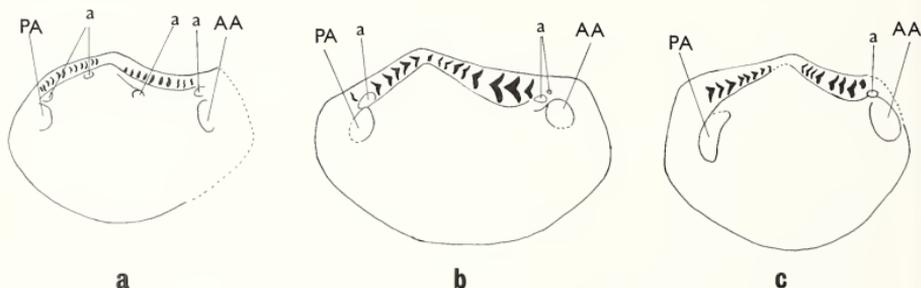
Type specimens. Holotype IGS GU 1893, internal mould of right valve, and paratypes IGS GU 1354, 1894, 1897, 1906, 3265, UM K4203, SM A16296, 3 left and 4 right valves; one a composite mould, the remainder internal moulds.

Horizon and locality. All specimens are from the Bardahessiagh Formation; GU specimens from the area of Mitchell's Bardahessiagh Formation collecting (Mitchell 1977), the others from uncertain localities to the south of Craigbardahessiagh.

Measurements

	L	H	H/L	AL/L	Angle
Max.	13.2 mm	11.0 mm	0.87	0.65	155°
Min.	7.8 mm	6.8 mm	0.61	0.50	130°
Mean	10.62 mm	8.15 mm	0.77	0.50	145°
Median	10.5 mm	8.9 mm	0.74	0.58	142.5°

Description. Ovate *Praenucula* with height about 0.7 of the length but variable. Umbo slightly posterior of centre, between the posterior two-fifths and mid-point, and extending slightly above the hinge-line. Convexity greatest slightly anterior to the umbo, maximum inflation of a single valve 2.4 mm seen in a valve 11 mm



TEXT-FIG. 3. *Praenucula* spp. based on internal moulds, *c.* $\times 5$. (a) *P. dispersa* sp. nov., IGS GU 1906, right valve. (b) *P. infirma* sp. nov., IGS NIL 8935, right valve. (c) *P. praeternissa* sp. nov., IGS NIL 8757, latex of left valve. Abbreviations: AA— anterior adductor muscle scar, PA— posterior adductor muscle scar, a— accessory muscle scar. Compare with Pl. 7, figs. 5, 12, 21. Note the differences in size of the adductor muscle scars and the differences in the size of the teeth and in their distribution on either side of the umbo. In each case, the finest teeth below the umbo are too small to be represented clearly.

long and 8 mm high. Angle between anterior and posterior hinge-plates about 140 to 145°. Posterior hinge-plate straight with 12+ uniformly sized teeth. Anterior hinge-plate concave towards the body of the shell, with 13+ teeth, increasing in size forwards. Slightly chevron-shaped teeth passing beneath umbo in a continuous series, chevrons directed towards the umbo. Anterior and posterior muscle scars clearly distinguished, equal in size the anterior more deeply impressed than the posterior and most deeply impressed at its posterior edge. Accessory muscles known (text-fig. 3a). Ligament and shell material unknown. Sculpture of fine concentric lines (c. 4 per mm) (Pl. 7, fig. 3).

Discussion. Nuculoid bivalves are poorly represented in the Bardahessiagh Formation, and those that are found are not well preserved. In particular, the very soft nature of some of the rottenstone has led to damage to, or loss of, the hinge-plate and teeth. The deformation apparent in other species from the Bardahessiagh Formation (e.g. *Cyrtodonta?* spp.) appears to have produced some variation among the *Praenucula* specimens; however, it is reasonable to regard them as belonging to a single species.

Praenucula dispersa is distinguished from the Killey Bridge Formation species, *Praenucula praetermissa* and *P. infirma*, by having smaller, less strongly chevron-shaped teeth. In the same way it can be differentiated from *P. costae* (Sharpe) as described by Bradshaw (1970, pp. 630–633) from the Llandeilo of Finistère. *P. dispersa* has more teeth than *P. clae* (Sharpe) (of Bradshaw 1970, pp. 633–636) and *Deceptrix pulchra armoricana* Babin and Melou (1972, pp. 81–82, pl. 8, figs. 4–7), and it lacks the posterior lobe seen in Hind's Drummuck species *Nuculana lobata* (1910, p. 519, pl. 4, figs. 1–3) and is less elongate than his *N. curta* (1910, p. 521, pl. 4, figs. 10–14) which is also from the Drummuck Group (Ashgill).

Ctenodonta albertina Ulrich and *C. filistriata* Ulrich (1894, pp. 598–599, pl. 42, figs. 76–82, text-fig. 44), both from the Cincinnati, have a pit beneath the umbo according to Ulrich's descriptions. Recent illustrations (Pojeta 1971, pl. 5, figs. 14–16; 1978, pl. 2, figs. 1–2) show a discontinuity in the dentition beneath the umbo not apparent in *P. dispersa*. *Nucula dispar* Barrande (1881, pl. 273, VII, figs. 1–14) is more rounded than *P. dispersa*.

Praenucula praetermissa sp. nov.

Plate 7, figs. 16, 21, 24; text-fig. 3c

Derivation of name. From the Latin *praetermittere*, to overlook, referring to the fact that the species has been overlooked by previous authors.

Type specimens. Holotype, IGS NIL 8757, composite mould of a left valve from the Killey Bridge Formation of the Crocknagargan Stream section (locality 1 of Mitchell 1977), Pomeroy, Co. Tyrone. Paratypes: 6 left and 6 right valves, internal, external, and composite moulds: IGS NIL 8687, 8747–8748, 8755, 8768, 8893, 8917, 8986, 8987 all from the same locality as the holotype; IGS NIG 482, Zs 2758 from locality 3 of Mitchell 1977, and IGS GU 1451 from his locality 2 (Warren Wood River). All from the Killey Bridge Formation.

Measurements	L	H	H/L	AL/L	Angle
Max.	11.0 mm	9.2 mm	0.83	0.70	160°
Min.	5.4 mm	3.6 mm	0.50	0.50	130°
Mean	8.6 mm	5.71 mm	0.72	0.60	143°
Median	8.2 mm	6.40 mm	0.66	0.60	145°

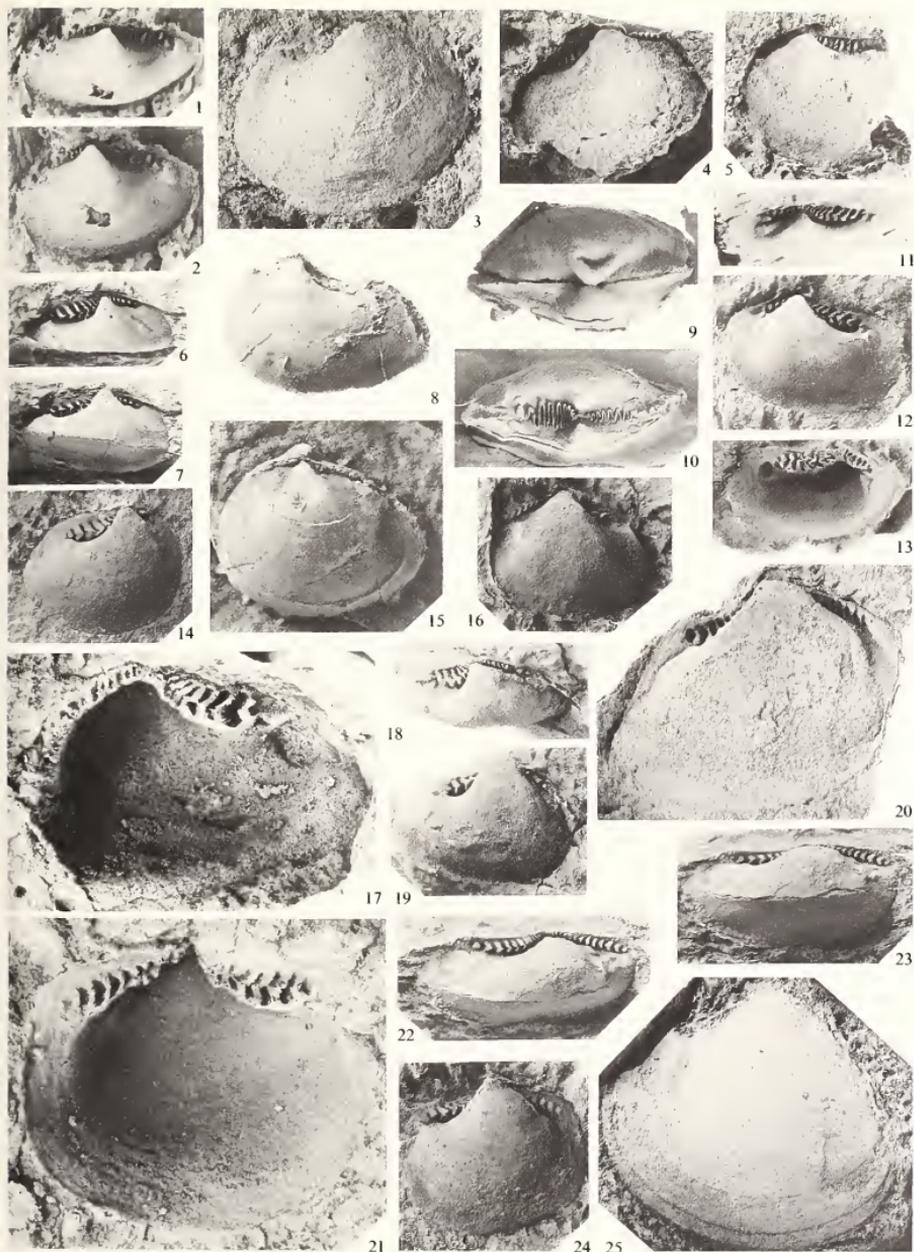
Description. Subovate to circular *Praenucula* in which the height is about 0.7 of the length. Maximum inflation of a single valve 1.4 mm seen in a valve 11.0 mm long and 9.2 mm high. The umbo is at about the posterior two-fifths. The shell is truncate behind and rounded in front. The anterior hinge-plate is broad and strongly arched towards the body of the shell. The anterior and posterior hinge-plates meet at an angle of about 145°, and usually bear the same number of teeth, up to nine. The teeth of the anterior hinge-plate are the larger and are strongly chevron-shaped; those of the posterior hinge-plate are markedly less so. The adductor muscle scars are subequal in size, the anterior scar being the more strongly impressed and lying below and slightly anterior to the anterior teeth with a diameter about one-quarter of the valve height; the posterior scar lies immediately below the end of the posterior dental series. Accessory muscle scars unknown, except for one anterior scar. Sculpture is of fine concentric lines, c. 16 per mm.

Discussion. This is a most distinctive form within the Pomeroy fauna, which, surprisingly, does not seem to have been seen by previous workers (Portlock, McCoy, Reed) and yet is well represented in recent collections, especially as fragments. *Praenucula praetermissa* is distinguished from *P. infirma*, described herein from the Killey Bridge Formation, by its larger adductor muscle scars and its more numerous posterior teeth, and from *P. dispersa* from the Bardahessiagh Formation by its larger and strongly chevron-shaped teeth. *P. praetermissa* lacks the lobate posterior of Hind's *Nuculana lobata* (1910, p. 519, pl. 4, figs. 1-3) and is less elongate than his *N. curta* (1910, p. 521, pl. 4, figs. 10-14), both from the Drummuck Group (Ashgill). It also lacks the pit beneath the umbo recorded in *N. curta* and in the American species *Ctenodonta albertina* Ulrich and *C. filistriata* Ulrich (1894, pp. 598-599, pl. 42, figs. 76-82, text-fig. 44).

It may be compared with other Ordovician *Praenucula* described from Europe: *Deceptrix pulchra armoricana* Babin and Melou, 1972 (= *D. cf. ciae* (Sharpe) of Babin and Robardet 1973) from the Caradocian rocks of Normandy, has a coarser sculpture than *P. praetermissa*, c. 6-8 lines per mm, grouped into 'faïsseaux' (Babin and Melou 1972, p. 82, pl. 7, fig. 7). *Praeleda pulchra* Pfab, 1934, is recorded by Havlíček and Vaněk 1966, from the Llanvirn, Caradoc, and Ashgill of Bohemia, and in shape resembles *Praenucula praetermissa* (Pfab 1934, p. 234, pl. 3, fig. 6) but Pfab gave no detail of dentition or hinge, and no sculpture is evident in his figure. *Nucula costae* (Sharpe) from Portugal, according to Sharpe's description (1853, pp. 148-149, pl. 9, fig. 4a, b) has more teeth than *P. praetermissa*, about 20 (given as 25-30 at one point and as a total of about 18 elsewhere) divided unequally between posterior and anterior, and shows the grouping of concentric striae also described in *D. armoricana*. The forms described by Bradshaw (1970, pp. 630-633) as *Praeleda costae* (Sharpe) from the Llandeilo of Finistère are closer in most respects to *Praenucula praetermissa*

EXPLANATION OF PLATE 7

- Figs. 1-5. *Praenucula dispersa* sp. nov. 1, 2, oblique dorsal view and lateral view, internal mould of right valve, holotype, IGS GU 1893. 3, ?composite mould of left valve, UM K4203. 4, internal mould of left valve, paratype, IGS GU 3265. 5, internal mould of right valve, paratype IGS GU 1906. All from the Bardahessiagh Formation (Caradoc), south of Craighbardahessiagh, Pomeroy, $\times 3$.
- Figs. 6-15, 17-19. *Praenucula infirma* sp. nov. 6, 7, oblique dorsal and lateral views, internal mould of left valve, IGS NIL 8824, Crocknagargan Stream section, Pomeroy (IGR c.H721737). 8, 15, internal mould and latex cast of external mould of right valve, IGS NIL 8682, 8682 *pars*, ditch exposure south of Craighbardahessiagh, Pomeroy (IGR H7195 7385). 9, 10, dorsal view of external mould and dorsal view of internal mould, conjoined valves, IGS NIL 8938, Crocknagargan Stream section, Pomeroy (IGR c.H721737). 11, 12, 13, dorsal and lateral views and latex cast of internal mould of right valve, holotype, IGS NIL 8935, Crocknagargan Stream section, Pomeroy (IGR c.H721737). 14, internal mould of left valve, IGS NIL 8754, Crocknagargan Stream section, Pomeroy (IGR c.H721737), $\times 3$. 17, 18, 19, internal mould of left valve, IGS NIL 8444, Tirnaskea Stream section, Pomeroy (IGR c.H727725); 17, latex cast, $\times 6$; 18, oblique dorsal view, $\times 3$; 19, lateral view, $\times 3$. All Killey Bridge Formation (Ashgill, Cautleyan), $\times 3$.
- Figs. 16, 21, 24. *Praenucula praetermissa* sp. nov. 16, internal mould of right valve, IGS NIL 8917, Crocknagargan Stream section, Pomeroy (IGR c.H721737), $\times 3$. 21, 24, left valve internal mould, holotype, IGS NIL 8757, Crocknagargan Stream section, Pomeroy (IGR c.H721737); 21, latex cast, $\times 6$; 24, lateral view, $\times 3$. All Killey Bridge Formation (Ashgill, Cautleyan).
- Fig. 20. *Praenucula* aff. *praetermissa* sp. nov. internal mould of left valve, IGS NIL 8972, Killey Bridge Formation (Ashgill, Cautleyan), Crocknagargan Stream section, Pomeroy (IGR c.H721737), $\times 3$.
- Figs. 22, 23. *Praenucula* aff. *praetermissa* sp. nov. Oblique dorsal view and lateral view of crushed internal mould of left valve, IGS NIL 8934, Killey Bridge Formation (Ashgill, Cautleyan), Crocknagargan Stream section, Pomeroy (IGR c.H721737), $\times 3$.
- Fig. 25. *Similodonta?* sp., composite mould of left valve showing fine concentric ornament and anterior adductor muscle scar, UM K4241, Bardahessiagh Formation (Caradoc), south of Craighbardahessiagh, Pomeroy, $\times 3$.



TUNNICLIFF, Ordovician bivalves

but also tend to have more teeth (17–22) and no detail of the sculpture is given. *N. ciae* Sharpe (1853, p. 149, pl. 9 fig. 5a–c) from Portugal has a similar number of teeth (c. 19) and is described as having fine concentric lines like *P. praetermissa*. However, *P. praetermissa* differs from Bradshaw's (1970, pp. 633–636) *Praeleda ciae* (Sharpe) in the posterior teeth: in Bradshaw's *P. ciae* and in Babin's *Ctenodonta ciae* (Sharpe) (Babin 1966, pp. 49–52, text-fig. 11) the posterior chevron-shaped teeth seem to point away from the umbo, in *Praenucula praetermissa* the chevrons point towards the umbo. In this respect *P. praetermissa* resembles Sharpe's *N. ciae*.

A single internal mould of a large left valve (IGS NIL 8972; Pl. 7, fig. 20) from the Killy Bridge Formation of the Crocknagargan Stream Section is like *P. praetermissa* in shape, but is 16 mm long and 13 mm high with a maximum inflation of 4 mm. The hinge-plates meet at an angle of 145° with 13 anterior and 15 posterior teeth meeting below the umbo. Its musculature is indistinct and sculpture unknown. Because of its large size and more central umbo, it is here recorded as *P. aff. praetermissa*.

A second specimen (IGS NIL 8934; Pl. 7, figs. 22, 23) from the same horizon and locality is also recorded as *P. aff. praetermissa*. It is large, 11.8 mm long, but crushed dorso-ventrally. The umbo is at the mid-point and the hinge-plates meet at an angle of 165° with 12 anterior and 14+ posterior chevron-shaped teeth meeting below the umbo. The adductor muscle scars are round and equal in size, about one-quarter of the valve height in diameter and each is close below and slightly anterior to the end of the corresponding dental series. The sculpture is unknown. It differs from *P. praetermissa* in its more central umbo and in having more teeth corresponding to its large size.

The collections at IGS contain a specimen (IGS PT 9049) from the Corona Beds, Dufton Shales (Caradoc, Longvillian) which is comparable with both *P. praetermissa* and *P. pulchra armoricana*.

Praenucula infirma sp. nov.

Plate 7, figs. 6–15, 17–19; text-fig. 3b

Derivation of name. From the Latin *infirma*, weak, referring to the small size of the adductor muscle scars.

Type specimens. Holotype, IGS NIL 8935, an internal mould of a right valve, from the Killy Bridge Formation of the Crocknagargan Stream section (locality 1 of Mitchell 1977) Pomeroy, Co. Tyrone. Paratypes: 9 left and 5 right valves, internal, external, and composite moulds: IGS NIL 8754, 8772, 8824, 8828, 8938, 8952 all from the same locality as the holotype; IGS NIL 8444–8445 from the Tirnaskea Stream section; IGS Zs 2729, 2737–2738 from locality 3 of Mitchell 1977; IGS NIL 8682, 8682 *pars* from a ditch exposure at IGR H 7195 7385. All from the Killy Bridge Formation.

Measurements	L	H	H/L	AL/L	Angle
Max.	12.4 mm	9.0 mm	0.81	0.64	160°
Min.	8.6 mm	4.2 mm	0.49	0.54	120°
Mean	10.4 mm	6.2 mm	0.68	0.59	145.5°
Median	10.5 mm	6.6 mm	0.65	0.59	140°

Description. Transversely subovate *Praenucula* in which the posterior end is slightly rounded or subtruncate and the front is rounded or somewhat angular. The height is usually between 0.6 and 0.7 of the length. The umbo is at about the posterior two-fifths. Maximum inflation of a single valve 2.2 mm seen in a valve 11.6 mm long and 9.0 mm high. The highest part of the shell is a little anterior of the umbo. The hinge-plates meet at an angle of about 140–145°; the anterior hinge-plate is broad and arched ventrally and bears up to eleven large teeth, the posterior hinge-plate bearing up to nine which are smaller and less markedly chevron-shaped. The dental series meet below the umbo. The adductor muscle scars are of equal size, in diameter about one-eighth of the valve height; the anterior scar is anterior to the end of the anterior hinge-plate and lies at the same height as the ventral edge of the plate. The posterior scar lies immediately below the end of the posterior hinge-plate. Both scars are distinct and quite strongly impressed. At least two umbonal muscle scars present. Sculpture of fine concentric lines, c. 16 per mm.

Discussion. The small size of the adductor muscle scars separates *Praenucula infirma* from other *Praenucula* species. In addition *P. infirma* is distinguished from *P. praetermissa* by its generally more elongate shape, and relatively shorter posterior hinge-plate with fewer teeth, and from *P. dispersa* by its larger, more strongly chevron-shaped teeth and more elongate shape. It bears some resemblance in shape to Hind's *Nuculana curta* (1910, p. 521, pl. 4, figs. 10-14, 14a, especially figs. 13, 14, 14a), but it lacks the central cartilage pit noted by Hind in that species. It differs in the same way from *Ctenodonta albertina* Ulrich and *C. filistriata* Ulrich (1894, pp. 598-599, pl. 42, figs. 76-82, text-fig. 44). It lacks the posterior lobe seen in *N. lobata* Hind (1910, p. 519, pl. 4, figs. 1-3). *P. infirma* shows no grouping of the growth lines as seen in *Deceptrix pulchra armoricana* Babin and Melou 1972 (= *D. cf. ciae* (Sharpe) of Babin and Robardet 1973) from the Caradoc of Normandy. Like *P. praetermissa*, *P. infirma* differs from *Praealeda ciae* (Sharpe) of Bradshaw (1970, pp. 633-636) and *C. ciae* (Sharpe) of Babin (1966, pp. 49-52, pl. 1, fig. 9) in the posterior teeth, the chevrons apparently pointing away from the umbo in the *C. ciae* specimens illustrated, but pointing towards it in *infirma*. This feature is, however, less marked than in *Praenucula praetermissa*. In this respect *P. infirma*, like *P. praetermissa*, resembles Sharpe's original *N. ciae* (1853, p. 149, pl. 9, figs. 5a-c).

GENUS DECEPTRIX Fuchs, 1919

Type-species. By monotypy, *Deceptrix carinata* Fuchs 1919, p. 79, pl. 7, figs. 1, 2. See discussion under Praenuculidae above.

Deceptrix sp.

Plate 8, figs. 15, 18

v. pars. 1843 *Arca regularis* Portlock, p. 427, pl. 34, fig. 2 [see *Deceptrix regularis*; IGS GSM 7805].

Material. Two left valves, IGS GU 1896 and UM K4202 and one right valve, IGS GSM 23215.

Horizon and locality. Bardahessiagh Formation; south of Craigbardahessiagh, Pomeroy, exact localities uncertain.

Description. Shell subquadrate, truncate posteriorly and slightly rounded to subtruncate anteriorly. The height to length ratio is between 0.62 and 0.68 and the umbo is at about the anterior two-fifths. Inflation of single valve 1.5 to 2.0 mm. The anterior and posterior hinge-plates meet at an angle of 140 to 150°. 4+ anterior and 10+ posterior teeth are visible in the specimens despite imperfect preservation. Anterior and posterior muscle scars indistinct, lying close below the ends of the hinge-plates. Sculpture of fine concentric lines of variable strength.

Discussion. Like other nuculoids, *Deceptrix* is uncommon in the Bardahessiagh Formation, and they can all be described under one heading. Lacking complete information on dentition and musculature, no specific name is proposed.

A specimen in the Sedgwick Museum (A16306; a left valve) is said to be from the Bardahessiagh Formation and may belong to the same species, but the anterior appears deformed and is very slender compared with the posterior.

A specimen collected by Fearnside, Elles and Smith, SM A16295, also from the Bardahessiagh Formation, was described by Reed (1952, p. 65) as *Ctenodonta cf. nitida* (Ulrich). It is a badly preserved left valve with 8+ posterior and 3+ anterior teeth, the dentition being obscured in part. Its height is 11 mm, and length 14 mm, giving height to length ratio 0.79. The umbo is at about the anterior third. The angle between the anterior and posterior hinge-plates is 115° and the inflation of the single valve is 2 mm. The musculature is unknown. It is unlike other *Deceptrix* from the Bardahessiagh Formation in having a more rounded outline and the umbo closer to the anterior. As Reed (1952, p. 65) observed, it bears a strong resemblance in form to *Ctenodonta nitida* (Ulrich 1894, p. 592, pl. 42, figs. 44-49), but he was clearly mistaken in suggesting that this specimen belongs to the same species as McCoy's *Arca quadrata* (see *Deceptrix apjohni*) and his comparison with *Nuculites dissimilis* (Portlock) is equally mistaken (see *N. cylindricus*).

Deceptrix apjohnni (Portlock 1843)

Plate 8, figs. 7, 8, 10, 11, 13, 14, 16, 17; text-fig. 4a

- v* 1843 *Pectunculus Apjohnni* Portlock, p. 429, pl. 34, fig. 8.
 v. 1843 *Pectunculus? ambiguus* Portlock, p. 430, pl. 34, fig. 11.
 v. 1846 *Pectunculus Apjohnni* Portlock; McCoy, p. 19.
 v. 1846 *Arca quadrata* McCoy, p. 20, pl. 2, fig. 5 (reversed).
 . 1878 *Ctenodonta ambigua* Portlock; Baily, p. 28.
 v. 1952 *Ctenodonta apjohnni* (Portlock); Reed, p. 60.

Type-specimens: IGS GSM 12409, Portlock's (1843, pl. 34, fig. 8) figured specimen, is here selected as lectotype of *Pectunculus apjohnni*; paralectotype UM K4219. The only known syntype of *P.? ambiguus* Portlock, IGS GSM 12410, is here selected as lectotype of *P. ambiguus*. The figured specimen of *Arca quadrata* McCoy NMI G.3. 1979, which is in the Griffith Collection, and which is the only known syntype, is here selected as lectotype of *A. quadrata*. All are from the Killey Bridge Formation, Pomeroy, exact locality uncertain, but possibly locality 3 of Mitchell, 1977.

Material: Sixteen specimens in IGS, BM, NMI, UM.

Horizon and locality. All from the Killey Bridge Formation (Ashgill, Cautleyan), with well-localized specimens recorded from the Crocknagargen Stream section (locality 1 of Mitchell 1977) and the Tirnaskea Stream section. Specimens from old collections are less well localized.

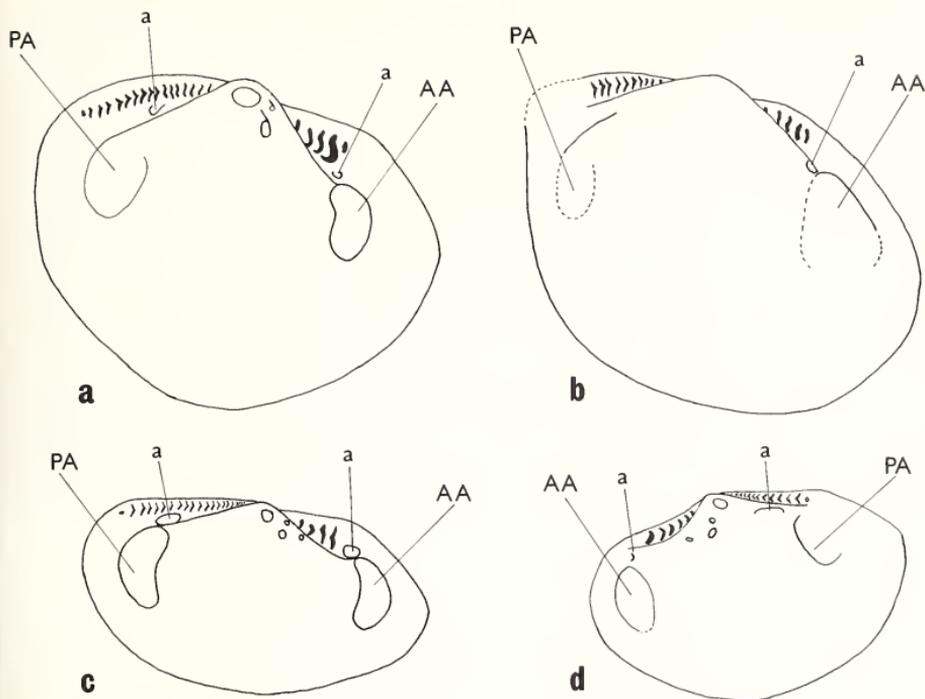
Measurements	L	H	H/L	AL/L	Angle
Max.	14.0 mm	14.0 mm	1.17	0.5	160°
Min.	4.8 mm	4.4 mm	0.81	0.32	125°
Mean	11.78 mm	10.23 mm	0.93	0.36	145°
Median	9.4 mm	9.2 mm	0.99	0.41	142.5°

Description. Rounded *Deceptrix*, occasionally subquadrate (as in *A. quadrata*), usually increasing in height towards the front. The postero-dorsal margin extends a little beyond the posterior hinge-line while the anterior hinge-plate occupies about half the length of the well-rounded antero-dorsal margin. The umbo is situated between the mid-point and the anterior third. Height occasionally greater than length but generally the height to length ratio is about 0.9-1.0. Maximum inflation of a single valve 4 mm seen in the lectotype, 14 mm long and 13 mm high. The posterior hinge-line is straight or gently curved, generally bearing up to 17 teeth (exceptionally 26 as in *A. quadrata*); the anterior hinge-plate is nearly straight or gently arched towards the body of the shell with 10+ teeth. The anterior and posterior hinge-plates meet below the umbo at an angle of 140-150°. The anterior adductor muscle scar is below the end of the anterior dental series, at about half the height of the shell and is one-quarter to one-third the height in diameter. The posterior adductor muscle scar is similar in size to the anterior scar and is close below the posterior dental series, a little anterior to its end. The scars of three umbonal accessory muscles are present (Pl. 8, fig. 17). Sculpture is of fine concentric lines, often of variable strength towards the margin. Pallial line not seen.

Discussion. Portlock (1843, p. 429) described his *Pectunculus apjohnni* as a 'very well marked species' and its well-rounded or subquadrate appearance is certainly distinctive in the Killey Bridge Formation fauna. It can only be confused, if fragmentary, with *Deceptrix semitruncata* but the two have distinctive forms, *D. apjohnni* more rounded and *D. semitruncata* more obliquely elongate and do not overlap in the range of their height-length ratios.

McCoy's *A. quadrata* is here regarded as synonymous with *D. apjohnni*. *A. quadrata* was described as 'rare' by McCoy (1846, p. 20) and only the type specimen is known and although it differs from Portlock's figured specimen of *D. apjohnni* in the manner outlined by McCoy, in particular its apparently square form (the result of the ventral margin being obscured by matrix), it is here considered to be an atypical specimen of *D. apjohnni*.

Reed (1952, pp. 60-61) likened *D. apjohnni* to several North American species which would now be regarded as *Similodonta*, and in this he was clearly misled by the general shape of the shell, for the dentition plainly shows *D. apjohnni* to be *Deceptrix*. In *Similodonta* the anterior and posterior teeth are equal in number and size. Of the described species of *Deceptrix*, none matches *D. apjohnni*



TEXT-FIG. 4. *Deceptrix* spp. based on internal moulds, $\times 5$. (a) *D. apjohni* (Portlock), IGS NIL 8910, right valve. (b) *D. semitruncata* (Portlock), IGS GSM 12421, right valve. (c) *D. subtruncata* (Portlock), IGS NIL 8971, right valve. (d) *D. regularis* (Portlock), IGS NIL 8919, left valve. Abbreviations as in text-fig. 3. Note the differences in size and positions of the muscle scars and the differences in number and distribution of teeth. Pedal accessory muscle scars are shown but not labelled in (a), (c), and (d).

so closely in shape as the type species *D. carinata* Fuchs, 1919, which has fewer anterior and more posterior teeth.

Deceptrix semitruncata (Portlock 1843)

Plate 8, figs. 9, 12; text-fig. 4b

- v* 1843 *Pectunculus semi-truncatus* Portlock, p. 429 (*pars*), pl. 34, fig. 7.
- . 1878 *Ctenodonta semi-truncatus* Portl. (probably *transversa*); Bailly, p. 28.
- v? 1910 *Ctenodonta semitruncatus* Portlock; Hind, p. 525, pl. 3, figs. 23–25.
- v. 1952 *Ctenodonta semitruncata* (Portlock); Reed, p. 60, pl. 3, fig. 3.

Type-specimens. Lectotype selected by Reed 1952, p. 60, IGS GSM 12421, the specimen figured by Portlock; from the Killey Bridge Formation, Pomeroy, exact locality uncertain. K4203, a syntype of *Pectunculus semitruncatus* is now identified as *Praenucula sp.* from the Bardahessiagh Formation.

Material, horizon, and localities: Seven specimens in IGS and UM, all from the Killey Bridge Formation, recorded from the Crocknagargan Stream section (locality 1 of Mitchell 1977) and in the Portlock Collection, exact locality uncertain.

Measurements	L	H	H/L	AL/L	Angle
Max.	17.0 mm	13.0 mm	0.8	0.52	160°
Min.	11.0 mm	9.0 mm	0.65	0.36	140°
Mean	15.29 mm	11.14 mm	0.73	0.44	150°
Median	14.0 mm	11.0 mm	0.72	0.44	150°

Description. Obliquely ovate *Deceptrix*, increasing in height towards the anterior, in which the height to length ratio is between 0.6 and 0.8 and maximum inflation of a single valve seen is 3 mm. The umbo is situated between the midpoint and the anterior third. The posterior margin is truncate and the anterior margin is produced obliquely and is sometimes angular antero-ventrally where it is met by a slight umbonal ridge. The posterior hinge-plate is straight or very gently curved, bearing 17+ teeth. The anterior hinge plate is straight or slightly arched towards the body of the shell with 11+ teeth. The anterior and posterior dental series meet beneath the umbo. The anterior and posterior hinge-plates meet at an angle of about 150°. Musculature indistinct: anterior adductor muscle scar is at about half the height of the shell, below and a little before the end of the anterior dental series; posterior adductor muscle scar is below the hind third of the posterior dental series. Sculpture is of fine concentric lines of variable strength.

Discussion. *D. semitruncata* is compared with *D. apjohnni* under that species. *D. semitruncata* is similar in shape to *Ctenodonta britannica* Babin (1966, p. 54, pl. 1, figs. 1, 2), which may be referable to *Deceptrix* but which has more numerous anterior teeth on a hinge-plate apparently arched away from the body of the shell. *C. socialis* Ulrich (1894, p. 594, pl. 37, figs. 59, 60) is also similar in shape to *D. semitruncata* but is a very small species with relatively fewer anterior teeth (6 out of 19, as opposed to 11 out of 17 in *D. semitruncata*). No other described species of *Deceptrix* is readily comparable with *D. semitruncata*.

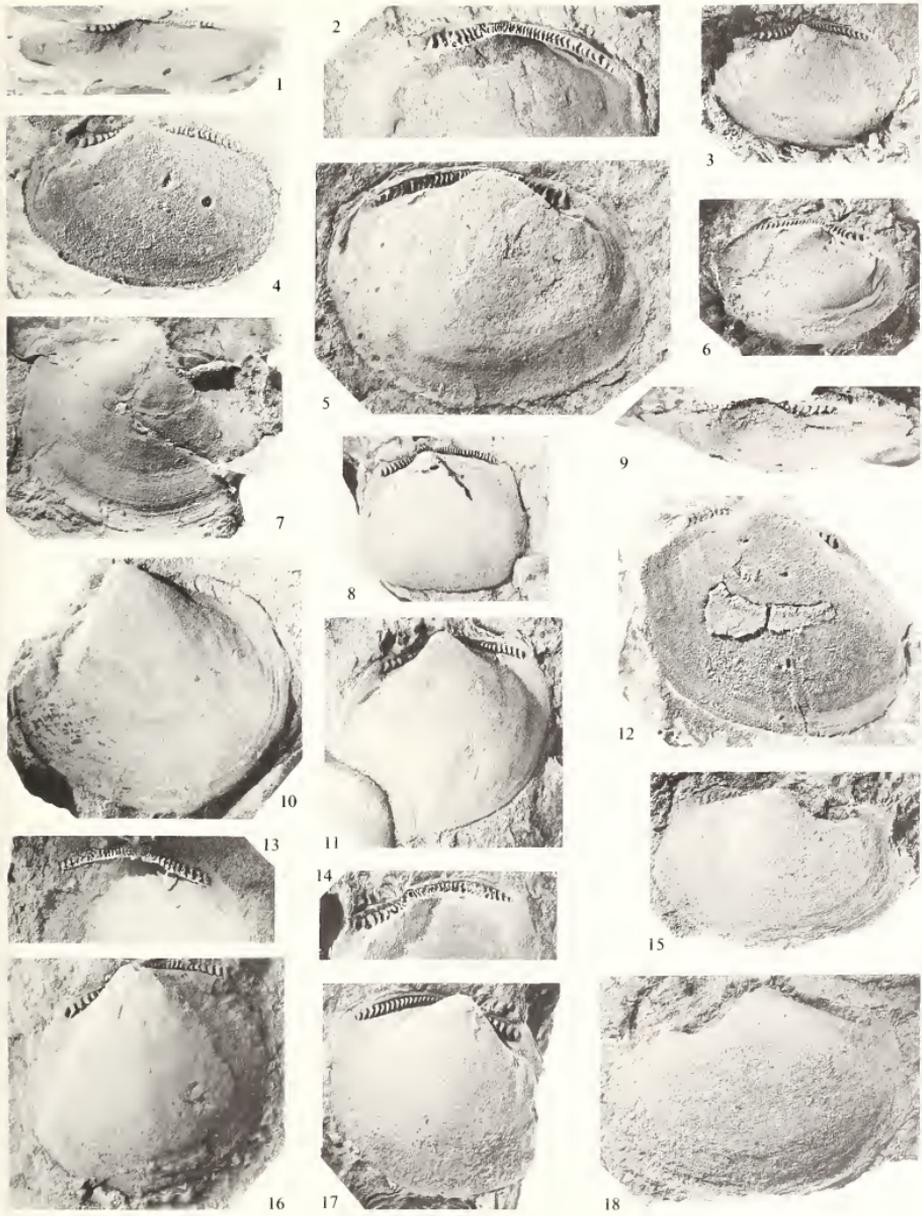
Deceptrix regularis (Portlock 1843)

Plate 8, figs. 1-6; text-fig. 4d

- v* pars 1843 *Arca regularis* Portlock, p. 427, pl. 34, fig. 2.
 . 1878 *Ctenodonta regularis* Portlock; Baily, p. 28.
 v pars. 1910 *Deceptrix regularis* Portlock; Hind, p. 524, ?pl. 3, figs. 15-17.
 v. 1952 *Ctenodonta regularis* (Portlock); Reed, p. 61, pl. 3, fig. 4.

EXPLANATION OF PLATE 8

- Figs. 1-6. *Deceptrix regularis* (Portlock 1843). 1, 4, oblique dorsal view and lateral view, internal mould of left valve, IGS GSM 12419, Pomeroy, exact locality uncertain. 2, 5, lateral view and latex cast, internal mould of right valve, IGS NIL 8803, Crocknagargan Stream section, Pomeroy (IGR c.H721737). 3, 6, lateral view and latex cast, internal mould of left valve, IGS NIL 8919, Crocknagargan Stream section, Pomeroy (IGR c.H721737). All Killely Bridge Formation (Ashgill, Cautleyan), × 3.
- Figs. 7, 8, 10, 11, 13, 14, 16, 17. *Deceptrix apjohnni* (Portlock 1843). 7, latex cast of external mould of right valve, IGS GSM 12410, lectotype of *Pectunculus ambiguus* Portlock, 1843, Pomeroy, exact locality uncertain, × 3. 8, internal mould of left valve, NMI G.3. 1979, lectotype of *Arca quadrata* McCoy, 1846, Pomeroy, exact locality uncertain, × 2. 10, internal mould of left valve, lectotype, IGS GSM 12409, Pomeroy, exact locality uncertain, × 3. 11, incomplete internal mould of left valve, UM K4253, Pomeroy, exact locality uncertain, × 3. 13, 16, latex cast of hinge and lateral view, internal mould of left valve BM LL40005, locality 3 of Mitchell, 1977 (IGR H72977268), × 3. 14, 17, latex cast of hinge and lateral view, internal mould of right valve, IGS NIL 8910, Crocknagargan Stream section, Pomeroy (IGR c.H721737), × 3. All Killely Bridge Formation (Ashgill, Cautleyan).
- Figs. 9, 12. *Deceptrix semitruncata* (Portlock 1843), oblique dorsal view and lateral view, internal mould of right valve, lectotype, IGS GSM 12421, Killely Bridge Formation (Ashgill, Cautleyan), Pomeroy, exact locality uncertain, × 3.
- Figs. 15, 18. *Deceptrix* sp. 15, composite mould of right valve, IGS GSM 23215. 18, composite mould of left valve, UM K4202. Both Bardahessiagh Formation (Caradoc), south of Craigbardahessiagh, Pomeroy, × 3.



TUNNICLIFF, Ordovician bivalves

Type-specimens. Lectotype (as 'holotype') inadvertently designated by Hind (1910, p. 524), IGS GSM 7805, probably the specimen figured by Portlock (1843, pl. 34, fig. 2); remaining syntypes IGS GSM 12419, 23215, UM K4202. GSM 23215 and K4202 are now identified as coming from the Bardahessiagh Formation, exact locality uncertain, and are referred to *Deceptrix* sp. The lectotype and remaining syntype are from the Killey Bridge Formation, Pomeroy, exact locality uncertain but possibly locality 3 of Mitchell 1977.

Material, horizon, and localities. Two specimens from the Portlock Collection, IGS GSM 7805, 12419 and two from recent collections, IGS NIL 8803, 8919. All are from the Killey Bridge Formation; the locality of the Portlock specimens is uncertain but the remaining specimens are from the Crocknagargan Stream section (locality 1 of Mitchell 1977).

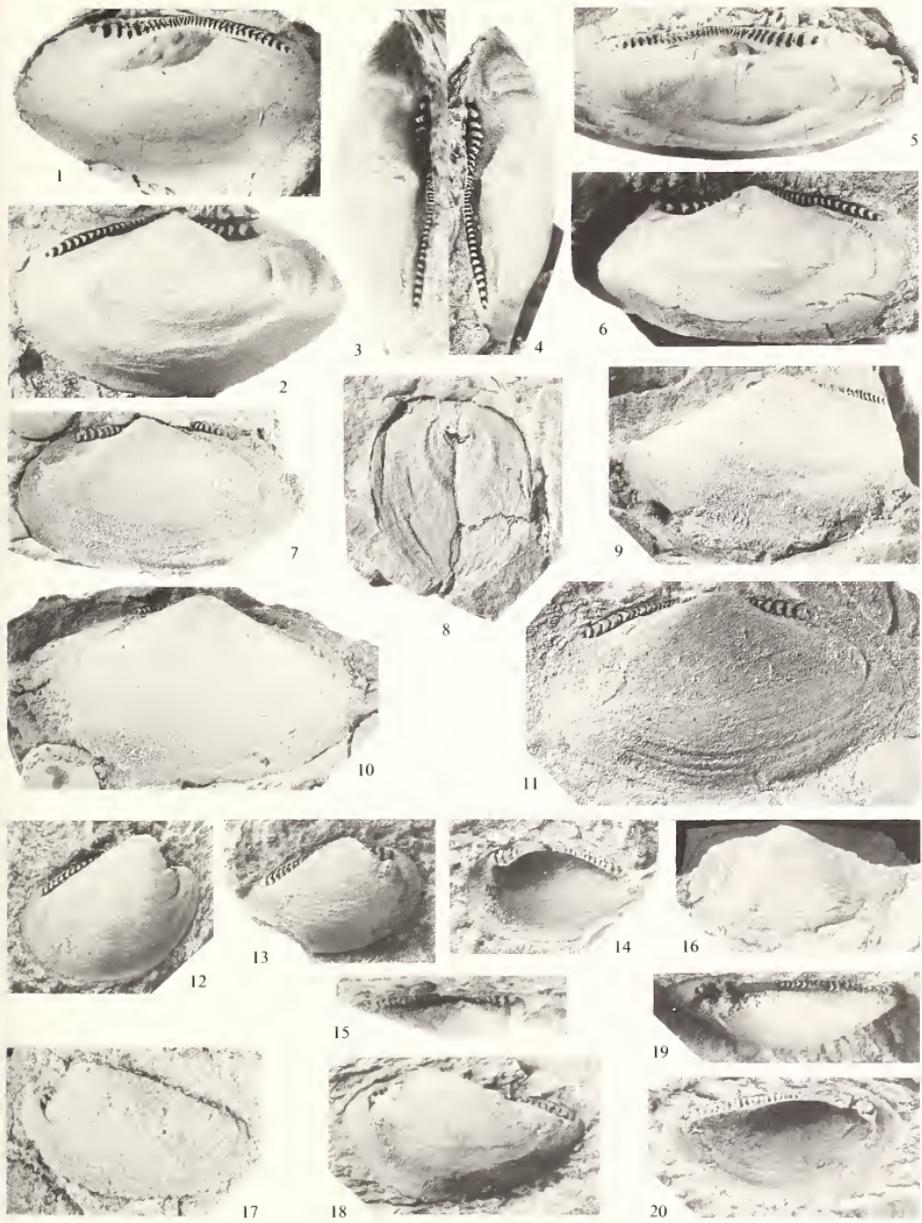
Measurements	L	H	H/L	AL/L	Angle
Max.	17.5 mm	13.0 mm	0.75	0.46	150°
Min.	10.5 mm	7.0 mm	0.64	0.36	145°
Mean	9.5 mm	13.5 mm	0.70	0.42	148.75°
Median	14.0 mm	10.0 mm	0.70	0.41	147.5°

Description. Transversely ovate *Deceptrix*, rounded at both anterior and posterior ends increasing in height slightly towards the rear. Height to length ratio about 0.7. The umbo is at about the anterior two-fifths. The maximum inflation of a single valve is 3 mm. The anterior and posterior hinge-plates meet below the umbo at an angle of 150° with a continuous series of nearly twice as many smaller posterior teeth than anterior teeth, up to 15 anterior and 25 posterior in a large specimen (Pl. 8, figs. 2, 5). The posterior hinge-plate is gently curved, the anterior is slightly arched towards the body of the shell. Adductor muscle scars vary from quite strongly impressed (Pl. 8, figs. 3, 6) to indistinct. Anterior scar lies below and a little in front of the end of the anterior teeth; the posterior scar lies a little anterior to the end of the posterior teeth. Three umbonal accessory muscle scars are present (Pl. 8, figs. 3, 6). Sculpture is not well seen in the specimens but appears to be of fine concentric lines.

Discussion. The lectotype of *Deceptrix regularis*, IGS GSM 7805, shows little other than the shape and is not illustrated here. It is perhaps surprising that Hind (1910, p. 524) regarded this as the type since GSM 12419 shows dentition, and there is no clear evidence which was the specimen figured by Portlock [see Tunnicliff 1980].

EXPLANATION OF PLATE 9

- Figs. 1-7, 9-11. *Deceptrix subtruncata* (Portlock 1843). 1-6, IGS NIL 8971, slab with internal moulds of both valves, Crocknagargan Stream section, Pomeroy, (IGR c.H721737): 1, 2, latex cast and lateral view of right valve; 5, 6, latex cast and lateral view of left valve (in fig. 6, difficulty in lighting the subject has resulted in a shortened appearance of the anterior); 3, 4, dorsal views of left and right valves juxtaposed. 7, internal mould left valve, IGS GSM 12413, holotype of *Ctenodonta deserta* Reed 1952, Pomeroy, exact locality uncertain. 9, oblique dorsal view and lateral view, damaged internal mould of left valve, IGS GSM 12423, lectotype of *Arca transversa* Portlock 1843, Pomeroy, exact locality uncertain. 10, internal mould right valve, IGS GSM 12422, Pomeroy, exact locality uncertain. 11, internal mould right valve, lectotype, IGS GSM 12424, Pomeroy, exact locality uncertain. All Killey Bridge Formation (Ashgill, Cautleyan), $\times 3$.
- Fig. 8. *Hippocardia praeprestis* (Reed 1952), holotype, IGS GSM 24147, Killey Bridge Formation (Ashgill, Cautleyan), Pomeroy, exact locality uncertain, $\times 3$.
- Figs. 12-20. *Concavodonta imbricata* (Portlock, 1843). 12, internal mould of right valve, IGS Zs 2790. 13-15, composite mould of right valve, IGS GU 1583; 15, dorsal view; 14, latex cast; 13, lateral view. 16, ?external cast of left valve, NMI G.1. 1979, lectotype of *Nucula subacuta* McCoy, 1846. 17, ?composite mould of left valve, NMI G.2. 1979, cited by McCoy 1846 as *Nucula protei* Münster. 18-20, composite mould of left valve, BM LL40003; 18, lateral view; 19, dorsal view; 20, latex cast. All Killey Bridge Formation (Ashgill, Cautleyan), figs. 12-15, 18-20, from locality 3 of Mitchell 1977 (IGR H7297 7268), figs. 16, 17, Pomeroy, exact locality uncertain. All $\times 4$.



TUNNICLIFF, Ordovician bivalves

Although in position of umbo and in height-length ratio *D. regularis* closely matches the range of *D. semitruncata*, it can be readily distinguished from that species by its transverse rather than oblique elongation and its increase in height towards the posterior end, while *D. semitruncata* is highest towards the anterior end. It is less easy to distinguish between *D. regularis* and *D. subtruncata*, but the latter is always more transverse with the highest part of the shell at the umbo rather than towards the posterior end, and has relatively larger adductor muscle scars and fewer teeth.

Pojeta's illustrations of his *Deceptrix* (*D.*) n. sp. 1 (1978, pl. 1 figs. 1, 2) show a close similarity to *D. regularis* except that the umbo is closer to the mid-point and the shell is highest a little anterior of the umbo and thus more closely resembles *D. subtruncata*. No other species of *Deceptrix* is closely comparable with *D. regularis*.

Deceptrix subtruncata (Portlock 1843)

Plate 9, figs. 1-7, 9-11; text-fig. 4c

- v* 1843 *Arca sub-truncata* Portlock, p. 427, pl. 34, fig. 1.
 v pars. 1843 *Arca transversa* Portlock, p. 428, pl. 34, fig. 4 [non IGS GSM 12425 *Nuculites* sp.]
 v. 1843 *Arca Eastnori?* (Murchison); Portlock, p. 427, pl. 34, fig. 3.
 v. 1846 *Arca subtruncata* Portlock; McCoy, p. 20.
 v. 1846 *Arca transversa* Portlock; McCoy, p. 20.
 . 1878 *Ctenodonta transversa* Portl.; Baily, p. 28.
 v non. 1910 *Ctenodonta* aff. *transversa* Portlock; Hind, p. 523, pl. 3, figs. 12-14.
 1910 *Ctenodonta eastnori* Portlock; Hind, p. 525, pl. 3, fig. 20, ?figs. 21, 22.
 ? 1946 *Ctenodonta transversa* (Portlock); Reed, p. 202.
 v. 1952 *Ctenodonta subtruncata* (Portlock); Reed, p. 62, pl. 3, fig. 6.
 v. 1952 *Ctenodonta transversa* (Portlock); Reed, p. 63.
 v. 1952 *Ctenodonta deserta* Reed, p. 64, pl. 3, fig. 8.

Type-specimens. IGS GSM 12424, the specimen figured by Portlock (1843, pl. 34, fig. 1) is here selected as lectotype of *Arca subtruncata*; paralectotypes IGS GSM 12422, TCD 14763. IGS GSM 12423, the specimen figured by Portlock (1843, pl. 34, fig. 4) was selected as lectotype of *A. transversa* by Reed 1952, p. 68; remaining syntypes IGS GSM 12425, TCD 7854. The holotype of *Ctenodonta deserta* Reed is IGS GSM 12413 by original designation (1952, p. 64). All from the Killey Bridge Formation, Pomeroy, exact localities uncertain but possibly locality 3 of Mitchell 1977.

Material, horizon, and localities. Many specimens in IGS, UM, SM, TCD, in both old and recent collections, are all from the Killey Bridge Formation. Recent collections contain specimens recorded from localities 1 and 3 of Mitchell 1977, while old collection material is less well localized.

Measurements	L	H	H/L	AL/L	Angle
Max.	19.4 mm	11.4 mm	0.64	0.51	170°
Min.	10.0 mm	5.4 mm	0.54	0.37	140°
Mean	17.3 mm	10.15 mm	0.59	0.48	153.8°
Median	16.76 mm	10.26 mm	0.59	0.44	153.6°

Description. Transversely elongate, subelliptical *Deceptrix*, with obliquely subtruncate anterior and rounded posterior end. Maximum height of shell below umbo. Height to length ratio about 0.6. Umbo nearly central. Maximum inflation of a single valve is 5.0 mm in a valve 17.5 mm long and 10.0 mm high. Hinge-line straight or slightly curved; anterior and posterior hinge-plates meet at an angle of about 155-160° in most specimens. The posterior dental series is straight with up to twenty teeth seen in both right and left valves. The anterior dental series is slightly arched towards the body of the shell with up to twelve teeth in the right valve and thirteen in the left (a single, tiny subumbonal tooth in the left valve is here counted as anterior). The dental series meet below the umbo. Adductor muscle scars are large, nearly half the height of the shell in diameter, and distinct, each lying slightly in front of, and below the end of, its corresponding dental series. Four umbonal accessory muscle scars are present in each valve (Pl. 9, figs. 1-6), three distinct, one less so. Sculpture of fine concentric lines of variable strength especially towards the margin. Pallial line not seen.

Discussion. There is no basis on which *A. transversa* Portlock (IGS GSM 12423) or the specimen which he labelled and described as *A. Eastnori* can be separated from *Deceptrix subtruncata* (Portlock). Despite Reed's observations (1952, p. 63) to the contrary, and Portlock's original description (1843, p. 428), the proportions of the shell in *A. transversa* are not greatly different from those of *D. subtruncata* although the type specimen of *A. transversa* is incomplete and its length must be estimated. Portlock's figures of the three species (1843, pl. 34, figs. 1, 3, 4) are poor and measurements taken from them are unreliable.

Reed (1952, p. 64) quite reasonably dissociated Portlock's specimen of *A. eastnori* (GSM 12413) from Sowerby's species, but he failed to recognize its affinities with *D. subtruncata* and created a new species, *C. deserta*. The second Portlock specimen of *A. eastnori* (GSM 12414) which Reed compared to *C. cingulata* Ulrich is *Nuculites* sp.

The differences between *D. subtruncata* and *D. regularis*, with which it might be confused, are discussed under the latter species. Of the published species of *Deceptrix* none compares so closely with *D. subtruncata* as that figured by Pojeta (1978, pl. 1 figs. 1, 2) as *D. (D.)* n. sp. 1 which has similar numbers of teeth, position of umbo, and, in the case of Pojeta's figure 2, a closely similar height to length ratio to the maximum seen in *D. subtruncata*.

Genus SIMILODONTA Soot-Ryen, 1964

Type-species. Designated by Soot-Ryen 1964, p. 498, *Tellinomya similis* Ulrich, 1892.

Similodonta? sp.

Plate 7, fig. 25

Material. Left valve, UM K4205 and a slab, UM K4241, bearing a left and a right valve; all composite moulds.

Horizon and locality. Bardahehsiagh Formation, locality uncertain but south of Craigbardahehsiagh, Pomeroy.

<i>Measurements</i>	H	L	H/L	AL/L	Angle
K4241 (both valves)	15.0 mm	16.0 mm	0.94	0.5	c. 110°
K4205	15.6 mm	14.0 mm	1.11	0.5	95–100°

Description. Triangular, equivalve, about as high as long with the umbo at the centre. Anterior and posterior hinge-plates meeting at about 100°. Details of hinge unknown. Anterior adductor muscle scar distinct, lying below anterior end of the anterior hinge-plate which is arched towards the body of the shell. Posterior adductor muscle scar not known. Auxiliary musculature unknown. Sculpture of fine concentric striae (about 7 per mm) with coarser striae developing at later growth stages.

Discussion. Reed's description (1952, p. 63) of *Ctenodonta perangulata* suggests that *C. perangulata* should be placed in *Similodonta*, but examination of his holotype (SM A16454) has shown it to be a *Nuculites* and it is here considered to be synonymous with *Nuculites cylindricus* (Portlock).

Genus CONCAVODONTA Babin and Melou, 1972

Type-species. Originally designated by Babin and Melou 1972, p. 83, *Nucula ponderata* Barrande, 1881, from the Vinice, Zahořany, and Bohdalec Formations (Caradoc) of Bohemia (Havlíček and Vaněk 1966), recorded again from Bohemia by Pfab 1934, and also recorded from the Upper Ordovician of Normandy (Babin and Robardet 1973), and, with doubt, the Caradoc of Brittany (Babin and Melou 1972).

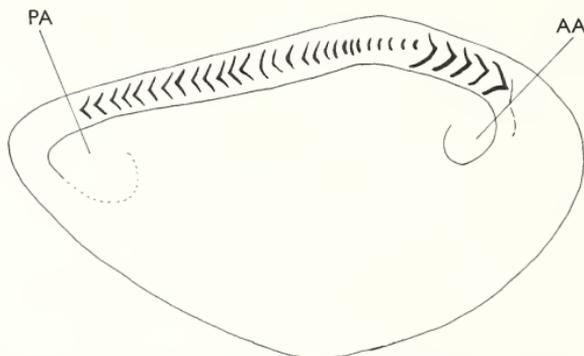
Diagnosis after Babin and Melou (1972, p. 83). Genus of Praenuculidae of fairly rounded shape, the posterior extremity being a little more slender than the anterior. Umbo prosogyrate. Imprints of adductor muscles subequal, the anterior more strongly impressed in the shell at its posterior edge. Pallial line complete. Teeth concavodont, that is, characterized by teeth in chevron with the concavities towards the umbo. Ornamentation fairly strong and regular, concentric.

Concavodonta imbricata (Portlock 1843)

Plate 9, figs. 12-20; text-fig. 5

- * 1843 *Nucula acuta?* (Sowerby) var. *imbricata* Portlock, p. 430, pl. 34, fig. 10.
 v. 1846 *Nucula protei* Münster; McCoy, p. 19.
 v. 1846 *Nucula subacuta* McCoy, p. 19, pl. 2, fig. 3 (reversed).
 v non. 1910 *Nuculana imbricata* Portlock; Hind, p. 519, pl. 4, figs. 4-7, 7a [none of these specimens is referable to *Concavodonta* but are referable to ?*Praenucula*. Name *imbricata* re-established].
 v. 1952 *Nuculana?* *imbricata* (Portlock); Reed, p. 66 [affirms the use of *imbricata*].
 v. 1952 *Ctenodonta* cf. *gibberula* (Salter); Reed, p. 65.

Type specimens. Portlock's type specimen remains untraced (Tunnicliff 1980). A lectotype for *Nucula subacuta* McCoy, 1846, is here designated NMI G.I. 1979, the only known syntype.



TEXT-FIG. 5. *Concavodonta imbricata* (Portlock), dentition and musculature based on composite mould, left valve, BM LL40003, c. $\times 10$. Compare with Pl. 9, fig. 20. Abbreviations as in text-fig. 3.

Material. Thirty-six specimens in IGS, UM, BM, SM, mostly internal moulds of single valves, some with counterparts, many apparently composite moulds showing the concentric ornament on the internal mould.

Horizon and localities. All specimens are from the Killiey Bridge Formation, of Pomeroy, Co. Tyrone. Most specimens are from locality 3 of Mitchell 1977. Others are from localities 1 and 2 of Mitchell and from the Tiraskea Stream section. Specimens from old collections are less precisely localized.

<i>Measurements</i>	L	H	H/L	AL/L	Angle
Max.	9.4 mm	6.6 mm	0.923	0.455	155°
Min.	3.8 mm	2.4 mm	0.517	0.250	100°
Mean	6.6 mm	4.5 mm	0.685	0.3367	131.1°
Median	6.6 mm	4.5 mm	0.720	0.3525	127.5°

Description. Ovate, equivalve nuculoid. Height generally about 0.7 of the length but variable. Prosogyrate umbo at about the anterior third and extending a little above the hinge-line. Convexity greatest below umbo, maximum inflation of a single valve 1.6 mm seen in a valve 9.4 mm long and 5.0 mm high. Angle between anterior and posterior hinge-plates about 130°. Posterior hinge-plate straight. Teeth concavodont (see generic diagnosis), anterior larger than posterior, apparently passing beneath umbo in a continuous series. 6+ anterior teeth in both valves, 19+ posterior teeth seen in right valve and 16+ in left valve (29 posterior teeth were seen in one large left valve (Pl. 9, fig. 20)). Anterior and posterior adductor muscle scars clearly distinguished; anterior slightly larger and more deeply impressed than posterior and most deeply impressed on its posterior

edge. Accessory muscles unknown. Pallial line probably represented by a change in convexity close to the ventral margin. Ligament and shell material unknown. Two forms of concentric sculpture observed; coarse (3 to 6 striae per mm) giving the imbricate appearance (Pl. 9, fig. 13), and fine (12 to 20 striae per mm) (Pl. 9, fig. 12).

Discussion. This is the first record of *Concavodonta* from the British Isles but material under study from Caradoc and Ashgill rocks in north Wales includes examples of *Concavodonta* sp. Specimens not showing the dentition may be distinguished from *Deceptrix* and *Praenucula* by the relatively coarse concentric sculpture, the position of the umbo and especially the straight posterior hinge-line. Ulrich's figures (1894, p. 589, pl. 38, figs. 25-28; pl. 42, figs. 38-40) of *Ctenodonta planodorsata* (Ulrich), from the Trenton Shale, show similar straight sets of concavodont teeth, but the angle between the anterior and posterior hinge-plates is more acute (105°) and the position of the posterior adductor muscle scar differs, being in line with the posterior hinge-plate in *C. planodorsata* but lying internally (i.e. antero-ventrally) to the teeth in *Concavodonta imbricata*. *C. ponderata*, as described and figured by Babin and Melou (1972), Babin and Robardet (1973), and by Pfab (1934), differs from *C. imbricata* only in that the posterior hinge-plate appears gently curved.

Superfamily NUCULANACEA H. Adams and A. Adams, 1858

Family MALLETHIDAE H. Adams and A. Adams, 1858

Genus NUCULITES Conrad, 1841

Type-species. Designated by Miller 1889, p. 496, *Nuculites oblongatus* Conrad, 1841, from the probable Middle Devonian (McAlester 1968, p. 37) of New York.

Nuculites cylindricus (Portlock 1843)

Plate 10, figs. 1-17

- ? 1841 *Nuculites planulatus* Conrad, p. 50 [see Bretsky and Bretsky 1977, for synonymy].
- v* 1843 *Arca cylindrica* Portlock, pp. 428, 759, pl. 34, fig. 9.
- v. 1843 *Arca dissimilis* Portlock, pp. 428, 759, pl. 34, fig. 5.
- v. 1843 *Arca obliqua* Portlock, pp. 429, 759, pl. 34, fig. 6.
- v pars. 1843 *Arca Eastnori* (Murchison); Portlock, pp. 427, 759, non pl. 34, fig. 3.
- v. 1846 *Arca cylindrica* Portlock; McCoy, p. 19.
- v. 1846 *Arca dissimilis* Portlock; McCoy, p. 20.
- v. 1846 *Arca obliqua* Portlock; McCoy, p. 20.
- 1875 *Ctenodonta obliqua* Portlock; Baily, p. 35, pl. 12, fig. 2.
- 1878 *Ctenodonta dissimilis* Portlock; Baily, p. 28.
- 1878 *Ctenodonta obliqua* Portlock; Baily, p. 28.
- v non. 1910 *Ctenodonta dissimilis* Portlock; Hind, p. 522, pl. 3, figs. 5-7.
- v non. 1910 *Ctenodonta eastnori* Portlock; Hind, p. 525, pl. 3, figs. 20-22.
- v non. 1910 *Ctenodonta obliqua* Portlock; Hind, p. 524, pl. 3, figs. 18, 19.
- ? 1946 *Clidophorus diu* Lamont, p. 365, pl. 1, fig. 3.
- v. 1952 *Clidophorus cylindricus* (Portlock); Reed, p. 66, pl. 3, fig. 9.
- v. 1952 *Ctenodonta dissimilis* (Portlock); Reed, p. 63.
- v. 1952 *Ctenodonta obliqua* (Portlock); Reed, p. 61, pl. 3, fig. 5.
- v. 1952 *Clidophorus occultus* Reed, p. 67, pl. 3, fig. 10.
- v. 1952 *Ctenodonta perangulata* Reed, p. 63, pl. 3, fig. 7.
- v pars. 1952 *Ctenodonta deserta* Reed, p. 65, non pl. 3, fig. 8 [IGS GSM 12414, non holotype IGS GSM 12413].

Type-specimens. Lectotype of *Nuculites cylindricus* (Portlock) here selected, IGS GSM 12416, the specimen figured and labelled by Portlock and described by Reed (1952, p. 66); paralectotypes are TCD 7876, 14761-14762, UM K4220, 4267. Lectotype of *Arca dissimilis* Portlock, selected Reed (1952, p. 63), IGS GSM 12411; paralectotype is IGS GSM 12412. For *A. obliqua* Portlock, Hind, (1910, p. 524) selected IGS GSM 12415 as lectotype, leaving paralectotypes IGS GSM 12417, 12418. The holotype of *Clidophorus occultus*

Reed is IGS GSM 12415 by original designation (*ocultus* becomes a junior objective synonym of *obliqua*). The holotype of *Ctenodonta perangulata* Reed is SM A16454 by original designation. The holotype of *Clidophorus diu* Lamont is Lamont Collection No. 1.

Material, localities, and horizon. Many specimens in IGS, TCD, UM, NMI, BM(NH), and SM, both in old and new collections. All are from the Killey Bridge Formation of Pomeroy. Apart from recently collected material especially from localities 1 and 3 of Mitchell (1977), specimens are generally poorly localized.

Measurements	L	H	H/L	AL/L
Max.	21.0 mm	16.0 mm	0.94	0.46
Min.	8.4 mm	3.8 mm	0.43	0.15
Mean	15.23 mm	9.1 mm	0.61	0.33
Median	14.7 mm	9.9 mm	0.68	0.30

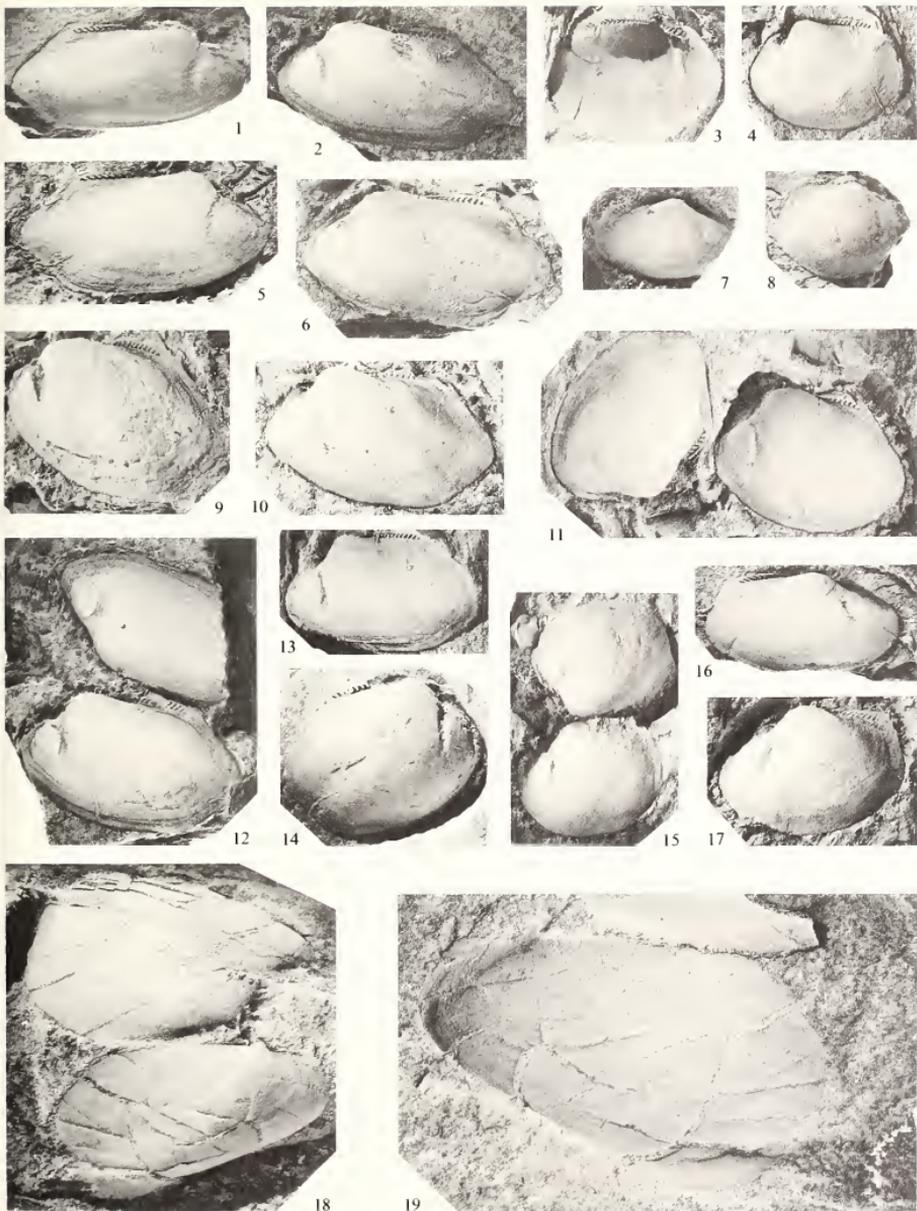
Description. *Nuculites* of very variable shape, from posteriorly elongate transversely or obliquely, or rounded, to more or less truncate posteriorly. Umbo between the mid-point and the anterior one-fifth. The height to length ratio varies between about 0.4 and 0.95. Many specimens show a posterior fold running from the umbo towards the postero-ventral margin (Pl. 10, fig. 5). Occasionally a weak anterior fold is developed running from the umbo towards the antero-ventral margin (Pl. 10, fig. 12), anterior to the position of the septum. Septal position indicated clearly by a strong impression on internal moulds and often evident on external moulds. The septum extends, usually vertically, from the hinge-line to half-way to the margin (e.g. Pl. 10, figs. 2, 9) but may appear to be directed slightly posteriorly (e.g. Pl. 10, figs. 1, 5) or more markedly towards the anterior end (e.g. Pl. 10, fig. 17). Posterior hinge-plate straight or slightly curved near the hind end (Pl. 10, fig. 9); anterior hinge-plate generally at an angle of about 150° to the posterior hinge-plate, but the angle is variable between 120 and 180°. Dentition taxodont: 3+ anterior teeth and 15+ posterior teeth. The anterior teeth are simple or slightly sigmoidal and are larger than the posterior teeth which are chevron-shaped pointing towards the umbo and becoming simpler towards the posterior end. Dentition below umbo obscured in all specimens. Maximum inflation of a single valve seen 3.5 mm in a valve 15.4 mm long. Anterior adductor muscle scar distinct and occupying much of the portion of the shell anterior to the septum: posterior adductor and other muscle scars unknown. Sculpture of fine (c. 16–20 per mm) concentric lines with some coarser lines interspersed, especially towards the margin in larger specimens.

Discussion. Bretsky and Bretsky (1977) have shown that *N. planulatus* Conrad, 1841, from the Upper Ordovician of Quebec is a highly variable species; Watkins (1978, p. 44) has done the same with the Silurian species *N. antiquus* (J. de C. Sowerby). This also appears to be the case with the Killey Bridge Formation species. As isolated specimens, the types of Portlock's *Arca cylindrica*, *A. dissimilis*, and *A. obliqua* appear to be different species but, seen in combination with the many other specimens of *Nuculites* both in old and recent collections, they appear to be extreme variants

EXPLANATION OF PLATE 10

Figs. 1–17. *Nuculites cylindricus* (Portlock 1843). All preserved as internal moulds. All Killey Bridge Formation (Ashgill, Cautleyan). 1, right valve, lectotype, IGS GSM 12416. 2, left valve, UM K4266. 3, 4, latex cast and lateral view, left valve, UM 1920–834. 5, right valve UM K4267. 6, left valve, UM K4226. 8, right valve, IGS GSM 12412. 9, left valve, IGS GSM 12418. 10, left valve, UM K4263. 11, left and right valves, probably of the same individual, UM K4264, lit from bottom right to accommodate both valves. 12, nearly conjoined valves, UM K4233. 14, right valve, IGS GSM 12415, lectotype of *Arca obliqua* Portlock 1843. 15, conjoined valves, IGS GSM 12411, lectotype of *Arca dissimilis* (Portlock 1843). 16, right valve, UM K4255. 17, left valve, UM K4231. All Pomeroy, exact locality uncertain, × 2½. 7, right valve, IGS GU 2087, 13, left valve, IGS GU 2061. Both locality 3 of Mitchell 1977 (IGR H7297 7268), × 2½.

Figs. 18, 19. *Nuculoid* gen. et sp. nov., IGS NIL 9240–1. 18, both valves, showing the fracturing of both and the greater displacement of parts of the left valve, × 2. 19, concave latex cast of composite mould, right valve showing the fine dentition, concentric ornament, and shallow sulcus, × 3. Tirnaskea Formation (Ashgill, Hirnantian), Crocknagargan Stream section, Pomeroy (IGR H722737).



TUNNICLIFF, Ordovician bivalves

of one form. There is no clear relationship between growth and height-length ratio that can be related to Portlock's species, and although many specimens may, by eye, be placed in one or other of Portlock's nominal species, there are others which fall between any two of the Portlock forms. I am unable to quantify any differences between these 'species' and choose therefore to place them in synonymy. There may be an argument for retaining Portlock's *obliqua* and *dissimilis* as terms for morphs.

Reed's (1952) *Clidophorus occultus* is a junior objective synonym of Portlock's *A. obliqua* and his *Ctenodonta perangulata* falls within the range of the *A. dissimilis* form. *Clidophorus diu* Lamont (1946), from the Lower Drummuck Group of Girvan, Ayrshire, appears from the figure and from Lamont's observations to fall within the range of the *A. cylindricus* form, differing only in the absence of the posterior fold commonly seen in specimens of that form.

Unfortunately, while Bretsky and Bretsky could relate the relative abundances of the different forms of *N. planulatus* to a known stratigraphic sequence, no such sequence is available in the Killey Bridge Formation, and each collection and locality is, in effect, isolated. Many specimens have only vague locality information.

On the basis of the description, figures, and measurements given by Bretsky and Bretsky it is not clear that *N. cylindricus* is distinct from *N. planulatus*, but Portlock's name is retained pending some closer comparison.

NUCULOID gen. and sp. nov.

Plate 10, figs. 18, 19; text-fig. 6

Material, horizon, and locality. A single specimen IGS NIL 9240-9241, showing nearly conjoined valves, crushed but apparently not distorted, preserved as a composite mould. From the Tirnaskea Formation (Ashgill, Hirnantian) of the Crocknagargan Stream section, Pomeroy, Co. Tyrone (IGR H722 737).

Description. Shell obliquely ovate and modioliform in appearance. For right valve, height 13.3 mm, length 22.9 mm giving a height-length ratio of 0.58. Inflation of the single valve at least 1.4 mm. The small, prosogyrate umbo is at the anterior three-tenths. A slight umbonal ridge runs to the postero-ventral angle at an angle of



TEXT-FIG. 6. Nuculoid gen. and sp. nov., based on latex cast of composite mould of right valve, IGS NIL 9240, $\times 6.5$. Compare with Pl. 10, fig. 19.

55° to the hinge-line, giving the shell its oblique appearance. A little posterior to the umbonal ridge is a shallow sulcus, reflected in the sculpture and sinus in the posterior margin. This sulcus is at an angle of 35° to the hinge-line. The posterior margin is otherwise rounded ventrally and obliquely slanted towards the hinge-line. The anterior margin is also obliquely slanted. The ventral margin is straight. The hinge-line is straight on both sides of the umbo, curving slightly at the posterior end. The anterior hinge-plate bears 3-4 thin blade-like parallel teeth, becoming shorter towards the anterior. The posterior hinge-plate bears 9+ similarly thin blade-like parallel teeth extending to the postero-dorsal angle. Musculature, ligament, pallial line unknown. Sculpture of fine regular concentric lines (about 7 per mm) more pronounced on the posterior slope of the shell.

Discussion. Bivalves are uncommon in the Tirnaskea Formation and are usually poorly preserved. It is unfortunate that this specimen, one of the best preserved from that horizon, should prove enigmatic. In outline it might be taken for *Modiolopsis* sp., but the presence of numerous taxodont teeth both before and behind the umbo precludes assignment to the Modiomorphidae. Suspicion that the teeth are the result of slight deformation can be dismissed since the anterior and posterior teeth are aligned contrariwise. This is endorsed by the way in which the posterior teeth of both valves can be seen in the specimen. Had these structures been produced by some post-depositional deformation, one would have expected them all to be parallel. It is possible but unlikely, that the structures are related to the ligament.

Although generally smaller in size than the Pomeroy specimen, *Silicula* Jeffreys, as described and illustrated by Allen and Sanders 1973, (pp. 263-309) and Allen 1978 (p. 394) shows many similar features: small umbones, ovate, flattened form, fine, elongate teeth. *Silicula* is a modern deep-sea protobranch of the family Siliculidae grouped by Allen (1978, p. 392) with the Malletiidae and others in the Nuculanoida. The strong resemblance in form to *Silicula* suggests that the Pomeroy specimen was a deep-water form, as would seem likely since the Tirnaskea Formation passes into the overlying graptolitic, presumably offshore, Llandovery strata (Mitchell 1977, p. 5).

Subclass PTERIOMORPHIA Beurlen, 1944

Order ARCOIDA Stoliczka, 1871

Superfamily CYRTODONTACEA Ulrich, 1894

Family CYRTODONTIDAE Ulrich, 1894

Genus CYRTODONTA Billings, 1858

Type species. *Cyrtodonta rugosa* Billings, 1858, by subsequent designation of Williams and Breger 1916, p. 149.

Cyrtodonta? expansa (Portlock 1843)

Plate 11, figs. 1, 3, 4, 9

- v* pars. 1843 *Modiola expansa* Portlock, p. 425, pl. 33, fig. 6 [pars: longer variety].
- v* pars. 1843 *Modiola Brycei* Portlock, p. 425, pl. 33, fig. 7 [pars: see *Cyrtodonta? securiformis* (Portlock)].
- v(?) 1843 *Modiola expansa* Portlock; McCoy, p. 18.
- v(?) 1875 *Modiolopsis expansa* Portlock; Baily, p. 35, pl. 12, fig. 2.
- 1878 *Modiolopsis expansa* Portlock; Baily, 1878 [includes *Brycei* in *expansa* with doubt].
- v. 1952 *Modiodesma expansum* (Portlock); Reed, p. 71, pl. 3, fig. 16.
- v. 1952 *Goniophora brycei* (Portlock); Reed, p. 78 [pars: see *Cyrtodonta? securiformis* (Portlock)].

Type-specimens. Lectotype here selected, IGS GSM 12445, the type of Portlock's long variety of *M. expansa* (1843, p. 425). For Portlock's small variety see *Cyrtodonta? securiformis* (Portlock). Lectotype of *Modiola brycei* Portlock here selected IGS GSM 12443, Portlock's figured specimen: other syntypes (paralectotypes) IGS GSM 12444, GSM 22038 (not certainly a syntype), UM K4206-4210, 4249. All from the Bardahessiagh Formation, Pomeroy, Co. Tyrone, exact localities uncertain, south of Craigbardahessiagh.

Material, localities, and horizon. A few specimens in IGS (GSM 12443-5) and UM (K4244, 4247, ?4248, ?4249) all from the Portlock Collection. Two specimens in the Griffith Collection at NMI may belong to this species. All composite moulds from the Bardahessiagh Formation, locality as above.

Measurements of type-specimen. IGS GSM 12445: H 29.6 mm, L 50.6 mm, AL 8.6 mm.

Description. Elongate, obliquely ovate, becoming higher towards the posterior end, with a height-length ratio between about 0.6 and 0.7. The straight hinge-line is about half as long as the total length of the shell. Antero-dorsal margin almost straight or gently curved and meeting the hinge-line at an angle of about 150°. Ventral margin almost straight. Umbones prosogyrate and placed at about 0.15 of the length from the front, projecting a little above the hinge-line. A rounded umbonal ridge extends backwards at about 35° from the hinge-line to the ventral margin at the point furthest from the umbo. Preservation poor, but two posterior lateral teeth can be seen at the posterior end of the hinge-line in the right valve and one in the left. anterior teeth are not known. The anterior adductor muscle scar is small, the posterior is unknown. Maximum inflation seen in a single undistorted valve is 4.1 mm in a valve 45 mm long. Sculpture of irregular concentric striae.

Discussion. *C.?* *expansa* and *C.?* *securiformis* (Portlock) show the effects of distortion more than other species from the Bardahessiagh Formation and this has influenced their nomenclatorial history. Portlock (1843, p. 425) noted two varieties of *M. expansa*; a longer variety, which he figured (1843, pl. 33, fig. 6), and a smaller variety which he described briefly. The smaller variety is now placed in *C.?* *securiformis*. Portlock's *M. brycei* (1843, p. 425, pl. 33, fig. 7) was based on specimens which he described as 'somewhat distorted by pressure' (1843, p. 426). Reed (1952) removed the specimens of Portlock's smaller variety from *M. expansa* and placed them in two new species, *Orthodesma tyronense* (1952, p. 71) and *Whiteavesia subexpansa* (1952, p. 72). These are now placed in *C.?* *securiformis*. Examination of Portlock's type material, some of which was not available to Reed, shows that those specimens which both Portlock and Reed placed in *brycei* are either *expansa* or *securiformis* which have been, as Portlock observed, crushed dorso-ventrally. In every case, the line of the umbonal ridge has proved the weakest and has produced, under pressure, a sharp keel-like appearance, described by Reed as 'acutely carinated'. It is clear that the specimens of *M. brycei* which Portlock figured and described belong to *C.?* *expansa*, while those which he described as 'young individuals' (1843, p. 426) are *C.?* *securiformis*.

Although the detail of the hinge is not well preserved, and the anterior teeth are not known, the position and appearance of the posterior lateral teeth suggests that *Cyrtodontia* is the appropriate genus for both *expansa* and *securiformis* but in the absence of the anterior dentition the genus remains doubtful. The presence of the posterior teeth, which Reed (1952, p. 71) apparently interpreted as a ligament groove, precludes the assignment of either species to the edentulous *Modiolopsis* [= *Modiodesma*, = *Orthodesma* Laroque and Newell, 1969, p. N397]. However, *C.?* *expansa* bears a strong resemblance in form to *Sphenolium* sp. as figured by Pojeta (1978, pl. 8, fig. 6) which, although previously placed in synonymy with *Modiolopsis* (as in the *Treatise etc.*, p. N397), Pojeta (1978, p. 235) now appears to regard as a cyrtodontid. The strongly prosocline form of *C.?* *expansa* distinguishes it from the species figured from North America by Ulrich, Pojeta, and others which, in illustration, tend to have a more rounded outline.

Cyrtodontia? securiformis (Portlock 1843)

Plate 11, figs. 5-7, 10, 12-14

- v* *pars.* 1843 *Modiola expansa* Portlock, p. 425 [*pars.*: smaller variety].
- v* 1843 *Modiola securiformis* Portlock, p. 425, pl. 33, fig. 8.
- v* *pars.* 1843 *Modiola Brycei* Portlock, p. 425 [*pars.*: see *Cyrtodontia? expansa* (Portlock)].
- v. 1846 *Modiola securiformis* Portlock; McCoy, p. 18.
- 1878 *Modiolopsis securiformis* Portlock; Baily, p. 28.
- ? *non.* 1946 *Whitella* cf. *brycei* (Portlock); Lamont, p. 366, pl. 1, figs. 1, 2.
- v* 1952 *Orthodesma tyronense* Reed, p. 71, pl. 3, fig. 17.
- v* 1952 *Whiteavesia subexpansa* Reed, p. 72, pl. 4, fig. 2.
- v* 1952 *Modiolopsis concentrica* Hall and Whitfield var. *simulans* Reed, p. 69, pl. 3, fig. 14.
- v. 1952 *Modiolopsis securiformis* (Portlock); Reed, p. 70, pl. 3, fig. 15.
- v. 1952 *Goniophora brycei* (Portlock); Reed, p. 78 [*pars.*: see *Cyrtodontia? expansa* (Portlock)].

Type-specimens. Lectotype of *Modiola securiformis* here selected, IGS GSM 12448, Portlock's figured specimen: paralectotype IGS GSM 12449. Type of *M. brycei*: see *Cyrtodonta? expansa* (Portlock). Holotype of *Orthodesma tyronense* IGS GSM 12447 by original designation of Reed (1952, p. 72). Holotype of *Whiteavesia subexpansa* IGS GSM 12446 by original designation of Reed (1952, p. 73). Holotype of *Modiolopsis concentrica simulans* Reed SM A16294a,b by original designation of Reed (1952, p. 70). All from the Bardahessiagh Formation, Pomeroy, Co. Tyrone, exact localities uncertain, south of Craighbardahessiagh.

Material, localities, and horizon. Specimens in IGS (GSM 12446-9, 22038, 24172, GU1880, Zf1021) and UM (1920-845, K4206-4210, 4245-4246). All composite moulds, from the same locality and horizon as given above.

Measurements. Type-specimen, GSM 12448, which is compressed dorso-ventrally; for left valve, the least distorted: H 13.6 mm, L 30.7 mm, AL 8.2 mm. GSM 12446, undistorted, H 30 mm, L 35.1 mm, AL 9.7 mm.

Description. Obliquely ovate, becoming broader towards the posterior, with a height-length ratio of about 0.9, but very variable in the distorted specimens available. Maximum inflation seen in a single undistorted valve is 3.9 mm in a valve 35.6 mm long. The hinge-line is straight or very gently curved and is about half as long as the total length of the shell. At the posterior end of the hinge-line are 2+ posterior lateral teeth in the right valve and 1+ in the left, but the preservation of the material prevents accurate description. The antero-dorsal margin is curved and meets the hinge-line at an angle of about 130°. The ventral margin is almost straight. Umbones prosogyrate, placed at about the anterior quarter projecting slightly above the hinge-line. A rounded umbonal ridge extends backwards at about 50° from the hinge-line to the ventral margin at its furthest point from the umbo. The anterior teeth are unknown. The musculature is unknown. Sculpture of irregular concentric striae.

Discussion. See discussion of *C.? expansa*. Portlock (1843, p. 425) described his specimens of *Modiola securiformis* as being 'partly distorted by pressure'. In the lectotype (GSM 12448), the right valve approaches the *M. brycei* Portlock form, with the umbonal ridge becoming sharpened; the left valve is less distorted and has the form of the smaller variety of *M. expansa*. Another specimen (UM K4245) shows two sets of distorted conjoined valves lying on the same plane, oriented at about 45° to each other. In each the left valve is *brycei*-like in form, while the right valve retains its shape with perhaps a reduction in height and an accentuation of the umbonal ridge. Reed's (1952) species *O. tyronense* and *W. subexpansa* are here interpreted as almost undistorted valves of *C.? securiformis*. The types (GSM 12446-12447) are so alike, apart from being opposite valves, that it is hard to understand why Reed separated them specifically, let alone generically. Portlock's 'younger individuals' of *M. brycei* are badly distorted *C.? securiformis*.

The reasons for referring *securiformis* to '*Cyrtodonta?*' are discussed under *C.? expansa*. While it is possible that *C.? expansa* and *C.? securiformis* may be synonymous, there are clear differences between them: *securiformis* is noticeably more truncate posteriorly in appearance, its postero-dorsal margin meeting the hinge-line at a steeper angle than in *expansa*, and its umbones being relatively more posterior.

Reed's (1952) *Modiolopsis concentrica simulans* seems to be a specimen of *C.? securiformis* which, as a result of distortion, is higher and shorter than normal. Hind's figure of *C. transversa* (1910, pl. 4, figs. 19, 19a, ?20) from the Drummuck Group (Ashgill) closely resembles *C.? securiformis*, but his specimen (BM L49860) is more inflated and slightly more prosocline than *securiformis*. The specimen from the Drummuck Group figured by Lamont (1946, pl. 1, figs. 1, 2) as *Whitella* cf. *brycei* (Portlock) should be compared with *C. transversa* rather than with *C.? securiformis*.

Cyrtodonta? sp.

Plate 13, fig. 1

v. ?1843 *Avicula orbicularis* J. de C. Sowerby in Murchison; Portlock, pp. 425, 755 (Synoptical Table) [pars: see *Cycloconcha? speciosa* (McCoy)].

Material, horizon, and locality. A single right valve, UM K4194 from the Bardahessiagh Formation, exact locality uncertain but south of Craighbardahessiagh, Pomeroy.

Measurements. L 26.2 mm, H 24.5 mm, AL 2.4 mm, inflation of the single valve 3.0 mm, obliquity 40°.

Description. Subcircular with the umbo at about the anterior one-tenth. Umbo incomplete. Obliquity of valve about 40°. The antero-dorsal margin meets the postero-dorsal margin at an angle of about 135°. Dentition poorly preserved but two parallel posterior lateral teeth are suggested by faint grooves; anterior teeth unknown. Anterior muscle scar faint, lying about half-way between the dorsal and ventral margins; posterior musculature unknown. Sculpture of fine concentric striae visible close to the anterior margin, and faint traces of a coarser concentric ornament ventrally.

Discussion. Although no Portlock label remains associated with this specimen it is almost certainly one which he likened to *Avicula orbicularis* Sowerby in Murchison 1839; in shape it compares quite well with the type of *A. orbicularis* (IGS Geol. Soc. Coll. 6888) but this is much larger with no visible posterior lateral teeth. Were it not for the more rounded shape, this specimen might have been placed in *?Cycloconcha speciosa*, but in that species one would expect to see three posterior lateral teeth in a right valve while in K4194 only two are apparent.

Genus *Vanuxemia* Billings, 1858

Type species. *Vanuxemia inconstans* Billings by subsequent designation of Miller 1889, from the Black River and Trenton Groups.

Vanuxemia? contorta (Portlock 1843)

Plate 13, figs. 4, 8

v* 1843 *Inoceramus contortus* Portlock, p. 422, pl. 33, fig. 5.

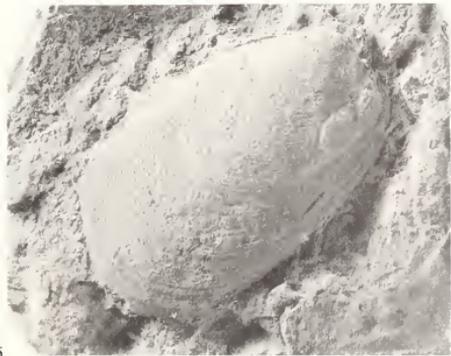
v. 1952 *Vanuxemia contorta* (Portlock); Reed, p. 68, pl. 3, fig. 12.

Type-specimen. IGS GSM 12435, holotype by monotypy; Portlock's brief description is of one shell.

Material, locality, and horizon. The type specimen (a fragmentary left valve) and a distorted right valve, IGS Zf 1020, both showing external features and both from the Killey Bridge Formation, Pomeroy, exact locality uncertain.

EXPLANATION OF PLATE II

- Figs. 1, 3, 4, 9. *Cyrtodonta? expansa* (Portlock 1843). 1, 4, conjoined valves, IGS GSM 12443, lectotype of *Modiola brycei* Portlock, 1843; 1, lateral view of left valve; 4, dorsal view of both valves. 3, right valve, UM K4247, probably the specimen figured by Baily, 1875, pl. 12, fig. 2. 9, left valve, lectotype, IGS GSM 12445. All preserved as ?composite moulds, Bardahessiagh Formation (Caradoc), south of Craighbardahessiagh, Pomeroy, $\times 1$.
- Fig. 2. Pterineid? gen. and sp. indet. ?external cast left valve IGS NIL 8981, Killey Bridge Formation (Ashgill, Cautleyan), Crocknagargan Stream section (IGR H721737), $\times 4$.
- Figs. 5-7, 10, 12-14. *Cyrtodonta? securiformis* (Portlock 1843). 5, right valve, IGS GSM 12447, holotype of *Orthodesma tyronense* Reed, 1952, $\times 1$. 6, left valve, IGS GSM 12446, holotype of *Whiteavesia subexpansa* Reed, 1952, $\times 1$. 7, 10, conjoined valves lectotype, IGS GSM 12448; 7, dorsal view, $\times 1\frac{1}{2}$; 10, lateral view of left valve, $\times 1\frac{1}{2}$. 12, external cast of left valve, SM A16294a, holotype of *Modiolopsis concentrica* var. *simulans* Reed, 1952, $\times 2$. 13, 14, slab bearing two conjoined pairs of valves, UM K4245; 13, dorsal view to show the distortion of both left valves which has produced the sharp 'umbonal ridge', leading to confusion in the past with *Goniophora*, $\times 1$; 14, lateral view of both right valves, $\times 1$. All except 12 preserved as ?composite moulds, Bardahessiagh Formation (Caradoc), south of Craighbardahessiagh, Pomeroy.
- Figs. 8, 11, 15. *Semicorallidomus?* sp. 8, latex cast of internal mould of left valve showing single small tooth, IGS GU 1739, $\times 4$. 11, composite mould of left valve, IGS GSM 12450, $\times 3$. 15, composite mould of right valve, IGS GSM 12451, $\times 3$. All Bardahessiagh Formation (Caradoc), south of Craighbardahessiagh, Pomeroy.



Measurements. Holotype incomplete. For Zf 1020 H 32.9 mm, L 25.1 mm, maximum oblique dimension 35.8 mm, apparent angle of obliquity 45 to 50°.

Description. Tall, the height being about 1.3 the length. Obliquity 45 to 50°. Length of hinge-line about half that of valve. Dentition and musculature unknown. Umbo anterior but not terminal, prosogyrate. Valve inflated to 8.7 mm in Zf 1020 after reduction by compression which has sharpened the umbonal ridge, especially towards the umbo. Sculpture of fine concentric striae, 3.5 per mm, becoming stronger towards the margin.

Discussion. Neither specimen is well preserved; the type shows only the posterior region and Zf 1020 is crushed. Portlock labelled Zf 1020 as 'indeterminate'. Reed did not use Zf 1020 when he assigned *contorta* to *Vanuxemia* with some reservation but the more complete Zf 1020, showing the anterior position of the umbones, supports his opinion. However, the nature of the material demands that the generic assignment be qualified with a ?. It is here proposed that the species be restricted to these specimens and that the species be regarded as otherwise unrecognizable.

Order PTERIOIDA Newell, 1965
 Suborder PTERIINA Newell, 1965
 Superfamily AMBONYCHIAEA Miller, 1877
 Family AMBONYCHIIDAE Miller, 1877

Remarks. In describing the ambonychiids, reference is made to Pojeta 1966, in which a terminology for certain angles and dimensions is standardized (text-fig. 7), and where a comprehensive review of North American ambonychiids is given.

Genus: AMBONYCHIA Hall, 1847

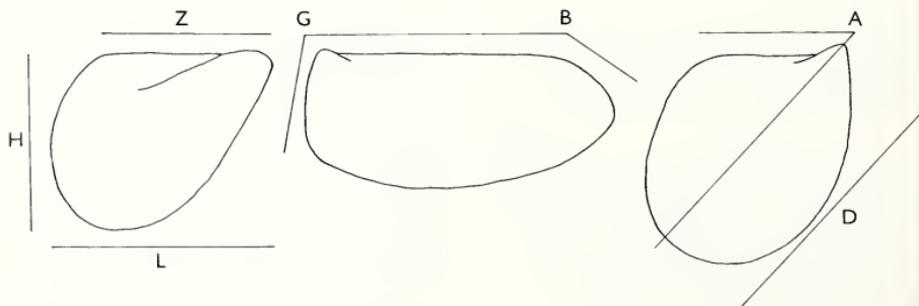
Type-species. *Ambonychia radiata* Hall, 1847, p. 163, by subsequent designation of Stoliczka (1871, p. 387).

Ambonychia arundinea sp. nov.

Plate 13, figs. 2, 3

Derivation of name. From the Latin *arundinea*, of reeds, reedy, referring both to the ornament and by allusion to F. R. C. Reed.

- v. 1843 *Uncites gryphus* Schlotheim var.; Portlock, p. 455, pl. 25A, fig. 8.
- . 1878 *Ambonychia gryphus*; Baily, p. 28.
- v? pars. 1910 *Byssonychia radiata* Hall; Hind, p. 487, pl. 1, figs. 20, 21, non figs. 19, 22.
- v. 1952 *Byssonychia gryphus* (Portlock); Reed, p. 77.



TEXT-FIG. 7. Linear and angular measurements used in describing Ambonychiids, after Pojeta, 1966. A—angle alpha, B—angle beta, G—angle gamma, L—length, H—height, D—greatest dimension, Z—length of hinge.

Type-specimens. Holotype, right valve IGS GSM 24302. Paratypes, left valves IGS GSM 24303, BM LL 40004, right valves IGS GU 1452, 1566-1567 (counterparts), and UM 1920-835 (larger specimen). All external moulds from the Killey Bridge Formation of Pomeroy, Co. Tyrone. GSM 24302, 24303 and UM 1920-835 are not precisely localized but probably come from locality 3 of Mitchell (1977), the Little River section (Irish grid ref. H7297 7268), the locality for GU 1566-1567. GU 1452 and BM LL 40004 are from locality 2 of Mitchell, Warren Wood River section (Irish grid ref. H7130 7128).

Description. Tall subrectangular *Ambonychia*. The greatest dimension at an angle of 50 to 55° to the hinge-line. Length about 0.7 of the greatest dimension and height about 1.25 the length. The hinge length is 0.4 of the length. Greatest inflation of a single valve seen is 4 mm in a valve 33 mm high (UM 1920-835). Proscloine, with an angle gamma of 80 to 85°. Umbones not rounded but carinate in the sense of Pojeta 1962 (i.e. the anterior portion of the valve is flattened antero-posteriorly), and projecting between 1.4 mm and 3.0 mm above the hinge-line. Valve surface mainly gently convex. The nature of the byssal gape is not discernible but the byssal sinus is shallow. Dentition unknown although what may be the damaged remains of the posterior laterals (? in right valve) are visible in GSM 24302. The ligament area is damaged or obscured in all the present specimens and none shows musculature. About forty costae (range seen 33+, 37+, 40, 41, 43).

Discussion. Portlock briefly described his specimens (GSM 24302, 24303) as brachiopods. Hind examined Portlock's specimens and assigned them, *in museo* to *Byssonychia*, as noted by Reed (1952, p. 78) who gave the first full description, but had only these two specimens before him. He discussed the similarity and differences between these specimens and those *Byssonychia* described from Girvan by Hind (1910, p. 487, pl. 19) and other species from North America. However, he chose to retain the specific name *gryphus*, and wrongly attributed its authorship to Portlock.

The North American Richmondian species *Byssonychia richmondensis* Ulrich, and *B. robusta* (Miller), as described by Pojeta 1962, and subsequently (Pojeta 1966) transferred to *Ambonychia*, have similar numbers of costae and similar dimensions to the Pomeroy specimens, but the Irish species has a more elongate appearance, the ratio of its length to its greatest dimension is 0.7 while for *Ambonychia richmondensis* and *A. robusta* it is 0.5-0.6 and 0.6-0.75 respectively (based on Pojeta's figures). Both the American species tend more towards the acline form by about 10°.

Of Hind's figures (1910, pl. 1, figs. 19-22) of *B. radiata*, which Pojeta (1962, p. 184) excluded from *B. radiata*, figs. 19, 22 are comparable to the Richmondian species *B. suberecta* Ulrich, but figs. 20, 21 (BM L49766-49767) are close in all respects to *A. arundinea* but have a slightly higher number of costae (44 to 48).

Genus CLEIONYCHIA Ulrich, 1892

Type species. By original designation *Ambonychia lamellosa* Hall, 1862.

Cleionychia transversa (Portlock 1843)

Plate 12, figs. 1-6

- v* 1843 *Inoceramus transversus* Portlock, p. 423, pl. 33, fig. 11.
- v pars. 1843 *Inoceramus vetustus* (J. de C. Sowerby) Var. *priscus* Portlock, p. 423, pl. 33, figs. 2, 3, non fig. 1.
- v. 1952 *Cleionychia subovalis* Reed, p. 76, pl. 4, fig. 7.
- v. 1952 *Cleionychia subquadrata* Reed, pp. 76-77, pl. 4, fig. 8.

Type specimens. Lectotype of *Cleionychia transversa* IGS GSM 12439, selected by Reed 1952, p. 77; holotype of *C. subovalis* Reed IGS GSM 12436 by original designation; lectotype of *C. subquadrata* Reed here selected, IGS GSM 12437, the specimen figured by Reed (1952, pl. 4, fig. 8). Paralectotypes of *transversa* IGS GSM 12440, UM K4199, all from the Portlock Collection; paralectotype of *C. subquadrata* IGS GSM 24304, from the Wyatt-Edgell Collection.

Other material. IGS GSM 24305, from the Wyatt-Edgell Collection.

Horizon and locality. All from the Bardahessiagh Formation, exact locality uncertain but south of Craighbardahessiagh, Pomeroy.

Measurements. For the lectotype IGS GSM 12439, L 67.6+ mm, H 40.1 mm, maximum inflation of the single valve 9.8 mm.

Description. Transversely elongate becoming relatively longer with increased size and with height about 0.6 of the length in large specimens. Inflation greatest below and slightly posterior to the umbo, gradually diminishing towards the back. Prosogyrate umbo anterior and almost terminal and rising above the hinge-line. Straight hinge-line about two-thirds of the valve length with duplivincular ligament area extending along dorsal margin. Anterior end truncate, angle gamma about 90°. Anterior slope meets commissure at about 90° but may form a distinctly obtuse angle in distorted specimens. Ventral margin curving rapidly up to anterior margin and more gently towards the posterior margin which is unclear in all the larger specimens available, but rounded and continuous with the ventral margin in smaller specimens. Angle beta about 140°. Musculature and dentition unknown. Sculpture of coarse concentric rugae, undulating in section.

Discussion. It is likely that the specimens on which Reed based his species *C. subovalis* and *C. subquadrata* (1952, pp. 76-77) are juveniles of *C. transversa*. This is supported by measurement of appropriate early growth stages of clear examples of *C. transversa*. It is found that the height to length ratio decreases from about 0.9 at 25 mm long growth stage to 0.6 at 60 mm.

Early growth stages of *C. transversa* closely resemble *C. undata* Emmons, but the latter has a slightly more acute angle gamma (apparently about 85° in Pojeta's illustrations, 1966, pl. 34, figs. 1-5) and there are no figures of late growth stages comparable to those seen in *C. transversa*.

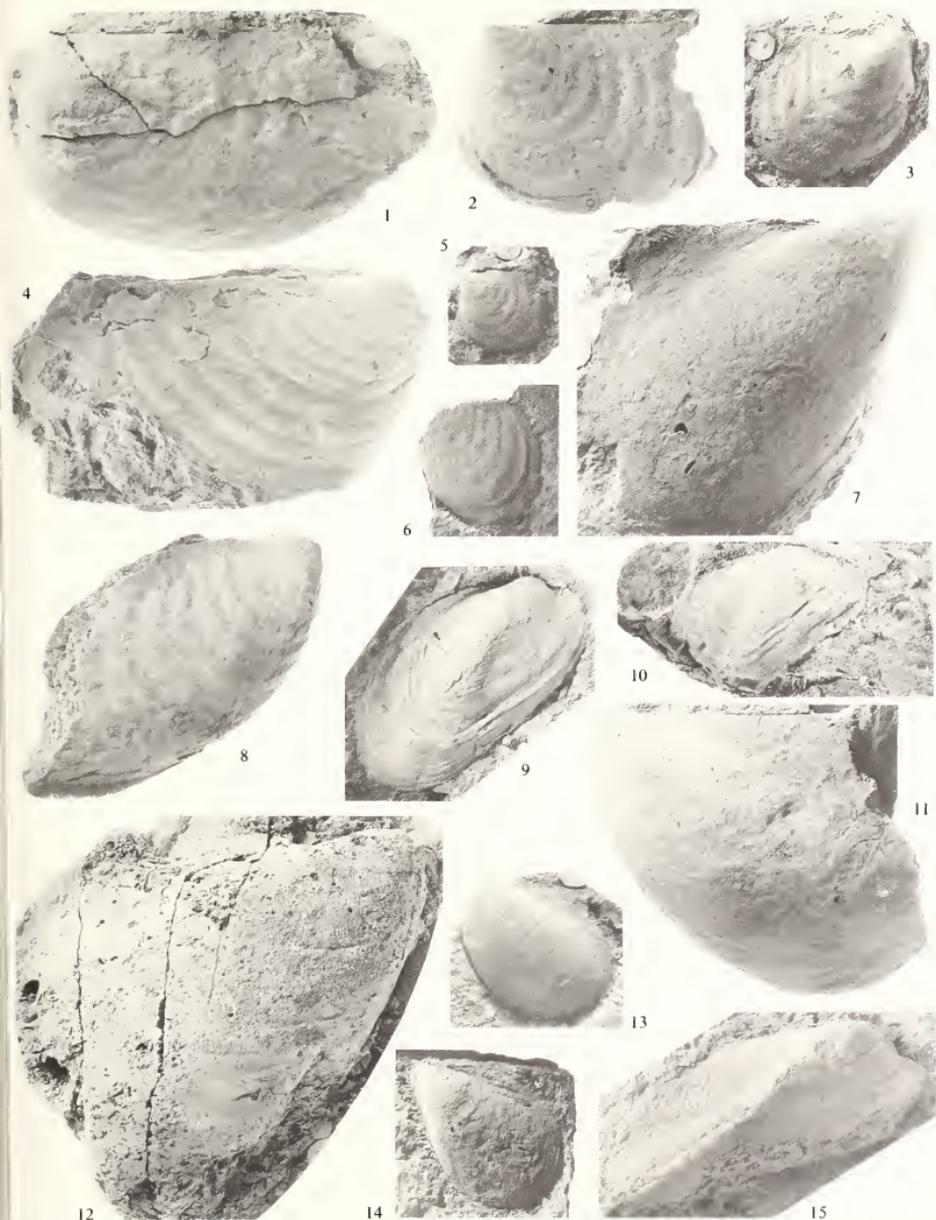
Cleionychia prisca (Portlock 1843)

Plate 12, figs. 8, 12

- v* pars. 1843 *Inoceramus vetustus* (J. de C. Sowerby) Var. *priscus* Portlock, p. 423, pl. 33, fig. 1, non figs. 2, 3.
 . 1878 *Ambonychia undata* Hall; Bailly, p. 28.
 v. 1952 *Ambonychia prisca* (Portlock); Reed, p. 73.

EXPLANATION OF PLATE 12

- Figs. 1-6. *Cleionychia transversa* (Portlock 1843). 1, left valve, lectotype, IGS GSM 12439. 2, left valve, UM K4199. 3, right valve, IGS GSM 12436, holotype of *Cleionychia subovalis* Reed, 1952. 4, right valve, IGS GSM 12440. 5, left valve, IGS GSM 12437, lectotype of *Cleionychia subquadrata* Reed, 1952. 6, left valve, IGS GSM 24304. All external casts, Bardahessiagh Formation (Caradoc), south of Craighbardahessiagh, Pomeroy, $\times 1$.
- Figs. 7, 11, 13. *Cleionychia incognita* sp. nov. 7, right valve, IGS GSM 24310. 11, left valve, holotype, IGS GSM 12441; note the bryozoan of the type referred by Portlock (1843, p. 360) to *Entobia antiqua* Portlock. 13, small left valve, IGS GSM 24311. All external casts, Bardahessiagh Formation (Caradoc), south of Craighbardahessiagh, $\times 1\frac{1}{2}$.
- Figs. 8, 12. *Cleionychia prisca* (Portlock 1843). 8, right valve, UM K4200. 12, right valve, lectotype, IGS GSM 12438. Both external casts, Bardahessiagh Formation (Caradoc), south of Craighbardahessiagh, Pomeroy, $\times 1$.
- Fig. 9. *Corallidomus concentrica* (Hall and Whitfield 1875), ?composite mould right valve, UM 1920-843, Killey Bridge Formation (Ashgill, Cautleyan), Pomeroy, exact locality uncertain, $\times 2$.
- Fig. 10. *Corallidomus*? sp. ?external cast of right valve, NMI G.4. 1979, Killey Bridge Formation (Ashgill, Cautleyan), Pomeroy, exact locality uncertain, $\times 2$.
- Fig. 14. *Ambonychiopsis suspecta* (Reed 1952), ?composite mould of left valve, holotype, IGS GSM 22103, Bardahessiagh Formation (Caradoc), south of Craighbardahessiagh, $\times 1$.
- Fig. 15. *Goniophora* sp., external cast of right valve, IGS Zs 2751, Killey Bridge Formation (Ashgill, Cautleyan), locality 3 of Mitchell 1977 (IGR H7297 7268), $\times 4$.



TUNNICLIFF, Ordovician bivalves

Type-specimens, horizon, and localities. Lectotype IGS GSM 12438, right valve, (with a second valve only partly visible) selected by Reed 1952, p. 74; paralectotype (not known to Reed) UM K4200. Both from the Bardahessiagh Formation from Portlock's locality 'sheet 37 no. 6' south of Craigbardahessiagh, Pomeroy.

Other material. A single specimen in the Griffith Collection, NMI; locality and horizon as for the type specimens.

Measurements. For the lectotype, L 66.5+ mm, H 60.2+ mm, maximum inflation of the single valve 12.2 mm, greatest dimension (oblique) 74.1 mm, angle alpha c. 55°, angle gamma c. 85°, angle beta c. 120°, length of hinge uncertain, height of umbo above hinge-line 8 mm.

Description. Obliquely ovate form, narrow anteriorly and expanding rapidly towards the posterior end. Height about 0.9 of length; precise length and detail of hinge-line unknown. Greatest dimension approximately 1.25 times length; angle alpha about 50°, angle gamma about 80 to 85°, angle beta about 120°. Maximum inflation seen in a single valve, in the lectotype 12.2 mm. Umbo terminal. Antero-ventral slope steep, meeting the plane of commissure at an angle of 90 to 100°. Posterior surface convex, becoming flatter towards the posterior end. Ligament, musculature, and dentition unknown. Sculpture of coarse concentric rugae undulating in section, about 2 per 10 mm along the plane of the greatest dimension.

Discussion. Although not well preserved, the specimens of *Cleionychia prisca* (Portlock) are sufficiently distinct to be separated from *C. transversa* and *C. incognita* sp. nov. While the sculpture in *C. prisca* is very like that in *C. transversa*, angle gamma is more acute in *C. prisca* and the shell has a generally more oblique and inflated appearance. Angle alpha in *C. prisca* is less acute than in *C. incognita* which lacks the strong concentric rugae of *C. prisca*.

Pojeta (1966, pp. 177, 180) pointed out that Reed's figures were poor and that it was not clear (despite his comments, 1952, p. 74) how Reed distinguished *Cleionychia* spp. from *Ambonychinia* spp. None of the specimens which Reed assigned to *Cleionychia* is greatly inflated but they have concentric undulating sculpture; those which he placed in *Ambonychinia* Isberg are more inflated, elongate obliquely, and have prominent umbones and a more acute angle gamma, but while having concentric ornament they apparently lack the radial costellae diagnostic of *Ambonychiopsis* Isberg although in shape they resemble the latter. The specimens treated by Reed as *Ambonychinia* are here assigned to *Cleionychia* following the suggestion inherent in Pojeta's remarks (1966, p. 177).

Reed (1952, p. 74) pointed out the similarity of *C. prisca* to one of Isberg's (1934, pl. 4, fig. 6) figures of *Ambonychinia corrugata* (Lindström) and also noted the different appearance of the remaining figures of *A. corrugata* (Isberg 1934, pl. 4, figs. 1-5, 7). The specimen in Isberg's pl. 4, fig. 6 appears to have stronger rugae than seen in *C. prisca* and each of its angles alpha, beta, and gamma is a little more acute than seen in *C. prisca*.

Cleionychia incognita sp. nov.

Plate 12, figs. 7, 11, 13

Derivation of name. From the Latin *incognita* unknown or unrecognized, referring to the nomenclatorial history of the type specimens.

- v. 1843 *Inoceramus trigonus* (Münster); Portlock, p. 422, pl. 33, figs. 4, 4a.
- . 1878 *Ambonychia trigona* Portlock; Baily, p. 28.
- v. 1952 *Ambonychinia* cf. *amygdalina* (Hall); Reed, p. 75, pl. 4, fig. 5.
- v. 1952 *Ambonychinia* cf. *intermedia* Isberg; Reed, p. 75, pl. 4, fig. 6.
- v. 1952 *Ambonychinia* cf. *volvans* Isberg; Reed, p. 74, pl. 4, fig. 4.

Type specimens. Holotype IGS GSM 12441, a left valve, figured by Portlock 1843, pl. 33, fig. 4; paratypes IGS GSM 24310, 24311 from the Wyatt-Edgell Collection, a right and a small left valve and IGS GSM 24306, 24307, 104237, three distorted specimens showing conjoined valves, all from the Wyatt-Edgell Collection.

Horizon and localities. Bardahessiagh Formation, exact localities uncertain but south of Craigbardahessiagh, Pomeroy.

Measurements. For the holotype, L 41.4 mm, H 34.7 mm, greatest dimension (oblique) 49.3+ mm, angle alpha c. 40°, angle gamma 75°, angle beta c. 120°, maximum inflation of the single valve 11.5 mm, length of hinge 29.6+ mm.

Description. Obliquely ovate to subquadrate in form, narrow anteriorly and expanding rapidly towards the posterior end. Height about 0.8 to 0.9 of length. Straight hinge-line about 0.7 to 0.75 length. Greatest dimension approximately 1.1 to 1.2 times length; angle alpha 40 to 50°. Angle gamma 70 to 80°, angle beta 115 to 135°. Maximum inflation of a single valve seen 11.5 mm in the holotype. Umbo terminal, rising above the hinge-line. Antero-ventral slope steep, meeting the plane of commissure at an angle of about 100° but varying with size and distortion of specimen. Posterior surface convex, becoming flatter towards the posterior end and with a plano-concave dorsal area below the hinge-line. Ligament, musculature, and dentition unknown. Sculpture of faint indistinct concentric lines and faint coarser rugae visible particularly on the antero-ventral surface.

Discussion. *Cleionychia incognita* is distinct from *C. transversa* and *C. prisca* in lacking the coarse rugae seen over the whole surface in those species. It is less transverse than *C. transversa* and less oblique than *C. prisca* which it closely resembles in general form but which does not show the flattened dorsal area seen in *C. incognita*.

Reed (1952, p. 75) compared IGS GSM 24310 with Hall's *Ambonychia amygdalina* and placed it in Isberg's genus *Ambonychia*. Pojeta (1966, p. 163) has described *amygdalina* as belonging to *Ambonychiopsis* Isberg. None of the present specimens of *C. incognita* shows the radial ornament or anterior lobe associated with *Ambonychiopsis*. *Ambonychia intermedia* Isberg, with which Reed (1952, p. 75) compared IGS GSM 12441 does bear a close resemblance to *C. incognita* but Isberg's figure (1934, pl. 9, fig. 1) shows more obtuse angles gamma (c. 90°) and beta (?140°) than seen in *C. incognita*. Similarly, there is a recognizable similarity between IGS GSM 24311 and *A. volvens* Isberg with which Reed (1952, p. 74) compared it, but *A. volvens* appears to have a small anterior lobe (Isberg 1934, pl. 2, fig. 4c) not seen in *C. incognita*. The flattened postero-dorsal area is not so pronounced in other species of *Cleionychia* except perhaps *C. intermedia*. The use of the generic name *Cleionychia* rather than *Ambonychia* is discussed under *C. prisca*.

Genus AMBONYCHIPSIS Isberg, 1934

Type-species. By original designation of Isberg 1934, p. 82, *Ambonychiopsis osmundsbergensis*.

Ambonychiopsis suspecta (Reed 1952)

Plate 12, fig. 14

v* 1952 *Vanuxemia? suspecta* Reed, p. 69, pl. 3, fig. 13.

Type specimen, horizon, and locality. Holotype by monotypy IGS GSM 22103, by original designation of Reed 1952, p. 69; a ?composite mould of a left valve, the only known specimen, from the Bardahessiagh Formation, exact locality uncertain, but south of Craighardahessiagh, Pomeroy.

Measurements. For the monotype L 26.9 mm, H 19.8 mm, greatest dimension (oblique) 29.1 mm, angle alpha c. 35°, angle gamma 60°, angle beta 150°, maximum inflation of the single valve c. 3 mm, length of hinge-line 17.9 mm.

Description. The specimen is lacking in detail but shows an obliquely ovate form, very narrow anteriorly and expanding rapidly towards the posterior end. Height is 0.7 of the length, hinge-line is 0.6 of the length and is apparently straight. The greatest dimension, along the plane of obliquity 35° to the hinge-line, is 1.1 times the length. Angles gamma and beta and inflation are given above. Anterior to the otherwise terminal umbo is a small anterior lobe. The posterior surface is gently convex. The steep antero-ventral slope meets the plane of commissure at an angle of about 60°. Ligament and musculature unknown. Dentition represented only by two doubtful posterior lateral grooves below and anterior to the postero-dorsal angle of the margin. Sculpture is poorly preserved and shows only irregular concentric striae.

Discussion. Portlock labelled this specimen '*Mytilus?—not specifically determined*'. Reed described two to three short cardinal teeth anterior to the umbo but these are not evident. The specimen has been developed a little since Reed examined it and part of the small anterior lobe now revealed

may have led Reed to his conclusions and suggested to him his determination *Vanuxemia? suspecta*. His use of a query (?) and the name *suspecta* both suggest that Reed remained doubtful as to the nature of this specimen. Some doubt is retained in applying the generic name *Ambonychiopsis* to *suspecta* but this assignment is justified by the ambonychiid nature of the form and sculpture, and the presence of the anterior lobe. However, there is a lack of the radial sculpture characteristic of *Ambonychiopsis*.

Ambonychia balclatchiensis Reed (1944, p. 213, pl. 2, fig. 2) from the Balclatchie Beds is probably an *Ambonychiopsis*: the illustration shows an anterior lobe, oriented such that it appears to be dorsal. Angles alpha (c. 30°), beta (c. 150°), and gamma (c. 70°) in Reed's figure are close to those of *A. suspecta* and its greatest dimension is 1.03 of its length (1.1 in *A. suspecta*), but the anterior lobe in *A. balclatchiensis* is larger.

The preservation of the specimen is such that comparison with other species presents great difficulty. It is here proposed that the name be restricted to the type specimen and the species be regarded as otherwise unrecognizable.

pterineid? gen. and sp. indet.

Plate 11, fig. 2

A single, very small specimen (IGS NIL 8981) from the Killey Bridge Formation of the Crocknagargan Stream section (Irish grid ref. H721737), is probably a pterineid. Although poorly preserved, it can be compared in outline and size to *Palaeopteria parvula* Whiteaves (1897, p. 181, pl. 20, figs. 1-3), from rocks of Black River-Trenton age (Caradoc) in the area of Lake Winnipeg. *Pterinea reticulata* Hind (1910, p. 494, pl. 1, figs. 7-8) from the Drummuck Group of Girvan has a distinctive ornament and is larger than the Irish specimen.

bivalve? gen. and sp. indet.

Plate 13, fig. 7

Material, horizon, and locality. A single specimen, IGS GSM 24308, from the Bardahessiagh Formation, exact locality unknown, south of Craighardaheesiagh, Pomeroy.

Description. A subtriangular fragment measuring 40.0 by 30.7 mm and showing 19+ coarse concentric rugae.

Discussion. This fragmentary specimen has in the past been referred plausibly to *Ambonychia undata* Hall, and indeed the coarse ornament on the specimen bears some resemblance to Hall's figure (1847, pl. 36, fig. 7a). It is considered, on the ornament alone, to resemble *Cleionychia*, but this view gives rise to difficulties of interpretation and a gastropod or cephalopod affinity is more probable. No comparable material is known from Pomeroy.

Subclass ISOFILIBRANCHIA Iredale, 1939
 Order MYTILOIDA Ferussac, 1822
 Superfamily MYTILACEA Rafinesque, 1815
 Family MODIOLOPSIDAE Fischer, 1887
 (after Pojeta and Gilbert-Tomlinson, 1978)
 Genus MODIOLOPSIS Hall, 1847

Type species. *Pterinea modiolaris* Conrad, 1838, by original designation of Hall 1847, p. 157.

Modiolopsis sp.

Plate 13, fig. 11

Material, horizon, and locality. A single, fragmentary, small internal mould of a right valve, IGS GU 1380, from the Killey Bridge Formation at the Crocknagargan Stream section (locality 1 of Mitchell 1977), Pomeroy, Co. Tyrone.

Description. Elongate, obliquely ovate, modioliform, with the umbo at about the anterior one-tenth to one-fifth. Height (12.5+ mm), about half of length (26.0+ mm). Inflation of the single valve 2.5 mm. The incomplete anterior end is narrow but the shell broadens rapidly towards the flat posterior which is also incomplete. The ventral slope and margin show a slight sinus a little posterior to the umbo. A rounded umbonal ridge runs towards the postero-ventral angle which is lost. An adductor muscle scar occupies much of the preumbonal portion of the shell and two umbonal muscle scars are present. Edentulous but with a dorsal longitudinal groove. Sculpture unknown except for a suggestion of concentric ornament on the antero-ventral slope.

Discussion. Although fragmentary, this specimen is similar in shape to two species figured by Hind (1910): *Modiolopsis exasperatus* (Phillips) (Hind 1910, pl. 2, fig. 15) and *M. scotica* Hind (1910, pl. 2, figs. 18–20) both recorded from the Drummuck Group (Ashgill) of Girvan. In both the Scottish species the valves become higher very rapidly towards the posterior as in the Irish specimen, but although the latter is incomplete, its postero-dorsal margin suggests that it is less elongate.

Genus CORALLIDOMUS Whitfield, 1895

Type species. *C. concentrica* (Hall and Whitfield 1875), by monotypy: the only Ordovician species assigned to the genus (Pojeta 1971, p. 6).

Corallidomus concentrica (Hall and Whitfield 1875)

Plate 12, fig. 9

- * 1875 *Modiolopsis concentrica* Hall and Whitfield, pp. 86–87, pl. 2, fig. 18.
- 1893 [1895] *Corallidomus concentricus* Whitfield, pp. 492–493, pl. 13, fig. 2 [on p. 493], pl. 13, [as n. gen., n. sp.].
- 1978 *Corallidomus concentrica* (Hall and Whitfield); Pojeta, pl. 12, figs. 12–14.

Material, horizon, and locality. A right valve, UM 1920–843, from the Killey Bridge Formation of Pomeroy, Co. Tyrone, exact locality uncertain.

Description. A small modioliform shell, nearly twice as long as high (12 mm high, 22 mm long) and inflated to nearly 2 mm at one point along the umbonal ridge. The shell broadens towards the posterior. The anterior margin is rounded, the posterior end is obliquely truncate. The ventral margin shows a slight flexure at about the mid-point. The umbo lies at about the anterior one-quarter. The preumbonal part of the shell is occupied by an adductor muscle scar. Dentition uncertain but there is a suggestion of a short, thin, posterior tooth immediately behind the umbo. The ornament is distinctive: the antero-ventral portion of the shell bears fine concentric lines which give way at the umbonal ridge to strong, coarse, fairly regular concentric rugae. The umbonal ridge becomes less marked away from the umbo but is defined by the change in texture and direction of the ornament.

Discussion. The specimen closely matches the descriptions and illustrations of Hall and Whitfield (1875, pp. 86–87, pl. 2, fig. 18) and the specimens figured by Pojeta (1978, pl. 12, figs. 12–14). Pojeta (1978, pl. 12, figs. 12–14) figured *Modiolopsis concentrica* as *Corallidomus concentrica*, treating it as synonymous with Whitfield's type species, and is followed here; however, Whitfield's (1893) figures and the lack of his material (Pojeta 1971, p. 30) do give rise to some doubt as to whether the two species are identical and therefore whether *M. concentrica* should be assigned to *Corallidomus*. Pojeta (1971, pp. 30–33) observed that the known occurrence of *Corallidomus* is restricted to the Richmondian, comparable to the Cautleyan age of the Killey Bridge Formation. The mode of life of *Corallidomus*, recorded by Whitfield as boring into masses of the coral *Labechia ohioensis*, is said by Pojeta (1971) to be unique among Ordovician bivalves and, although the present specimen is not in life position, it is worth noting that masses of the tabulate coral *Catenipora tapaensis* (Sokolov) [identified by Dr. D. E. White, IGS] were collected by Portlock (IGS GSM 103460, 104183, 104184) from the Killey Bridge Formation, possibly from locality 3 of Mitchell 1977.

A left valve, NMI G.4. 1979, in the Griffith Collection is from the same horizon as UM 1920 843 but also lacks exact locality details and is here recorded as *Corallidomus?* sp. (Pl. 12, fig. 10). It lacks the characteristic coarser ornament on the posterior portion of the shell and has a more central umbo than *C. concentrica*.

Subclass PALAEOHETERODONTA Newell, 1965
 Order MODIOMORPHOIDEA Newell, 1969
 Superfamily MODIOMORPHACEA Miller, 1877
 Family MODIOMORPHIDAE Miller, 1877
 Genus GONIOPHORA Phillips, 1848

Type species. *Goniophora cymbaeformis* (J. de C. Sowerby) by original designation of Phillips 1848, p. 264.

Goniophora sp.

Plate 12, fig. 15

Material, locality, and horizon. A single specimen, IGS Zs 2751, external cast of a right valve collected by Mr. R. P. Tripp from the Killy Bridge Formation, at locality 3 of Mitchell (1977), the Little River Section (Irish grid ref. H7297 7268).

Measurements. H 6.0 mm, L 13.8 mm, AL 2.8 mm; inflation of the single valve 1.8 mm; obliquity, measured along umbonal ridge, 35–40°.

Description. Small *Goniophora*; transversely elongate with a pronounced, slightly sigmoidal umbonal ridge or carina running from the umbo to the postero-ventral angle; height to length ratio 0.43; umbo barely protruding above the hinge-line and situated at about the anterior one-fifth. Dentition and musculature unknown. The surface anterior to the carina shows concentric striae of irregular strength and spacing but the posterior surface has a well-developed concentric sculpture, regularly spaced, with 3–4 striae per mm. The posterior surface also shows a flexure close behind the carina.

Discussion. This remains the only known *Goniophora* specimen from the Ordovician of Pomeroy; *Goniophora brycei* (Portlock) of Reed (1952, p. 78) is a *Cyrtodonta*? (see *Cyrtodonta*? spp.). In the absence of any detail of the hinge, there is some doubt as to whether *Goniophora* or *Goniophorina* Isberg is the more appropriate genus for this specimen; but it is reasonable to place it in the more familiar *Goniophora*. The lack of radial costae precludes it from being *Cosmogoniophora* McLearn.

Specimens of a comparable form from Caradocian rocks in north Wales are under study.

Genus COLPOMYA Ulrich, 1894

Type species. Monotype, *Colpomya constricta* Ulrich by original designation of Ulrich 1894, pp. 522–523.

Colpomya simplex (Portlock 1843)

Plate 13, fig. 14

- v* 1843 *Cypricardia? simplex* Portlock, p. 426.
- v pars. 1910 *Grammysia undata* J. de C. Sowerby; Hind, p. 540, pl. 5, fig. 14, ?non figs. 13, 15, 16.
- v. 1952 *Cuneomya simplex* (Portlock); Reed, p. 79, pl. 4, fig. 10.

Type-specimen. The only known syntype, a left valve, IGS GSM 24290, from the Killy Bridge Formation, is here selected as lectotype; locality given by Portlock as his 'sheet 37 no. 2', probably locality 3 of Mitchell (1977), the Little River section, Pomeroy (Irish grid ref. H7297 7268).

Measurements. H 22.9 mm, L 39.5 mm, AL 14.00 mm, inflation of the single valve is 7.8 mm; obliquity, measured along the umbonal ridge, 35°.

Description. Transversely elongate, rounded at posterior and anterior ends, with dorsal and ventral margins subparallel; posterior broader than anterior. The height is about 0.6 of the length and the umbo is at about the anterior one-third. The single valve is inflated to 7.8 mm in the type-specimen. A slightly sigmoidal rounded umbonal ridge at an angle of 35° to the hinge-line meets the postero-ventral margin below the posterior end of the hinge-line. The prosogyrate umbo extends above the hinge-line and is flattened, the flat area corresponding to the very faint sulcus developed towards the margin anterior to the umbonal ridge. Lunule present but

escutcheon not clearly differentiated. Dentition and musculature unknown. Sculpture of coarse, rather irregular concentric rugae, pronounced anterior to the sulcus and becoming fainter and even indistinguishable on the posterior surface.

Discussion. Portlock (1843, p. 426) and Hind (MS, see Reed 1952, p. 79) compared this species to *Cypricardia impressa* J. de C. Sowerby (in Murchison). As Portlock observed, the sulcus in *C. simplex* is much less pronounced than in *C. impressa*. *Colpomya simplex* differs from *Cuneamya* in that the umbo is not terminal (cf. *Cuneamya miamiensis* Hall and Whitfield as figured in the *Treatise*, p. N821 and Pojeta 1971, pl. 15, figs. 9, 10), but it is closely comparable to the type species of *Colpomya*, *C. constricta* Ulrich (1894, p. 523, fig. 41) from the upper Trenton of Kentucky. The specimen figured by Hind (1910, pl. 5, fig. 14) from the Drummuck Group (BM L49889) may be conspecific with *C. simplex*.

Genus SEMICORALLIDOMUS Isberg, 1934

Type species. Semicorallidomus whitfieldi Isberg by original designation of Isberg 1934, pp. 175, 180 from the Ordovician of Sweden.

Semicorallidomus? sp.

Plate 11, figs. 8, 11, 15

- v. 1843 *Modiola Nerei* (Münster); Portlock, p. 424, pl. 33, fig. 10.
- v. 1843 *Mytilus? Nerei* (Münster); Portlock, p. 424.
- 1878 *Modiolopsis Nerei* Münster; Baily, p. 28.
- ? 1952 *Modiolodon speciosus* (McCoy); Reed, p. 72, pl. 4, fig. 1.
- v. 1952 *Paramodiola?* sp.; Reed, p. 73, pl. 4, fig. 3.

Material. IGS (Portlock and Mitchell collections) GSM 12450-12452, GU 1739, 1741; UM (Portlock and Grainger collections) 4125 and counterpart, K4169, 4195, 4197-4198, 4242; NMI (Griffith collection); TCD 7871 (Portlock collection); ?SM A16461.

Localities and horizon. All from the Bardahessiagh Formation, south of Craighardahessiagh, Pomeroy, exact localities uncertain.

Measurements	L	H	H/L	AL/L
Max.	20.0 mm	14.0 mm	0.85	0.15
Min.	10.0 mm	7.2 mm	0.62	0.07
Mean	14.63 mm	10.4 mm	0.71	0.11
Median	15.0 mm	10.6 mm	0.74	0.11

Description. Subovate, modiomorphoid, with a height-length ratio about 0.7. Umbo not prominent and at about the anterior one-tenth to one-fifth. Some specimens show a slight flexure of the posterior surface. Obliquity about 30°. Apparently isomyarian with the anterior adductor muscle scar almost below the umbo and the posterior scar poorly defined. Single valve inflated to about 2.5 mm in the larger specimens. Concentric ornament of varying strength, with an average of five striae per mm on the most inflated part of the shell along the plane of obliquity. Precise nature of the hinge unknown, but the left valve apparently bears a tooth below the umbo (IGS GU 1739, Pl. 11, fig. 8).

Discussion. The name *Paramodiola*, used by Reed (1952) for this form, is rejected here in view of the apparent presence of a tooth in the left valve (GU 1739); *Paramodiola* is said to be edentulous. A diagnostic characteristic of *Semicorallidomus* is the presence in the left valve of a socket, the reverse of what is seen in the Pomeroy form. In outline, the Irish specimens most closely resemble the type species *Semicorallidomus whitfieldi* Isberg. The specimen described and figured by Reed (1952, p. 72, pl. 4, fig. 1) as *Modiolodon speciosus* (McCoy) (SM A16461) was not available for study at the time of writing, but his figure resembles the known specimens of *Semicorallidomus?*: McCoy's specimen of *M. speciosus* is in the NMI (see *Cycloconcha? speciosa*).

Subclass ACTINODONTIA Douvillé, 1912 (after Pojeta 1978)

Family CYCLOCONCHIDAE Ulrich, 1884

Genus CYCLOCONCHA Miller, 1874

Type species. By original designation *Cycloconcha mediocardinalis* Miller, 1874, p. 231.

Cycloconcha? speciosa (McCoy 1846)

Plate 13, figs. 5, 6, 9, 10, 12, 13

v. 1843 *Avicula obliqua* J. de C. Sowerby in Murchison; Portlock, p. 425.

v. 1843 *Avicula orbicularis* J. de C. Sowerby in Murchison; Portlock, pp. 425, 755 (Synoptical Table) [pars: see *Cyrtodontia? sp.*].

v* 1846 *Pullastra speciosa* McCoy, p. 17, pl. 2, fig. 2 (reversed).

?non 1952 *Modiolodon speciosus* (McCoy); Reed, p. 72, pl. 4, fig. 1.

Type specimen. The original of McCoy's figure (1846, pl. 2, fig. 2) is in the NMI Griffith Collection and as the only known syntype is here selected as Lectotype, NMI G.5. 1979.

Material. Five right valves; GSM 21919, 21920, 104236, UM K4213, 4214. Four left valves; GSM 104235, UM K4212, 4216 and the type specimen. All are composite moulds.

Horizon and locality. All from the Bardahessiagh Formation, exact localities uncertain but south of Craighardahessiagh, Pomeroy.

<i>Measurements</i>	L	H	H/L	AL/L	Obliquity
Max.	24.2 mm	22.0 mm	0.94	0.38	55°
Min.	16.0 mm	13.0 mm	0.72	0.29	45°
Mean	22.4 mm	18.6 mm	0.83	0.34	50.6°
Median	20.1 mm	17.5 mm	0.83	0.34	50°

EXPLANATION OF PLATE 13

Fig. 1. *Cyrtodontia? sp.* ?composite mould of right valve, UM K4194, Bardahessiagh Formation (Caradoc), south of Craighardahessiagh, Pomeroy, $\times 1\frac{1}{2}$.

Figs. 2, 3. *Ambonychia arundinea* sp. nov. 2, external cast of right valve, IGS GSM 24302. 3, external cast of left valve IGS GSM 24303. Both Killy Bridge Formation (Ashgill, Cautleyan), Pomeroy, exact locality uncertain, $\times 1\frac{1}{2}$.

Figs. 4, 8. *Vanuxemia? contorta* (Portlock 1843). 4, external cast of left valve, holotype, IGS GSM 12435. 8, external cast of right valve, IGS Zf 1020. Both Killy Bridge Formation (Ashgill, Cautleyan), Pomeroy, exact locality uncertain, $\times 1$.

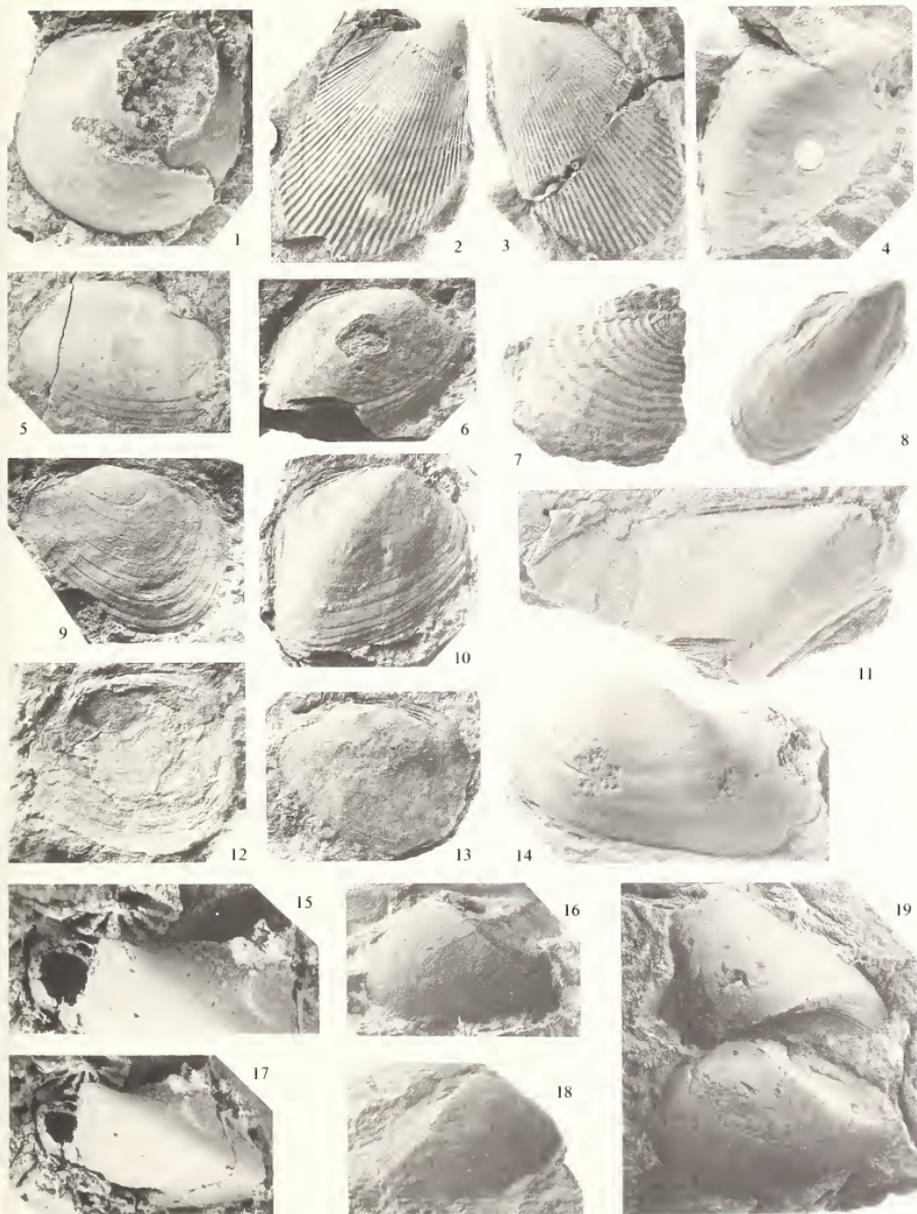
Figs. 5, 6, 9, 10, 12, 13. *Cycloconcha? speciosa* (McCoy 1846). 5, left valve, lectotype NMI G.5. 1979. 6, right valve, UM K4214. 9, left valve, UM K4212. 10, right valve, IGS GSM 21920. 12, right valve, IGS GSM 21919. 13, left valve, UM K4216. All preserved as composite moulds, Bardahessiagh Formation (Caradoc), south of Craighardahessiagh, Pomeroy, $\times 1\frac{1}{2}$.

Fig. 7. Bivalve? gen. and sp. indet. ?external cast IGS GSM 24308, Bardahessiagh Formation (Caradoc), south of Craighardahessiagh, $\times 1$.

Fig. 11. *Modiolopsis* sp. internal mould of right valve, IGS GU 1380, Killy Bridge Formation (Ashgill, Cautleyan), Crocknagargan Stream section, Pomeroy (IGR H721737), $\times 2\frac{1}{2}$.

Fig. 14. *Colpomya simplex* (Portlock 1843), external cast of left valve, lectotype, IGS GSM 24290, Killy Bridge Formation (Ashgill, Cautleyan), Pomeroy, exact locality uncertain, $\times 1\frac{1}{2}$.

Figs. 15-19. *Lyrodesma radiatum* (Portlock 1843). 15, 17, left valve, internal mould, IGS GU 3264; 15, oblique dorsal view to show dentition, lit from bottom left, $\times 6$; 17, lateral view, lit from bottom left, $\times 4$. 16, external cast of left valve, lectotype, IGS GSM 22178, $\times 2$. 18, external cast of right valve, IGS GSM 22177, $\times 2$. 19, composite mould of conjoined valves, IGS GSM 104185, $\times 2$. All Bardahessiagh Formation (Caradoc), south of Craighardahessiagh, Pomeroy.



TUNNICLIFF, Ordovician bivalves

Description. *Cycloconcha?* of slightly variable subovate shape, the posterior end being somewhat truncate, with height between 0.72 and 0.94 of the length. Slight umbonal ridge is at about 50° to the hinge-line. The anterior dorsal margin is at an angle of 145 to 155° to the posterior dorsal margin. The prosogyrate umbones are at about the anterior one-third. Maximum inflation of a single valve seen is 2 mm in a valve 24.2 mm long. Hinge-line shows two or three lamellar posterior lateral teeth in the left valve and three in the right valve, subparallel to the margin, and at least one anterior lateral tooth in each. Anterior adductor muscle scar faint, about half-way between umbo and anterior; posterior musculature unknown. Sculpture of regular concentric striae with more prominent lines at intervals of about 2.4 mm along the umbonal ridge especially towards the margin.

Discussion. This species is placed, with some reservation, in *Cycloconcha* since it possesses straight anterior and posterior teeth, although no cardinal teeth are visible in the available specimens. I have not seen Reed's specimen of *Modiolodon speciosus* (SM A16461, 1952, p. 72, pl. 4, fig. 1), and doubt whether it should be placed in *C.? speciosa*. Reed noted radial striation, stating that this appeared to be present in McCoy's specimen but he was working only from McCoy's figure and no radial striation is apparent in the type specimen. He also mentioned a deeply impressed anterior muscle scar but in the specimens of *C.? speciosa* available the anterior muscle scar can at best be described as faint. His comparison of his specimen with *Modiolopsis? consimilis* Ulrich, *Modiolodon obtusus* Ulrich, and *M. truncatus* (Hall) all suggest that we should regard his specimen as distinct from *C. speciosa*.

In shape, *C.? speciosa* resembles *Cyrtodonta parva* Ulrich (1894, p. 541, pl. 39, figs. 24, 25) from the Trentonian of Minnesota but it is larger and the posterior teeth are longer. In this last respect, comparison may be made with the upper Trenton shale form *Cypricardites tenellus* Ulrich (1892, p. 237) from Minnesota. The teeth in *C. tenellus*, later referred to *Cyrtodonta* by Ulrich (1894, p. 546, pl. 40, figs. 15-19), are similar in form to those of *Cycloconcha speciosa*, but only two are recorded in the right valve.

Family LYRODESMATIDAE Ulrich, 1894
Genus LYRODESMA Conrad, 1841, p. 51

Type-species. By monotypy *Lyrodesma planum* Conrad, 1841, p. 51.

Lyrodesma radiatum (Portlock 1843)

Plate 13, figs. 15-19

- v* 1843 *Nucula? radiata* Portlock, p. 430, pl. 36, fig. 11.
v. 1846 *Nucula radiata* Portlock; McCoy, p. 19.
1878 *Ctenodonta radiata* Portlock; Baily, p. 28.
v. 1952 *Lyrodesma radiatum* (Portlock); Reed, p. 67, pl. 3, fig. 11.

Type-specimen. Lectotype selected here IGS GSM 22178, the specimen figured by Portlock (1843, pl. 36, fig. 11) and used by Reed (1952, p. 67) in his redescription.

Material, localities, and horizon. Specimens in IGS, TCD, and NMI, including six Portlock syntypes. Mostly external moulds, or composite moulds. All from the Bardahessiagh Formation, south of Craighbardahessiagh, Pomeroy, exact localities uncertain except IGS GU 3264, Mitchell Collection, from Mitchell's Bardahessiagh collecting area (Mitchell 1977, p. 5).

Measurements

	L	H	H/L	AL/L	Angle between antero- and postero-dorsal margins
Max.	20.0 mm	12.6 mm	0.69	0.40	c. 150°
Min.	13.0 mm	8.0 mm	0.50	0.26	c. 125°
			compressed dorso-ventrally		
Mean	16.24 mm	9.86 mm	0.60	0.34	
Median	16.5 mm	11.0 mm	0.60	0.33	

Description. *Lyrodesma* of elongate, ovate form with height-length ratio about 0.6. Maximum inflation of a single valve is about 2 mm in a valve 20 mm long. The umbo lies at about the anterior one-third. The anterior margin is rounded, the posterior end is subtruncate and obliquely carinate. Postero-dorsal surface bearing 17+ radial striations of variable strength and arranged somewhat irregularly. Anterior portions of the surface show very faint concentric growth lines. Umbones rather small. Six radiating crenulate teeth of similar size below umbo in left valve. A faint line or ridge is seen on the internal mould running from the umbo to the ventral margin anterior to the umbonal ridge. Posterior and anterior adductor muscle scars situated dorsally, the posterior scar being a little larger than the anterior. Accessory muscle scars poorly discerned in the present specimen.

Discussion. As Reed noted (1952, pp. 67-68) Portlock's description and figure of *Lyrodesma radiatum* were poor, but Reed saw only two of the Portlock syntypes and had no specimens showing the dentition. In shape and the number of teeth, *L. radiatum* resembles *L. majus* (Ulrich) and Reed likened it to *L. cincinnatiense* Hall (of Ruedemann 1926) and to *L. poststriatum elongatum* Stewart, 1920, but until more material is available to provide further detail of the internal structure, no close comparison can be made with other species.

Class ROSTROCONCHIA Pojeta, Runnegar, Morris and Newall, 1972

Order CONOCARDIOIDEA Neumayr, 1891

Superfamily CONOCARDIACEA Miller, 1889

Family HIPPOCARDIIDAE Pojeta and Runnegar, 1976

Genus HIPPOCARDIA BROWN, 1843

Type species. By monotypy *Cardium hibernicum* Sowerby, 1815. The classification used here is that of Pojeta and Runnegar 1976.

Hippocardia praepristis (Reed), 1952

Plate 9, fig. 8

v* 1952 *Conocardium praepristis* Reed, p. 80, pl. 4, fig. 11.

v. 1976 *Hippocardia praepristis* (Reed); Pojeta and Runnegar, p. 76.

Type specimens. Holotype by original designation, IGS GSM 24147, the only specimen known to Reed and to the present author. The specimen is part of the Portlock Collection (Tunnicliff 1980) and bears a label reading 'Cypricardia—Analogous to *C. cymbaeformis* but differs from it and also from *Cardium carpo-morphum* (J. P.)' but Portlock (1843) published no reference to it.

Locality and horizon. The horizon of this specimen is uncertain, but Reed likened the matrix to that of the Tirnaskea Beds (Tirnaskea Formation). If this is correct, a likely locality would be the Tirnaskea Stream section or perhaps the Crocknagargan Stream section, both of which have exposures of Tirnaskea Formation (Ashgill, Hirnantian) but there is no record of Portlock having specimens from the latter and there is evidence that he had none from the Tirnaskea Stream section (Portlock 1843, p. 230 '...on the Tirnaskea or small river there are thin calcareous layers of three or four inches thick mixed with quartzose bands, no fossils, however, occurring in them...'). Lithologically, the specimen resembles known Killy Bridge Formation specimens, and it must be assumed that the specimen is from that horizon, but the locality is unknown.

Description. Adequate description is provided by Reed (1952), and Pojeta and Runnegar (1976) placed *praepristis* in *Hippocardia* on this basis. The specimen is figured here to supplement Pojeta and Runnegar.

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JUVENILE SPECIMENS OF THE ORNITHISCHIAN DINOSAUR *PSITTACOSAURUS*

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ABSTRACT. Hitherto undescribed specimens of *Psittacosaurus mongoliensis* from the Oshih Fm., Mongolian Peoples' Republic, include two almost complete skulls and numerous postcranial elements. A rostral bone, present in these and other specimens of *Psittacosaurus*, is a cranial element otherwise known only in ceratopsians, and its presence indicates a sister group relationship for the Psittacosauridae and Ceratopsia. Each of the two new specimens of *Psittacosaurus* is a juvenile, and are among the smallest dinosaur specimens yet described. Parental attendance of nests was common, possibly universal among dinosaurs, but post-hatching parental care is uncertain. Juveniles of *Psittacosaurus*, as well as those of other dinosaurs, may have formed sibling groups.

Two skeletons of small bipedal ornithischians collected by the Third Asiatic Expedition (1922) of the American Museum of Natural History were described by Osborn (1923, 1924) as the types of *Psittacosaurus mongoliensis* (Oshih Fm.) and *Protiguanodon mongoliense* (Andai Sair Fm.), thought to be a primitive ankylosaur and a primitive iguanodontid, respectively. To the family Psittacosauridae, erected for reception of these two species (Osborn 1923), have been added several new species of *Psittacosaurus* and additional fragmentary remains from various localities in Mongolia and northern China (Young 1931, 1958; Bohlin 1953; Maleev 1954; Rozhdestvensky 1955; Chao 1962). Described below are two additional specimens of *Psittacosaurus* from the same locality as the type of *P. mongoliensis*.

MATERIAL

AMNH 6535 (= American Museum of Natural History, New York), partial skull and jaws.

AMNH 6536, almost complete skull and jaws with numerous distarticulated postcranial elements including: cervical, dorsal, and caudal vertebrae; ribs; scapulae; coracoid; partial ilium and ischium; humeri; femora; tibiae; fibulae; and an almost complete left pes. The postcranial material belongs to several individuals (there are fourteen distal ends of tibiae) of at least two different sizes (some femoral fragments are tiny and more compatible in size with the skull AMNH 6535). Rather than allot separate numbers to every element, all of the postcranial material is arbitrarily assigned to AMNH 6536.

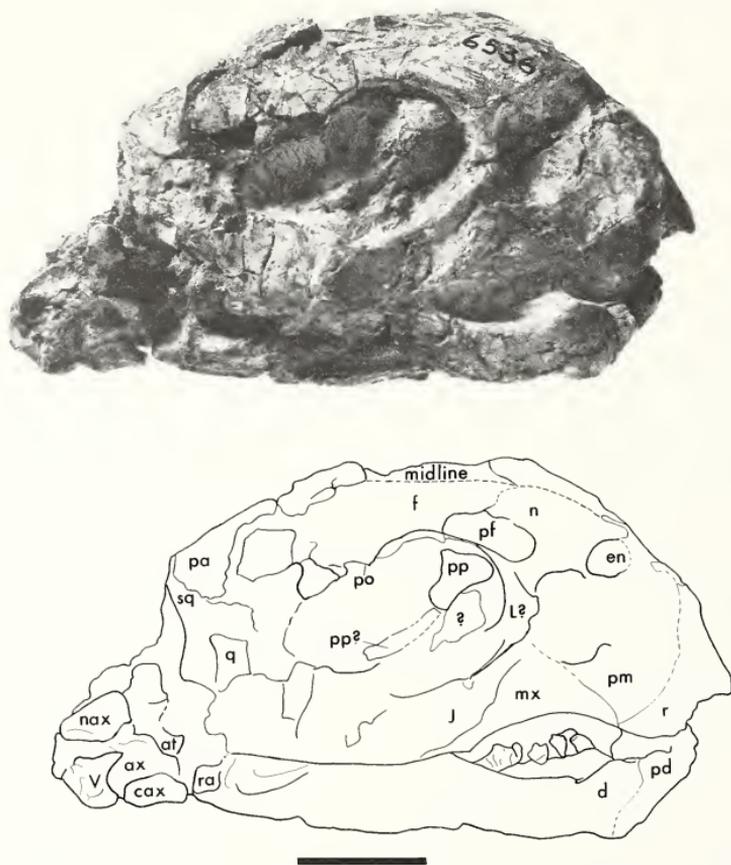
Locality. Both specimens come from the Oshih Fm., Artsa Bogdo basin, western Mongolian Peoples' Republic, and were apparently collected at the same time and in the same place as the type of *Psittacosaurus mongoliensis* (Osborn 1923, 1924).

DESCRIPTION

Skull, general. In lateral view the skull is arched dorsally, truncated posteriorly, and has a short snout (text-figs. 1, 3, 4). AMNH 6536 is laterally crushed, but AMNH 6535 retains the characteristic triangular shape of psittacosaur skulls, with the greatest breadth across the flaring jugals and a sharply pointed apex at the beak (Pl. 14). The apparent relatively large size of the brain in AMNH 6535 is a juvenile character (Pl. 14, figs. 1 and 2). The diameter of the orbit equals 33% of cranial length in AMNH 6536; 38% in AMNH 6535, the relatively large orbit also being a juvenile characteristic. The nostril is clearly delineated only on the right side of AMNH 6536, on which it is small, circular, and approximately at the level of the upper half of the orbit.

Cranial fenestrae. Both skulls are damaged posteriorly and borders of all temporal fenestrae are incomplete. The left supratemporal fenestra of AMNH 6536 is oval with its long axis paralleling the midline. The braincase is broad and devoid of a sagittal crest between the upper fenestrae (Pl. 14). Lateral temporal fenestrae are

evidently tall and narrow, and considerably smaller than the orbit, unlike the condition in adult *Psittacosaurus* in which the fenestrae are larger than the orbit (e.g. Osborn 1923, fig. 2). AMNH 6536 has a shallow depression, its depth somewhat exaggerated by crushing, between nostril and orbit in the region where an antorbital fenestra might be located, but there is no opening into the interior of the skull (text-fig. 1). AMNH 6535 is badly crushed in the immediate pre-orbital region, but it appears that a true antorbital fenestra was not present.



TEXT-FIG. 1. AMNH 6536, skull, lower jaws, and anterior cervical vertebrae; right side with key drawing. Abbreviations: at, atlas; ax, neural arch of axis; cax, centrum of axis; d, dentary; en, external naris; f, frontal; j, jugal; L, lacrimal; mx, maxilla; n, nasal; nax, neural spine of axis; pa, parietal; pd, prefrontal; pf, prefrontal; pm, premaxilla; po, postorbital; pp, palpebral; q, quadrate; r, rostral; ra, retroarticular process; sq, squamosal; and v, cervical vertebrae (post-atlas). Length of reference line = 1.0 cm (approximately twice natural size).

Rostral. Following Maryańska and Osmólska (1975, p. 172), the most anterior element of the snout is identified as a rostral, a bone diagnostic of ceratopsians, rather than as a premaxilla (as suggested by Osborn (1923; see also Young 1958; Chao 1962). The rostral, best preserved on the smaller skull (text-fig. 4), is roughly triangular in lateral view with an ascending ramus that curves posteriorly to terminate near the ventral margin of the nostril. Most of the cutting margin of the beak is composed of the rostral, but it is unclear to what extent the rostral contributes to the anterior palatal shelf.

Premaxilla. Exact limits of the premaxillae are unclear, but the bone probably intervenes between the rostral and the external nares and forms all the ventral border of the latter opening (text-fig. 3; Maryańska and Osmólska 1975). Because other authors have identified the rostral as the premaxilla, the true premaxilla has been identified as part of the maxilla. In consequence, *Psittacosaurus* has been reconstructed with a very large maxilla that separates the premaxilla from the lacrimals as well as from the margin of the nostril (Osborn 1923, fig. 2A; Young 1958, fig. 51; Chao 1962, fig. 1) a pattern atypical for ornithischians. The alternative interpretation presented here (text-fig. 3) indicates extensive contact of premaxilla and lacrimal with exclusion of the maxilla from the border of the nostril, a pattern common among ceratopsians and ornithischians in general (Lull 1933; Romer 1956). Ornithischians typically have a bony roof to the anterior part of the buccal cavity composed of premaxillae, maxillae, and sometimes the vomers. In the Ceratopsia the rostral bone forms much of the cutting edge of the beak, but forms only a small segment of the anterior palatal shelf (Lull 1933, figs. 5 and 30; Maryańska and Osmólska 1975, fig. 9). *Psittacosaurus* may have a similar arrangement, but sutures are unclear on the present specimens (Pl. 14, figs. 3 and 4).

Maxilla. Anteriorly the maxilla may contact the posterior limit of the rostral along the edge of the mouth in the present specimens, but contact is lost in adult *Psittacosaurus*. Maxillary teeth, numbering at least five in AMNH 6535 and at least six in AMNH 6536, are withdrawn medially, so that the maxilla forms a lateral shelf thus delineating the dorsal border of a 'cheek-pouch', a common feature among ornithischians (Galton 1973).

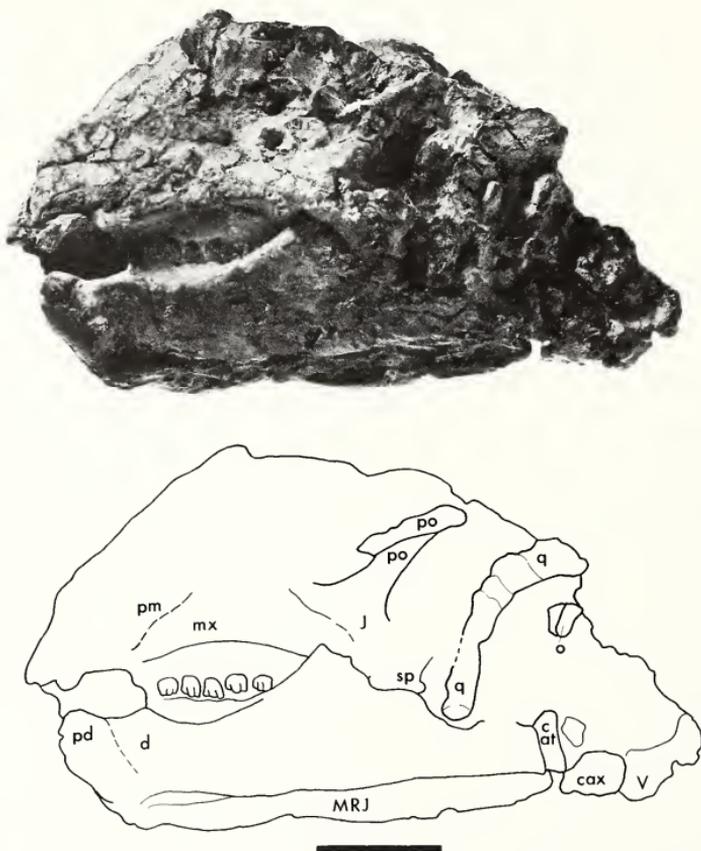
Jugal. All the ventral margin of the orbit is formed by the jugal, the suborbital bar being relatively slender in AMNH 6535, considerably wider and giving an impression of massiveness in AMNH 6536, but in neither skull is the jugal as wide as in adult *Psittacosaurus*. A ventro-laterally projecting jugal spine, located below the lateral temporal fenestra, is present on the left jugal of AMNH 6536 (text-fig. 2), but is considerably smaller than the prominent flange of adult *Psittacosaurus* skulls (Osborn 1923, 1924; Young 1958; Chao 1962). A slender ascending ramus of the jugal forms part of the postorbital bar. A quadratojugal presumably intervened between the jugal and the ventral end of the quadrate, but the element cannot be distinguished on either of the present specimens.

Quadrate. The elongate quadrate curves anteriorly from its dorsal, squamosal articulation and is two to three times wider than the postorbital bar (text-figs. 2 and 3). The mandibular cotylus is compressed antero-posteriorly and has a bulbous lateral region adjacent to a narrower medial area (Pl. 14, figs. 3 and 4). The cotylus projects below the level of the tooth row, as in most ornithischians.

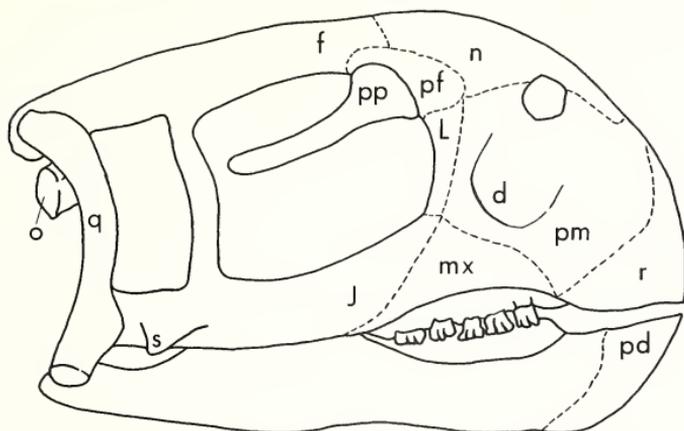
Skull roof. The nasals presumably form the narrow bar between the nostrils as well as the wider region immediately posterior to them, but sutures of the nasals with rostral, maxillae and premaxillae are not visible on either specimen. Chao (1962) illustrates *P. youngi* with the nasals excluded from the narial border (text-fig. 7c), but this is not true of the type of *P. mongoliensis* (text-fig. 7d). A prefrontal nestles into the antero-dorsal margin of the orbit excluding the nasal from the orbital rim (right side of AMNH 6536, text-figs. 1 and 3). Ventrally the prefrontal contacts the lacrimal and premaxilla, but sutures are indistinct. A displaced palpebral ('supraorbital' of Osborn 1923; 'prefrontal' of Chao 1962; see Coombs 1972) originally articulated with the prefrontal at the anterior rim of the orbit (text-figs. 1 and 3). The palpebral has an expanded base and a tapered posterior extension that is incompletely preserved. Posterior to the indistinct contact of nasals and frontals above the orbits the skull roof widens and the postorbital contacts the lateral edge of the frontal. A slender descending rod of the postorbital bone forms most of the postorbital bar. The relative contributions of the postorbitals, frontals, and parietals to the margins of the supratemporal fenestrae cannot be determined. Parietals form most of the arched posterior skull roof, without the sagittal crest present in adult skulls (see also skull of *Psittacosaurus osborni* Young, 1931, fig. 2). The parietals bend sharply downward at the posterior margin of the skull roof to form the most dorsal surface of the occipital region.

Occipital area. Very little of this region is exposed. The rugose distal tip of the left opisthote of AMNH 6536 projects from matrix well below the level of the skull roof and the dorsal tip of the quadrate (text-fig. 2). The element is roughly triangular in section, not as flattened as is typical for Ornithischia.

Palate. Some palatal details are visible on the smaller skull (Pl. 14, figs. 3 and 4). An anterior palatal shelf is formed partly of the rostral and partly of the premaxillae, and is roughly semicircular in shape, being less pointed and less triangular than in adult *Psittacosaurus*. The vomers form a median vertical plate that dominates the interior palatal region. The ventral keel of this plate extends below the level of the tooth rows, a condition found in several ornithischians (e.g. the ankylosaur *Panoplosaurus*; Russell 1940). A narrow shelf from the maxillae appears to contact the vomer keel anteriorly, thus shifting the internal nares posteriorly. The internal nares are bounded laterally and anteriorly by maxillae, medially by the vomer keel, and are bounded posteriorly by a broad plate of bone that slants obliquely anteriorly and upward toward the skull



TEXT-FIG. 2. AMNH 6536, skull, lower jaws and anterior cervical vertebrae; left side with key drawing. Abbreviations: cat, centrum of atlas; cax, centrum of axis; d, dentary; J, jugal; MRJ, medial side of right lower jaw; mx, maxilla; o, opisthotic; pd, pre-dentary; pm, premaxilla; po, postorbital; q, quadrate; sp, spine of jugal; v, cervical vertebra (post-atlas). Length of reference line = 1.0 cm (approximately twice natural size).



TEXT-FIG. 3. Restoration of a juvenile *Psittacosaurus* skull based primarily on AMNH 6536. Abbreviations: d, depression in premaxilla; f, frontal; j, jugal; L, lacrimal; mx, maxilla; n, nasal; o, opisthotic; pd, predentary; pf, prefrontal; pm, premaxilla; pp, palpebral; q, quadrate; r, rostral; and s, spine of jugal.

roof. The latter plate is composed of pterygoid, ectopterygoid, and palatine bones, but sutures are unclear. The palatal structure of *Psittacosaurus* is similar to that of many Ornithischia, especially the quadrupedal forms, and may be compared particularly to the palate of *Bagaceratops* (Maryańska and Osmólska 1975, fig. 9).

Basicranium. The partially exposed basicranium of AMNH 6535 (Pl. 14, figs. 3 and 4) is broad relative to other skull dimensions (a juvenile feature), and has a median longitudinal depression that is flanked by anteriorly converging ridges. A small, subspherical, posteriorly directed occipital condyle projects only slightly below the level of the basicranial floor.

Lower jaw. The deep, massive lower jaw has a straight ventral margin and medially displaced dentary teeth (text-fig. 1). A curved shelf marks the ventral border of the cheek pouch. The predentary and dentary bones are fused together. Posteriorly there is a pointed coronoid process projecting upward medial to the most anterior ventral corner of the lateral temporal fenestra. A short retroarticular process projects backward from the articular (text-fig. 1).

Teeth. Anterior maxillary teeth have three ridges on the lateral surface that upon wear produce the 'tribolate' cutting margin described by Osborn (1924; text-fig. 2). Posterior maxillary teeth may have four ridges and are generally larger but less worn than anterior teeth. All teeth that are adequately exposed on the two skulls are worn to some degree. There are no premaxillary teeth.

Vertebrae. Cervical vertebrae attached to the skull of AMNH 6536 include the axis, which has a low, laterally compressed, elongate neural spine as described in the type of *Protiguanodon mongoliense* (AMNH 6253; Osborn 1924). A small block of bones (part of AMNH 6536) contains several vertebrae, mostly dorsals (text-fig. 5). The centra are laterally compressed, with expanded, roughly heart-shaped articular ends. The neural arches are not fused to the centra, a juvenile characteristic. A particularly well-preserved neural arch of a dorsal(?) vertebra has about the same length as its centrum; the incomplete zygapophyses arch upward and there is an almost circular diapophysis high on the side of the neural arch. A sacral vertebra in the same block has a centrum similar in shape to dorsal centra, and has a low, broad neural arch with an elongate, laterally compressed neural spine most of which is broken off. The sacral rib articulated on anteroposteriorly compressed diapophyses positioned at the extreme anterior end of this sacral, which judged from the sacral



TEXT-FIG. 4. AMNH 6535, skull, partial lower jaw, and fragmentary anterior cervicals, right side. Length of reference line = 1.0 cm (approximately twice natural size).

series of *Protoceratops* (Brown and Schlaikjer 1940), is from the middle of the sacral series. Another sacral vertebra in the block also has an elongate, compressed diapophysis but it is oriented almost horizontally, suggesting that this vertebra belongs to the posterior end of the sacral series. A group of three caudal centra (text-fig. 6N), all lacking the neural arch, are smaller than either dorsals or sacrals but have similar shape and proportions. Transverse processes are not present on any of the caudals. The largest of these three caudal centra is about 4.5 mm in length.

Ribs. Rib fragments embedded in the block with other postcranial elements have cross sections that are either circular (proximal ends) or compressed (distal ends, text-fig. 5). One proximal end fragment has a large, almost circular head that matches in size and shape the articular surface on the dorsal vertebra described above, and a very small tubercle positioned a short distance from the head.

Pectoral girdle. Scapulae are represented by two almost complete elements (text-fig. 5), plus a partial scapular blade. The scapulae are elongate and narrow, with a much wider, slightly concave area adjacent to the glenoid and coracoid articulation. The upper end of the blade is broad but flattened. A low scapular spine arises from the extreme anterior edge of the scapula directly opposite the glenoid. The glenoid articulation is short, broad, slightly concave, and has a rather massive dorsal lip. The coracoid articulation is elongate and

EXPLANATION OF PLATE 14

Two views of AMNH 6535, a skull, partial lower jaw and fragments of anterior cervical vertebrae.

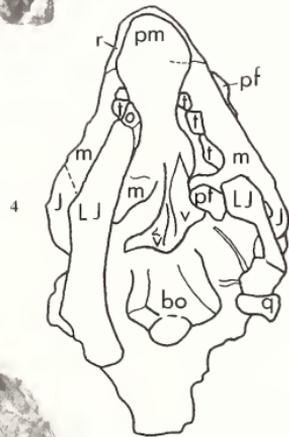
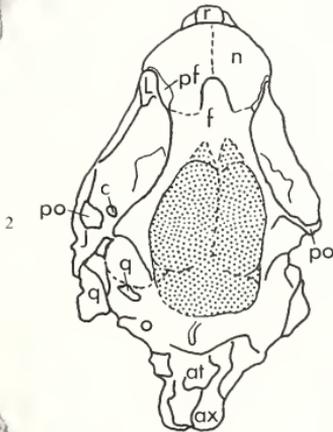
Fig. 1. Dorsal view, stereo pair.

Fig. 2. Key to structures visible in the dorsal view. Stippling indicates the approximate extent of a natural endocranial cast that has been partially exposed through loss of some dorsal cranial bones. The anterior limit of the endocranial space was determined in part by examination of AMNH 6536 which has the anterior tip of a natural endocranial cast exposed through loss of some skull bones.

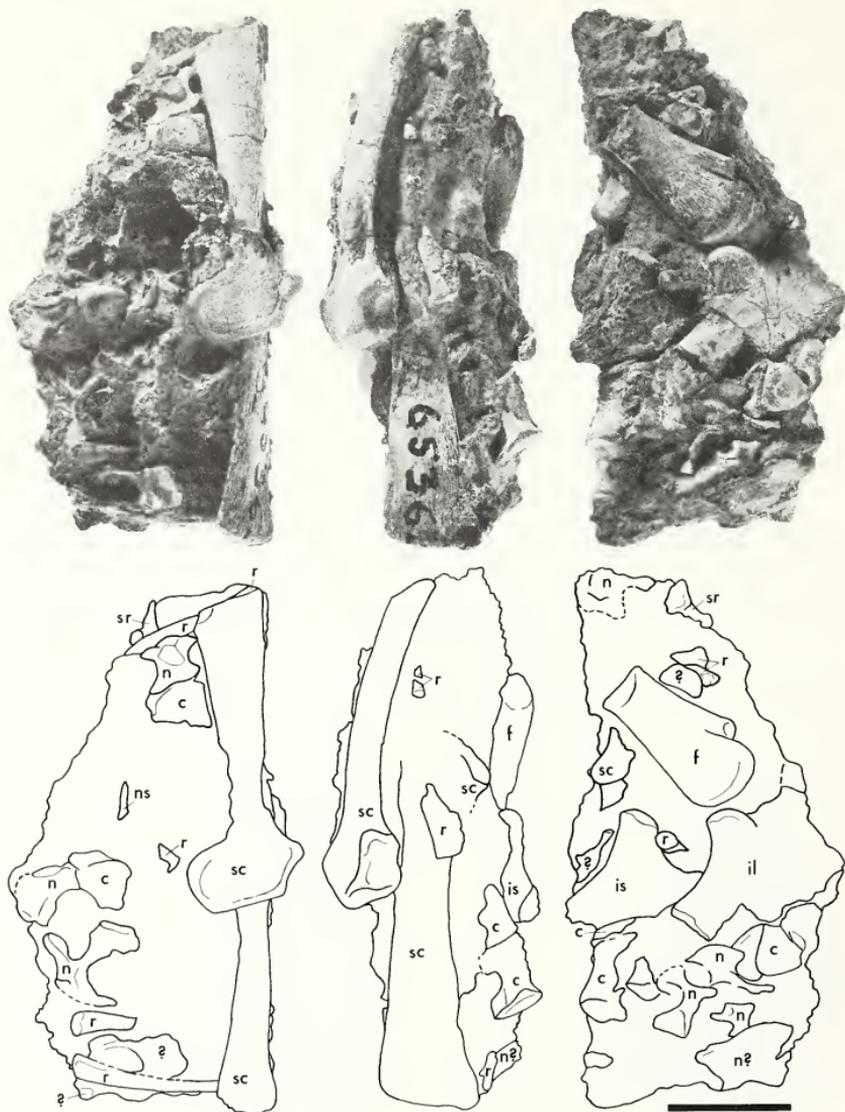
Fig. 3. Ventral view, stereo pair.

Fig. 4. Key to structures visible in ventral view. Abbreviations: at, atlas; ax, axis; bo, basioccipital; c, left coronoid process (protruding through matrix); f, frontal; j, jugal; L, lacrimal; LI, lower jaw; m, maxilla; n, nasal; o, opisthotic; pm, premaxilla; po, postorbital; pt, pterygoid; q, quadrate; r, rostral; t, tooth. Length of reference line = 1.0 cm (approximately twice natural size).

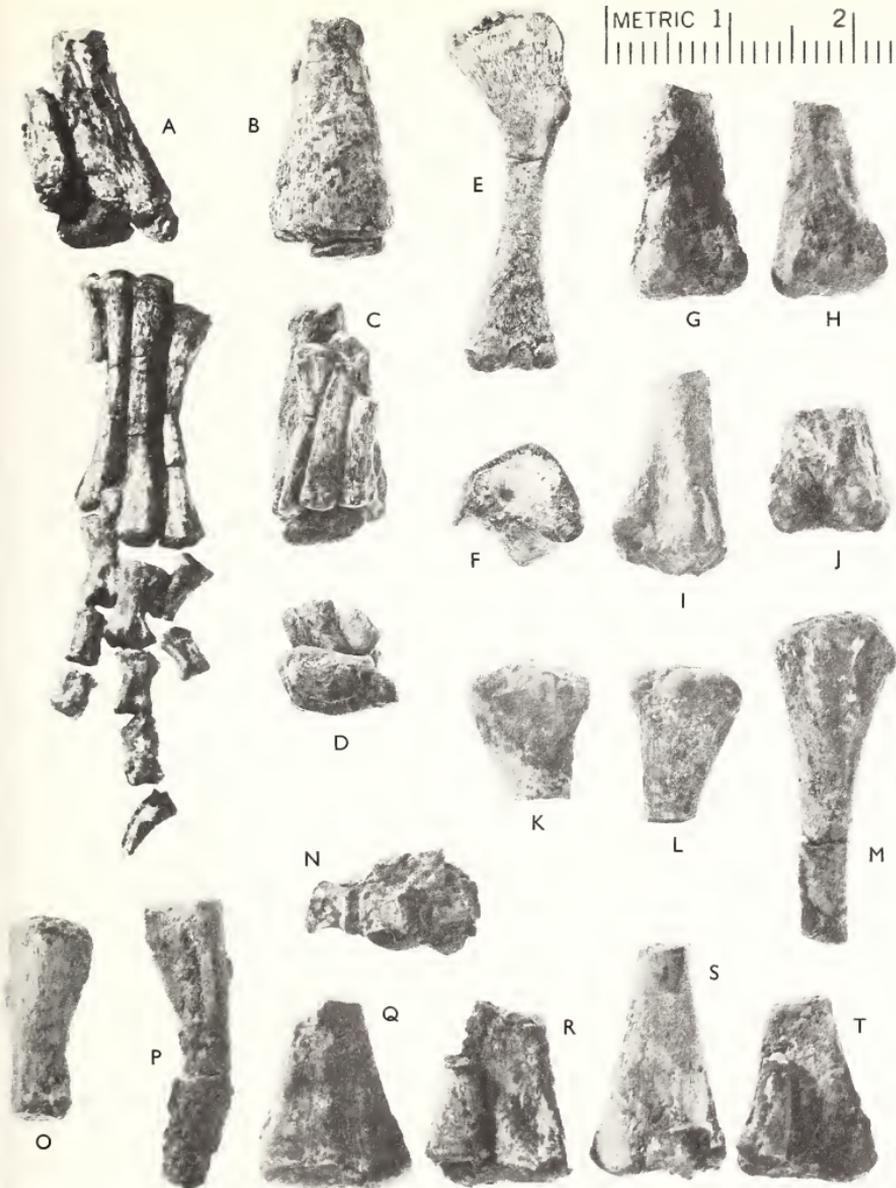
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TEXT-FIG. 5. AMNH 6536, three views of a block containing various postcranial elements, with key drawings. Abbreviations: c, centrum; f, femur; il, ilium; is, ischium, n, neural arch, r, rib; sc, scapula; sr, sacral rib; and a question mark denoting an unidentified fragment. Length of reference line = 1.0 cm (approximately twice natural size).



TEXT-FIG. 6. AMNH 6536, various postcranial elements. A, partial left pes with distal ends of tibia and fibula; B, posterior view of a partial left tibia with astragalus and metatarsals II, III, and IV; C, same as B in anterior view; D, same as B in distal view; E, left humerus, flexor surface; F, right coracoid, lateral view; G, H, I, and J, distal ends of four femora, posterior views; K, L, and M, proximal ends of three tibiae, anterior views; N, block containing three caudal centra; O and P, proximal ends of two small femora, anterior views; Q, R, S, and T, distal ends of four tibiae, anterior views, with distal ends of fibulae on R and T. Scale divisions in mm (approximately twice natural size).

triangular, exactly matching an associated left coracoid (text-fig. 6F). The coracoid has a broad, slightly concave glenoid and a foramen that is roughly equidistant from the glenoid and scapular articulations. There is a prominent biceps tuberosity on the anterior edge of the coracoid, from which a ridge extends posteriorly toward the glenoid. Below the biceps tuberosity the coracoid has a shallowly concave, medially inclined surface that is the probable region of coracobrachialis origin. Clavicles have been reported for *Psittacosaurus mongoliensis* (Osborn 1924) and *P. sinensis* (Young 1958), but there are no clavicles associated with the scapulae of the present specimens (text-fig. 5). In view of the jumbled condition of the bones, the clavicles could well be displaced and easily mistaken for rib fragments.

Pelvic girdle. Of the pelvic girdle there is one fragmentary piece each of ilium and ischium (text-fig. 5). The ilial fragment is flat with a blunt, ventrally projecting ischial peduncle and a laterally compressed, rather thin postacetabular segment. Only the base of the pubic peduncle is preserved. The ischial fragment includes an elongate, laterally compressed pubic articulation, and an ilial articulation that appears to be more compact and rounded, although most of the latter is hidden below the ilial fragment. The ischial blade slants posteriorly and is narrow and laterally compressed. Most of the distal part of the ischium is missing.

Forelimb. In addition to a perfect left humerus (text-fig. 6E), there are two proximal ends of right humeri, one about the same size as the left humerus and one considerably smaller. Proximally, the humerus is broad, but it tapers quickly to a roughly circular shaft, then widens at the distal articulations which are rotated relative to the head such that the extensor surface is twisted medially. A deltopectoral crest projects ventrally and is rather close to the proximal end of the humerus. No other forelimb elements have been identified.

Hindlimb. There are numerous fragments, but unfortunately there is no association of a particular femur with a particular tibia, nor with the pes described below, so that hindlimb proportions cannot be established. The proximal end of a relatively large femur has a compressed, crest-like greater trochanter with an adjacent, finger-like lesser trochanter separated from the former by a deep furrow, and an irregularly circular shaft (text-fig. 5). Two much-smaller femora have a virtually identical set of trochanters and a medially displaced head that is as much cylindrical as spherical (text-fig. 6O, P). The femoral shaft is curved with the convex surface lateral, a common shape for femora of bipedal Ornithischia. None of the eight distal femoral pieces included in AMNH 6536 can be fitted on to any of the proximal ends. Distal articulations follow the usual bipedal ornithischian pattern of a larger lateral and smaller medial articular surface (text-fig. 6G, H, I, J).

There are seven proximal and fourteen distal ends of tibiae (text-fig. 6K, L, M, Q, R, S, T). Proximally, the tibia has an antero-posteriorly elongated articular surface that has a smoothly curved medial surface and a notched lateral surface that gives the proximal end a trilobate shape viewed end-on. The tibial shaft tapers to a slender rod of almost circular cross-section. Distally, the tibia is strongly compressed antero-posteriorly, creating a wide articular surface that is a little thicker medially and has a slight depression near the centre for reception of the astragalus. There is a slight ventral projection at the lateral corner of the distal end, marking the fibular articulation. Fibular fragments still attached to two of the tibiae (text-fig. 6R, T) are oval in section, only a fraction of the diameter of the tibial shaft, and fit into a shallow depression on the antero-lateral edge of the distal end of the tibia.

Pes. The astragalus is compressed against and covers about two-thirds of the distal end of the tibia (text-fig. 6A, B, C, D) leaving a small space laterally for the calcaneum. The lateral edge of the astragalus is notched for reception of the calcaneum, and anteriorly the astragalus curves up on to the flexor surface of the tibia. A roughly cup-shaped calcaneum nestles against the ventrally projecting lateral corner of the tibia (text-fig. 6A), and as preserved does not contact either the astragalus or fibula. A distal row of tarsals is not present.

As is typical of bipedal ornithischians, the metatarsals are long, slender, and fit tightly together, especially at their proximal ends (text-fig. 6A, C, D). As in the types of *Psittacosaurus mongoliensis* and *P. sinensis*, metatarsals I through IV are present, but there is no trace of metatarsal V nor is there an articular surface for it on metatarsal IV. Metatarsal I is strongly compressed at the proximal end and through the upper two-thirds of the shaft. Metatarsal II is about double the width of metatarsal I proximally, but is still somewhat compressed. Metatarsal II has a wider shaft and is longer than metatarsal I. Metatarsal III has an irregularly square proximal articular surface and is the longest, straightest, and most massive of the metatarsals. Metatarsal IV is about the same length as metatarsal II, but is more compressed at the proximal end, and its shaft curves slightly away from the axis of the pes running through metatarsal III. Phalanges have the typical form found in small bipedal ornithischians (text-fig. 6A). All are relatively long (length greater than diameter) and are circular to subrectangular in cross-section, not dorsoventrally compressed. One almost complete ungual of digit III is slightly longer than the adjacent phalanx and has a narrow, semi-claw shape as in *Leptoceratops* (Brown 1914; Brown and Schlaikjer 1942) rather than the broad, hoof-like unguals of *Protoceratops* (Brown

and Schlaikjer 1940). The pes is narrow, long, and gracile (text-fig. 6A), suggesting a relatively fleet animal. Of interest is the manner in which the pes is folded against the anterior surface of the tibia in one specimen (text-fig. 6B, C, D), a post-mortem posture also found in the types of *Psittacosaurus mongoliensis*, *Protiguanodon mongoliense*, and *Stenopelix valdensis* (Osborn 1923, 1924; Meyer 1857; Koken 1887). When these animals died, they settled on to their belly with the hindlimbs folded into a sharp 'Z', the knee projecting forward, ankle backward, femur atop the tibia, and pes pressed against the anterior surface of the tibia and apparently set flat against the ground (this posture is imperfectly preserved also in specimens of *Psittacosaurus sinensis*: Young 1958, figs. 52, 53, and 54). The imprint of the pes would conform to the sitting dinosaur trackways from the Connecticut Valley (e.g. *Sauropus barrattii* and *Anomoepus scambus* specimens described by Lull 1953). The belly-down position is not common among bipedal ornithischians. The skeletons of *Iguanodon* and most hadrosaurids are typically found lying on their side with the knee and ankle both flexed rearward, or with the pes almost aligned with the tibia. Psittacosaurus apparently had great mobility of the knee and mesotarsal joint, with hyperextensibility of the ankle permitting the entire length of the pes to be laid flat on the ground. The difference in joint mobility in psittacosaurus and large bipeds may be related to total body size, the larger ornithischians sacrificing some ankle extensibility for the sake of rigidity necessary for weight-bearing.

DISCUSSION

Taxonomy. Rozhdestvensky (1955) regarded *Psittacosaurus mongoliensis* Osborn (1923) as the senior synonym of the following: *Protiguanodon mongoliense* Osborn (1923 = *Psittacosaurus protiguanodonensis* of Young 1958); *Psittacosaurus osborni* Young (1931); ?*Psittacosaurus tingi* Young (1931); and *Protiguanodon* cf. *mongoliense* (of Young 1931). Trivial differences among these species are reasonably regarded as stemming from ontogenetic state and individual variation. *Psittacosaurus sinensis* Young (1958) and *P. youngi* Chao (1962) may also be junior synonyms of *P. mongoliensis* although, without having all the specimens in hand for detailed comparison of measurements and proportions not available in extant descriptions, formal suppression of all but one species is premature. *Stenopelix valdensis* Meyer (1857; see also Koken 1887; Huene 1908) from Wealden deposits (Swinton 1936) of northern Germany was originally classified in the Hypsilophodontidae (Huxley 1870), but has also been suggested as a ceratopsian (Huene 1909; Lull 1910) and a psittacosaur (Romer 1956). The reported absence of a postpubic process and the exclusion of the pubis from the acetabulum in *Stenopelix* are features unknown in psittacosaurus, but have been reported for the pachycephalosaur *Homalocephale* (Maryńska and Osmólska 1974), and *Stenopelix* has been classified in the Pachycephalosauridae (Galton 1976; Olshevsky 1978). Contact of the ischium with the pubic peduncle with resultant exclusion of the pubis from the acetabulum may also be common among ankylosaurs, although obscured in most specimens by fusion of the pelvic elements, and ankylosaurs have a very short postpubic process. In any case, assignment of *Stenopelix* to the Psittacosauridae cannot be defended on the basis of common derived characters, and the genus is here considered as Ornithischia, *incertae sedis*. The family Psittacosauridae is therefore regarded as having a single genus, *Psittacosaurus*, with the type species *P. mongoliensis*, and other species being of questionable validity.

AMNH 6535 and 6536 come from the same stratigraphic and geographic locality as the type of *Psittacosaurus mongoliensis*. While the two new skulls differ in detail from the type of *P. mongoliensis*, the differences are of a kind and magnitude that are reasonably expected in such juvenile specimens, as may be appreciated by studying the hypothesized growth series (text-fig. 7). AMNH 6535 and 6536 are therefore assigned to the species *Psittacosaurus mongoliensis*.

Phylogenetic position of the Psittacosauridae. Bipedality has long been the justification for inclusion of several families, including the Psittacosauridae, within the suborder Ornithopoda, despite recognized peculiarities and the absence of critical features. Maryńska and Osmólska (1974) argued that bipedality alone was insufficient evidence for such a grouping, and removed pachycephalosaurs from the Ornithopoda (see also Olshevsky 1978). If the general dogma that bipedality is primitive (plesiomorphic) for the order Ornithischia is true (e.g. Galton 1978), then it is unsuitable as a

unifying character for the suborder Ornithopoda. Moreover, psittacosaur, like pachycephalosaurs, have no obturator process on the ischium, a feature apparently synapomorphic for the Ornithopoda *sensu stricto*. Psittacosaur has been recognized as ceratopsian-like by several authors (Rozhdestvensky 1955, 1960; Romer 1956; Gregory 1957; Young 1958; Colbert 1965; Maryańska and Osmólska 1975) but Steel (1969) noted that the absence of premaxillary teeth removed *Psittacosaurus* from the immediate ancestry of *Protoceratops*, and the peculiar structure of the *Psittacosaurus* manus (Osborn 1924) is a further barrier to placing the genus in a position ancestral to any known ceratopsian.

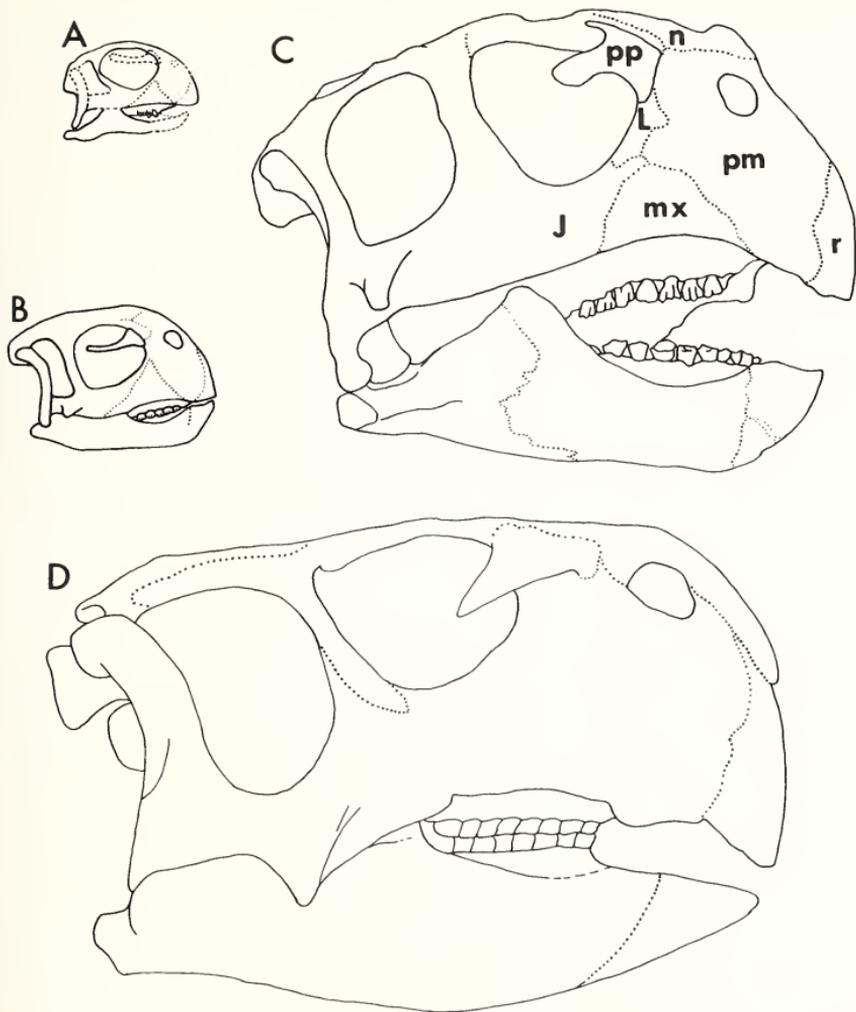
Maryańska and Osmólska (1975) recognized that the substantial similarity in general cranial morphology shared by psittacosaur and ceratopsians outweighed any arguments on the unsuitability of the former as 'ancestors' for the latter. They also realized that failure to identify a rostral bone in *Psittacosaurus* was the single major objection to transferring the Psittacosauridae to the suborder Ceratopsia, and they boldly suggested that the snout of *Psittacosaurus* had been incorrectly interpreted by Osborn (1923, 1924) and others (Young 1958; Chao 1962). Maryańska and Osmólska (1975) contended that a rostral bone is in fact present in *Psittacosaurus*, an opinion with which I fully concur (see also Olshesky 1978).

The rostral of ceratopsians probably originated as an epidermally induced ossification, with the large, overlying epidermal scale eventually becoming a thick, heavily keratinized upper beak. The rostral and upper beak thus correspond to the prementary and associated beak of the lower jaw in origin and function. In *Psittacosaurus* the rostral is ill defined and in large part fused to the premaxillae, similar to the way in which epidermal ossifications overlie and are fused to the skull roof of ankylosaurs (e.g. Maryańska 1971, 1977). The *Psittacosaurus* rostral is not, therefore, a completely separate cranial element as it is in advanced ceratopsians, but it is nevertheless present. Revised identifications of psittacosaur skull bones (text-figs. 3 and 7c) may be compared with identifications in original descriptions.

The family Psittacosauridae is here regarded as belonging in the suborder Ceratopsia rather than in the Ornithopoda, but further refining of its position among ceratopsians is difficult. Many taxa included in the Protoceratopsidae share synapomorphies with the Ceratopsidae, for example the development of a posterior parietal-squamosal frill and at least incipient development of horns, features not present in psittacosaur. On the other hand, absence of premaxillary teeth in *Psittacosaurus* is possibly a derived character shared with the Ceratopsidae, but not with the Protoceratopsidae some of which have premaxillary teeth. The peculiar manus of *Psittacosaurus*, and the related bipedal stance, are unique developments among ceratopsians, but whether these are derived characters defining the basal sister group split of the suborder, or merely retention of primitive features by *Psittacosaurus*, is unclear. Potentially, at least, the Psittacosauridae could be the sister group of all other Ceratopsia, such a position leaving uncertain the question as to whether bipedal or quadrupedal posture was the primitive condition for the suborder.

Juvenile features. Differences between adult and juvenile ceratopsian skulls (Brown and Schlaikjer 1940; Maryańska and Osmólska 1975; Dodson 1976) provide a basis for recognition of juvenile features in the two *Psittacosaurus* skulls under consideration. Among these features are the following: orbit very large; braincase relatively large; skull roof more curved than in adult; snout short; rostral approaches and may contact maxilla, thus excluding premaxilla from border of mouth; small, narrow lateral temporal fenestrae; no sagittal crest; suborbital bar slender; and jugal flange small or absent. General changes in cranial proportions can be seen in the hypothetical ontogenetic series (text-fig. 7). Quantification of allometric relationships is not justified in view of the small sample for each age category. Consideration of juvenile features in AMNH 6535 and 6536 serves less for establishment of growth trends than for confirmation of these specimens as young *Psittacosaurus mongoliensis* and not a new taxon of small dinosaur.

Smallest dinosaur. AMNH 6535 and 6536 are each smaller than any previously reported dinosaur specimen. A listing of the smallest dinosaurs based on basal skull length yields the following



TEXT-FIG. 7. A hypothetical ontogenetic series of *Psittacosaurus* skulls based upon A, AMNH 6535; B, AMNH 6536; C, the type of *P. youngi* (after Chao 1962); and D, AMNH 6254, the type of *P. mongoliensis* (after Osborn 1923). Readily observed are a decrease in relative size of the orbit, a lengthening of the snout (pre-orbital region of skull), and a shift from a rounded to a flat-topped cranial contour. Revised identifications of some cranial elements are given in C. Abbreviations: J, jugal; L, lacrimal; mx, maxilla; n, nasal; pm, premaxilla; pp, palpebral; and r, rostral.

sequence: *Lesothosaurus diagnosticus*, 94 mm (Galton 1978; = *Fabrosaurus australis* of Thulborn 1970); *Protoceratops andrewsi*, 76 mm and 62 mm (respectively AMNH 6419 and ZPAL MgD II/7; Brown and Schlaikjer 1940; Dodson 1976; Maryńska and Osmólska 1975); *Compsognathus longipes*, 70 to 75 mm (Huene 1925; Ostrom 1978); *Bagaceratops rozhdestvenskyi*, 47 mm (ZPAL MgD I/123; Maryńska and Osmólska 1975); juvenile prosauropod(?), 32 mm (Charig 1979); *Psittacosaurus mongoliensis* 42 mm and 28 mm (respectively AMNH 6536 and 6535). An estimate of total body length for the two *Psittacosaurus* juveniles can be obtained by scaling down the dimensions of the two large, almost complete skeletons described by Osborn (1923, 1924), using comparisons of median skull length. The calculated snout to tail tip length for AMNH 6536 is about 390 mm, and that for AMNH 6535 is about 265 mm. Possible allometric changes in skull size relative to body length were not considered in these estimates but, since the skull is proportionately larger in juveniles, the calculated total body lengths probably err on the high side. Scaling the complete *Psittacosaurus* skeleton based on a comparison of humeral length (using the humerus shown in fig. 5) gives an estimated total length for AMNH 6536 of 340 mm. Allowing for some allometric changes in skull size, I would estimate the total body length of AMNH 6535 at about 230 mm. For comparison with the size of these two juvenile psittacosaurus, the famous skeleton of *Compsognathus longipes*, also probably a juvenile, has a length of between 750 and 810 mm (based on restorations by von Huene 1925, 1926; Ostrom 1978). The smaller *Psittacosaurus* specimen described herein (AMNH 6535) belonged to a dinosaur slightly smaller than a common pigeon (*Columba livia*).

Parental care. Recently it has become fashionable to ascribe mammalian or avian behaviour patterns to dinosaurs despite the reptilian aspect of the brains of all dinosaurs except small theropods (Hopson 1977) and the acknowledged difficulty of deducing habits from osteology even for living animals. Among behavioural patterns considered for dinosaurs is parental care of young (e.g. Horner and Makela 1979). In attempting an objective analysis of parental care in dinosaurs, three points must be kept in mind. First, there is no such thing as an 'accepted interpretation'. The suggestion that dinosaurs abandoned their eggs as do modern chelonians is a hypothesis that requires proof as rigorous as that required to prove that dinosaurs cared for their young in the manner of modern ducks or ungulates. Casting aspersions on arguments favouring parental care does not constitute proof of the alternate hypothesis. Second, the morphologic diversity and long evolutionary history of dinosaurs makes it exceedingly unlikely that every species practiced a similar amount of parental care. Indeed, the egg-laying pattern of the hadrosaur *Rhabdodon* has been interpreted as precluding parental care (Ginsburg 1980) while nests of the hadrosaur *Maiaosaurus* have been interpreted as requiring parental care (Horner and Makela 1979). Dinosaur parental behaviour should be approached on a case-by-case basis, and generalities applicable to all dinosaurs will necessarily be few. Finally, the selection of modern analogues to interpret dinosaur behaviour is a subtle trap that encourages interpretations far beyond what can reasonably be concluded from actual data. This problem has been discussed elsewhere (Coombs 1975), but the warning merits repetition. The mental image of the relationship between adult and juvenile dinosaur is greatly altered if described as being: (1) like elephants; (2) like opossums; (3) like ducks; (4) like crocodiles; or (5) like mouth-breeding fishes. Use of modern analogues must be approached with great caution.

In the absence of contrary evidence it is assumed that most dinosaurs laid eggs (Hopson 1977). *Coelophysis* specimens from Ghost Ranch, New Mexico (Colbert 1961), are sometimes cited as demonstrating dinosaurian viviparity, but are more likely a case of cannibalism in so far as jumbled, disarticulated juvenile skeletons are enclosed in almost perfectly articulated adult skeletons (making parental care unlikely for *Coelophysis*). The supposed juvenile within the type of *Compsognathus longipes* is in fact a skeleton of the lacertilian *Bavarisaurus* (Ostrom 1978). Dinosaur egg morphology indicates nests buried in leaf litter or sand (Seymour 1979; Seymour and Ackerman 1980), a construction pattern similar to that of both crocodylians and megapode birds (Frith 1956, 1962; Seymour and Ackerman 1980). Megapode nesting habits are regarded as primitive among birds

(Welty 1963) and are thus an appropriate analogue for at least the primitive pattern of dinosaur nest-building behaviour. Parental attendance of buried nests, involving protection (crocodilians), temperature regulation (megapodes), and assistance to young at hatching (both crocodilians and megapodes) may be a primitive archosaurian behaviour pattern that is reasonably inferred for dinosaurs. Hatchlings of crocodilians, megapodes, and ground-nesting birds in general (excluding those relatively free of terrestrial predator threat, e.g. most insular, Arctic, and Antarctic marine birds) are generally precocial (mobile, self-feeding, and fast maturing). Megapode hatchlings are notoriously precocial, at least one species being capable of flight within 24 hours of hatching (Frith 1962). The *Psittacosaurus* juveniles had been feeding on abrasive material, probably vegetation, for some time prior to death, as evidenced by wear on teeth of both skulls (similar conclusion for juvenile *Maiasaurus*: Horner and Makela 1979). It is therefore probable that the juveniles of *Psittacosaurus* were precocial; parental offering of transported, pre-masticated, or regurgitated food is unlikely, implying that parental care was unnecessary at least for feeding.

A great difference in physical size between juvenile and adult increases liability of injury to young in species having large adults and parental care after hatching. Habits and posture also play a part. Some crocodilians practice extended parental care after the young hatch, but crocodilians are semi-aquatic, with young more aquatic than adults, and the posture is sprawling to semi-erect quadrupedal with long, slender, flexible toes. The danger of injury to a juvenile crocodilian is thus far less than to juveniles of terrestrial, bipedal dinosaurs that have a compact foot and digitigrade stance. Among both mammals and birds that are ground dwellers and that have precocial young, the minimum relative newborn size (= newborn body mass expressed as a percent of adult body mass, and hereafter abbreviated RNS) is about 0.9% (in *Struthio*; Welty 1963). RNS values for mammals with precocial young range from about 1 to 12% (calculated from data in Walker 1968) with typical values of about 3-5% (e.g. *Odocoileus*, *Giraffa*, *Rhinoceros*, *Antilocapra*, *Rangifer*, *Taurotragus*, and *Loxodonta*: Walker 1968; Case 1978). Adult body size has little influence on RNS for mammals with precocial young. Relatively immobile, altricial young whose position and movements are either limited or controlled by the parent have much lower RNS values (e.g. 0.33% in *Euaretos*: Walker 1968; Case 1978). The recent death of a zoo-born *Ailuropoda*, apparently by smothering under a careless (inexperienced) adult female, points up the potential dangers to young of very low RNS and terrestrial habits. RNS values of modern reptiles follow a different pattern: values decline as adult body mass increases (Table 1). The RNS of *Psittacosaurus* is 0.7 to 0.8% (calculated by cubing equivalent linear dimensions of adult and juvenile) which is low compared to precocial young of mammals or birds, but is high compared to that of modern reptiles of similar adult body mass (10 to 100 kg category, Table 1). RNS values for other dinosaurs include 0.24% for *Protoceratops* and 0.06% for *Hypselosaurus* (Case 1978). Thus dinosaurs appear to follow the reptilian pattern of declining RNS at high adult body mass. The combination of low RNS and mobile, self-feeding habits of *Psittacosaurus* contrasts with the pattern for mammals and birds that practice parental care after birth or hatching and that have active, mobile young. On the basis of RNS values, parental care is marginally possible, but not probable for *Psittacosaurus*, and is very unlikely for dinosaurs of high adult body mass.

TABLE 1. Data from Case (1978) showing the decline in relative newborn size (RNS) at higher adult body masses among modern reptiles.

Adult mass	Number of species averaged	Average RNS
Less than 1 kg	6	3.8%
1-10 kg	7	1.9%
10-100 kg	5	0.42%
Over 100 kg	7	0.04%

Indirect support for the hypothesis that some dinosaurs did not care for their young after hatching comes from Triassic-Jurassic trackways known as *Selenichnus* (text-fig. 8). The footprint maker was a tridactyl biped with a tail sufficiently long to occasionally imprint, and the animal was probably a juvenile of one of the many large bipedal dinosaurs that are so ubiquitous in the Connecticut Valley (e.g. *Eubrontes*, *Gigandipus*, *Anomoepus*, *Anchisauripus*, or *Sauropus*; Lull 1953). The *Selenichnus* trackmaker was intermediate in size between the two juvenile *Psittacosaurus* described herein, although in view of the disparity in geologic age, *Selenichnus* trackways could not belong to *Psittacosaurus*. The five slabs at the Pratt Museum (Amherst College, Amherst, Massachusetts, U.S.A.) that contain *Selenichnus* tracks have the following characteristics in common: (1) there are no instances of 'adult' footprints in company with *Selenichnus*; and (2) there are no instances of two or more *Selenichnus* tracks on a single bedding plane, headed in roughly the same direction. Insufficient numbers of *Selenichnus* tracks are known to draw unequivocal conclusions, but the evidence indicates that tiny dinosaurs, the size of small juvenile *Psittacosaurus*, travelled alone, unaccompanied by either adults or fellow hatchlings, at least sometimes. This evidence suggests that at least some dinosaurs did not practice post-hatching parental care.



TEXT-FIG. 8. *Selenichnus brevisculus*, trackway made by a small tridactyl, bipedal dinosaur that at least sometimes left a sinuous tail trace (pseudo-tail traces are sometimes made by dragging the tip of one toe through soft sediment, but that does not appear to be the case with this specimen). This particular trackway was made on a raindrop splattered surface. According to Lull (1953) the average print length for this species is 46 mm and the average step length is 58 mm. I estimate the size of the trackmaker to be a little smaller than AMNH 6536, the larger *Psittacosaurus* specimen described herein. Lull (1953) regarded these tracks as pertaining to a theropod. Specimen in the collection of the Pratt Museum, Amherst College (Amherst, Massachusetts, U.S.A.).

Association of adult and juvenile skeletons might be taken as an indication of parental care. The remarkable assemblage of *Protoceratops andrewsi* at Djadochta includes numerous individuals of every age category, unhatched eggs to old adults (Brown and Schlaikjer 1940; Dodson 1976) and association of adults and juveniles in life is thus indisputable. Horner and Makela (1979) interpreted a group of juvenile hadrosaurs (*Maiaosaurus*) as requiring parental guidance to remain a coherent group, and an adult specimen was unearthed reasonably nearby. As noted above, the juvenile *Psittacosaurus* described herein were excavated in the vicinity of the type of *P. mongoliensis*, although exactly how close is difficult to ascertain from available records. Association of adults and juveniles in fossil assemblages has little bearing on the question of parental care in so far as such an association would sometimes occur even if the adults abandoned their eggs immediately after laying. Only if nests were constructed far from the normal range of the adult (note arguments of Horner and Makela 1979), and if the juveniles lived entirely outside of adult habitats would the incidence of adult-juvenile association in fossil assemblages be reduced to nil. While such a set of conditions may have existed for some dinosaurs, it is unlikely it was a universal situation.

Thus the association of adult and juvenile skeletons even in a single quarry is not sufficient proof of extended post-hatching care.

Parental care, summary. Available evidence for parental care by dinosaurs is scant and equivocal. Moreover, there is no clear indication of what constitutes necessary and sufficient proof of either competing theory (i.e. that dinosaurs did, or that dinosaurs did not, care for their young). On the basis of the data and arguments developed above, the following conclusion might be drawn: (1) guarding of nests may be a general archosaurian pattern inherited as the primitive behaviour of dinosaurs; (2) nests of some dinosaurs were buried and may have required parental attendance for temperature regulation and perhaps for assisting the young at hatching; (3) egg distribution of other dinosaurs seems to preclude parental care after laying; (4) adult–juvenile size disparity makes parental care unlikely for very large dinosaurs, but for smaller genera the size disparity may not have been a problem; (5) footprints indicate that at least some tiny dinosaurs, probably juveniles, were independent of adults; and (6) for *Psittacosaurus*, available evidence is inconclusive.

Sibling groups. One of the two juvenile *Psittacosaurus* specimens is a composite of several skeletons, with fourteen distal ends of tibiae indicating a minimum of seven individuals represented. The jumbled, broken, incomplete condition of the skeletons suggests a post-mortem assemblage, yet the majority of bones are from juveniles of similar, indeed almost identical, size (text-fig. 6). Such an assemblage could result from mechanical sorting processes, or from the simultaneous deaths of several individuals of a sibling group. Horner and Makela (1979) described an assemblage of juvenile hadrosaurs probably derived from a single clutch, and footprints possibly belonging to juvenile dinosaurs travelling in unison have been reported (Currie and Sargeant 1979; contra *Selenichmus* evidence described above). Therefore juveniles, possibly clutch mates of some dinosaurs, may have formed cohesive aggregates, for which the term 'sibling group' is proposed in preference to 'herd' or 'flock' or 'school' all of which imply behavioural interactions not yet proven for dinosaurs. A behavioural complexity similar to that of modern gregarious reptiles (e.g. *Amblyrhynchus*) is sufficient to explain sibling groups among dinosaurs. Aggregates of adult dinosaurs might have resulted from persistence of bonds formed in juvenile sibling groups.

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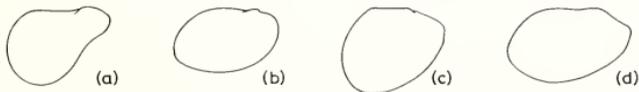
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A DESCRIPTION OF THE GENERATING CURVE OF BIVALVES WITH STRAIGHT HINGES

by MARGARET JENNIFER ROGERS

ABSTRACT. A method of describing the whole of the generating curve of a lamellibranch is sought. When lengths and angles are used to describe an outline, much of the outline remains undefined. A curve can be fitted to an outline and the coefficients in the particular approximation employed then define the outline. Reasons are given for fitting a Tchebychev polynomial, rather than a spline, or Fourier series containing both sine and cosine terms. Polar coordinates r and θ are calculated for each point on a digitized outline. $\cos \theta$, rather than θ is chosen as the independent variable when the Tchebychev coefficients are calculated. It is found that about 100 irregular spaced data points are required to produce stable coefficients, and that adequate numerical accuracy is obtained when the outline is described by the first six coefficients. These six coefficients can also be used as shape discriminators. As the value of c_0 is a measure of size, it can be used to standardize the other coefficients. The standardized coefficients can be used to compare the shape of the generating curve of shells of different sizes.

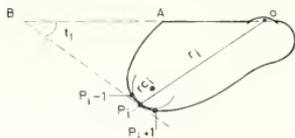
DESCRIPTIONS of the morphology of organisms should, ideally, be objective, reproducible, and enable different forms to be distinguished. In this article the description of the lateral outline, or generating curve (Raup 1966) of the Carboniferous non-marine bivalve genera *Naiadites* and *Curvirimula* is discussed. The general form of the generating curve is elliptical. A point (the origin of growth, or tip of the umbo) and a line (the hinge-line, which is straight, or only slightly curved in the genera studied) define the orientation of these shells to which further descriptions can be related. A coarse separation of shapes can be made qualitatively by simple terms such as outline approximately triangular (text-fig. 1a), rectangular (text-fig. 1b), or semicircular (text-fig. 1c, d). The distinction between text-fig. 1c and text-fig. 1d is more difficult to describe qualitatively. Measurements of various lengths and angles have proved useful in describing and distinguishing shell forms



TEXT-FIG. 1. Outlines of four shells which can be described qualitatively as approximately (a) triangular, (b) rectangular, (c) and (d) semicircular.

(Davies and Trueman 1927; Deleers and PASTIELS 1947; Trueman and Weir 1955; Eager 1973; Hajkr, Lukasova, Ruzicka, and Rehor 1974), but only a few points on the shell outline are defined. As Bookstein (1978) notes, techniques which use 'landmarks', inter-landmark distances, and angles ignore much of the shape of the outline. Between the landmarks the outline is undefined and cannot be reproduced.

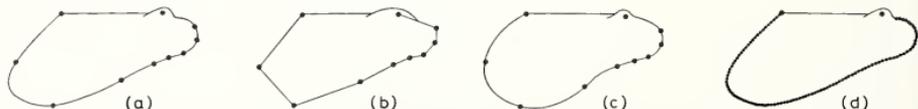
Papin and Khoroshev (1974) measured the radius of curvature (text-fig. 2, rc_i) of successive parts of the outline, indicating that sections of the curve should be described, rather than interpoint distances. The value of the radius of curvature at P_i , when calculated from the position of three successive points P_{i-1} , P_i , P_{i+1} (text-fig. 2) on the curve, is highly sensitive to the actual position of the points P_{i-1} , P_{i+1} . Accordingly, it is virtually impossible to obtain a reliable estimate of this



TEXT-FIG. 2. Measurements on a shell outline. The hinge OA is produced to B . P_{i-1} , P_i , P_{i+1} are three consecutive points on the outline. rc_i is the radius of curvature, t_i the tangent angle, and r_i the distance from O of point P_i .

quantity. For this reason the radius of curvature, and a related measurement, the tangent angle t_i (text-fig. 2) are not suitable as shape descriptors. Error in the measurement of the length r_i (text-fig. 2), from the umbo to the point P_i is due to the accuracy of the measuring device used and is not related to the shape of the curve at P_i . It is essential to choose a property of the curve which can be measured accurately as a basis of a reproducible description. The length r_i satisfies this condition.

With the advent of more sophisticated devices such as a digitizing table, the (x, y) coordinates (text-fig. 6) of many points on an outline can be recorded with ease. A large number of unequally spaced data points will yield an accurate reproduction. If the recorded points are used to redraw the outline (text-fig. 3), a few equally spaced data points may not reproduce the outline accurately. Although a large number of data points produce an accurate reproduction, for the purposes of comparison it is necessary to look for a more economical way in which to represent the outline. A variety of curve-fitting techniques exist which allow a numerical approximation to the fossil outline to be derived. A set of numbers which represent the coefficients in the particular approximation employed can then define the outline. For reasons which are discussed below, the curve-fitting method chosen here is the Tchebychev polynomial. The purpose of this article is to determine the reliability of the Tchebychev coefficients as shape descriptors and discriminators in the practical context of bivalves with a straight hinge.



TEXT-FIG. 3. Reproduction of shell (a) from data points taken at 20° intervals and joined by (b) curved and (c) straight lines. (d) is reproduced from many unequally spaced data points.

CURVE FITTING TECHNIQUES

All descriptive, curve fitting techniques seek a solution to the equation

$$y = f(x) \text{ over a specified range of } x$$

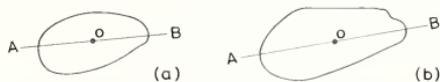
where x is the independent variable and y the dependent variable. A length, r_i (text-figs. 2 and 6), called the radial length below, can be measured with reasonable accuracy and is a suitable dependent variable. The angle θ_i (text-fig. 6) at the origin between the radial length and the reference line AOB is an appropriate independent variable since, once this angle is known, the value of the dependent variable is precisely defined.

With these coordinates, the equation representing a circle is $r = a \cos \theta$, but the outline of a bivalve shell is, in general, too complex to be represented by such a simple equation. Accordingly, techniques such as splines and Fourier series have been used. A spline curve may be fitted to a series of data points provided there are no marked inflections. If such inflections occur, the data points are chopped up into segments at the turning-points. These turning-points are called knots. Suitable positions for knots (x) are shown on two shell outlines in text-fig. 4. Each part of the shells would be accurately described by the coefficients of the appropriate spline function, but these coefficients cannot be used to compare the shapes of the shells (which may belong to the same species) because each function relates to a different range of the independent variable.

TEXT-FIG. 4. Fitting spline curves to a shell outline. x mark the position of knots.



Fourier series coefficients have been used to define the outlines of ostracodes (Kaesler and Waters 1972), Bryozoa (Anstey and Delmet 1973), blastoids (Waters 1977), and sand grains (Ehrlich and Weinberg 1970). As yet palaeontologists cannot readily understand what outline is being described by a particular set of coefficients. This led Scott (1980), in his study of Foraminifera, to calculate radii from the origin to the outline at 10° intervals from the Fourier series representation of an outline. The thirty-six measurements allow the outline to be visualized, but the description is not economical and the outline is undefined between the radii. A Fourier series in which both sine and cosine terms are used is periodic, the value of the independent variable ranging from 0 to 360° , and is well suited for describing the closed curves found in the above examples, provided the origin and orientation are defined. In the case of a sand grain (text-fig. 5a) a choice of origin and orientation can be made on the basis of its geometry. The line of orientation could be its longest axis (AOB) and the origin its mid-point. In radially symmetric organisms, the centre is a point of morphologic significance and the orientation can be defined in morphologic terms. As in the case of the sand grain, the origin and orientation of a bivalve can be defined geometrically (text-fig. 5b), but it is not clear that such definitions would be homologous, or have any morphologic relevance. Biological reference points within the curve, such as muscle insertions, are rarely preserved in fossil material and are thus unsuitable. In those bivalves having a straight hinge, an origin and orientation can be chosen which are morphologically homologous and are usually visible in fossil material. Since they lie on, rather than within, the outline, a periodic function may not fit the outline most economically.



TEXT-FIG. 5. Geometric method of defining the origin and orientation of an outline. AOB = longest axis, O being the centre. (a) sand grain, (b) bivalve.

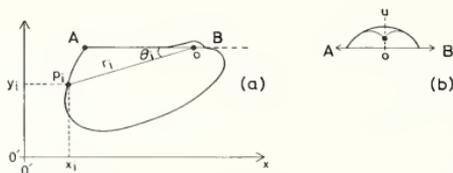
The Tchebychev series provides a function in which the independent variable lies in the range -1 to $+1$ and the NAG Library routine EO2ADF enables this function to be fitted to an arbitrary set of data points. For these reasons it was decided to use the coefficients of the polynomials of a Tchebychev series to describe the generating curve of several bivalves. Experiments were designed to discover how many data points are needed to ensure that the calculated coefficients are the same wherever the data points are taken, and by whom. Further, how many coefficients are needed to give a good representation, whether θ or a transform of θ as the independent variable gives better results; how sensitive the coefficients are to a change of range in the initial data points, and how effective they are as shape discriminators. The results of these experiments are given below.

The basic objective of this study is to create attributes (shape descriptors) which can be used to study variation within populations and as aids to classification.

METHODS OF TAKING DATA POINTS AND CALCULATING THE TCHEBYCHEV COEFFICIENTS

A digitizing table consists of a plane surface over which a pointer may be moved. In the device used for this study, the pointer consists of the intersection of a pair of cross wires. When a button is pressed the x, y coordinates of the pointer are recorded to an accuracy of 0.025 mm. The cursor must lie on the table when the coordinates are recorded. Thus the outline to be digitized must be drawn on a piece of paper, be photographed, or be a projected image. Material embedded in matrix cannot be digitized directly.

Initially, outlines of shells, scaled to be about 4 cm square, were drawn using a camera lucida. The origin of the polar coordinates system, O , was taken as the projection of a perpendicular from the tip of the umbo on to the hinge (text-fig. 6b) and this was the first point digitized. When the specimen consisted of an external representation of the shell, this origin is concealed by the umbonal swelling and its position must be inferred from growth lines. The hinge AOB (text-fig. 6a) is the line of orientation and the posterior end of the hinge (A) was the second point digitized. Subsequent points, i.e. P_i (text-fig. 6a) were digitized from A to B .



TEXT-FIG. 6. Diagram showing the orientation of a shell for digitizing. AOB = hinge line, u = tip of umbo, O = origin of the polar coordinates, O' = origin of x, y coordinates. x_i, y_i are the rectangular coordinates, and r_i, θ_i the polar coordinates of the point P_i .

The (x_i, y_i) coordinates can be used to calculate the polar coordinates (r_i, θ_i) of the point P_i . The shape is then defined by the polar equation:

$$r = r(\theta)$$

where θ is the independent variable and r is the single valued function of θ . An approximation to this function may be made by a Tchebychev series of the form

$$r = \frac{1}{2}c_0T_0(v) + \sum_{m=1}^{\infty} c_mT_m(v)$$

where v , the independent variable, is θ or a transform of θ , $T_m(v)$ is the Tchebychev polynomial of degree m , and the c_m are the coefficients whose values define the particular function $r(\theta)$ in each case. A full account of the Tchebychev polynomials can be found, for example, in Fröberg (1965). The general polynomial is defined as $T_m(v) = \cos(m \arccos v)$ and the first few polynomials are

$$\begin{aligned} T_0(v) &= 1 \\ T_1(v) &= v \\ T_2(v) &= 2v^2 - 1 \\ T_3(v) &= 4v^3 - 3v \end{aligned}$$

When $v = \cos \theta$, $T_m v = \cos(m\theta)$ and the expansion is effectively a Fourier cosine series, the form of which is

$$r = \frac{1}{2}b_0 + \sum_{n=1}^{\infty} b_n \cos(n\theta)$$

where b_n are the coefficients of the Fourier cosine series. In this case it is a simple matter to calculate the area of a specimen, provided θ ranges from 0 to π radians (0–180°).

$$\text{The area} = \frac{\pi}{4} \left(\frac{c_0^2}{2} + \sum_{m=1}^{\infty} c_m^2 \right)$$

The coefficients were calculated using the NAG library routine EO2ADF which computes the least-squares approximation to an arbitrary set of data points. The introductory remarks to this routine states that more points should be recorded where the outline changes markedly, and also at the ends of the range. The independent variable is scaled so that its value ranges from -1 to $+1$ by the linear transform

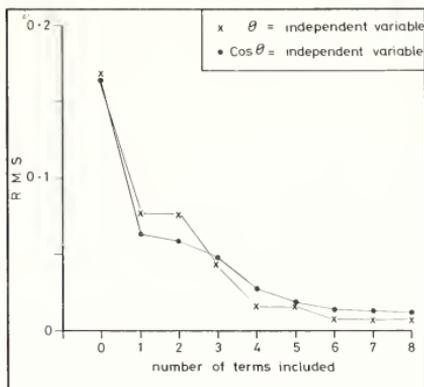
$$V = (2v - v_{\max} - v_{\min}) / (v_{\max} - v_{\min}) \text{ where } V = \text{scaled independent variable}$$

$$v_{\max} = \text{maximum value of } v$$

$$v_{\min} = \text{minimum value of } v$$

Thus, if θ ranges from 0 to 180° and $v = \cos \theta$ then $V = \cos \theta$.

TEXT-FIG. 7. Root mean square residual (R.M.S.) plotted against number of terms included.



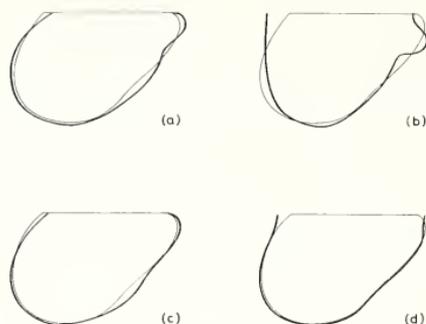
The root mean square residual (R.M.S.) is a measure of the departure of the fitted curve from the original data points. Initially the residuals decrease rapidly as successive terms are used (text-fig. 7); thereafter they decrease more slowly, and indeed may increase slightly as unwanted fluctuations are produced. The number of terms in the series required to give adequate accuracy is the number after which the residuals decrease only slowly. In the case shown in text-fig. 7, six or seven terms give an adequate fit.

NUMBER OF COEFFICIENTS REQUIRED AND CHOICE OF THE INDEPENDENT VARIABLE

The polar coordinates r and θ of a digitized outline were used to calculate the coefficients of the polynomial of the Tchebychev series from degree zero to degree eight. The plots of the R.M.S. (text-fig. 7) for the two cases when $v = \theta$ and $v = \cos \theta$ are typical and show that c_2 has little effect on the accuracy of the fit of the polynomial. Thereafter the accuracy of the fit improves continuously as terms are added when $v = \cos \theta$. The R.M.S. decreases irregularly when $v = \theta$, and it is difficult to identify where significant flattening of the curve occurs. The values of the coefficients when $v = \cos \theta$ are given in Table I. It can be seen that when a new coefficient (c_i) is added, the value of the preceding one, c_{i-1} changes considerably but the value of c_{i-2} is only slightly altered. The addition of a new coefficient can cause a marked change in the value of all the preceding coefficients when $v = \theta$.

TABLE I. Value of the coefficients when polynomials of different degree are evaluated
 $v = \cos \theta$ is the independent variable

Degree, m of polynomial	Terms included								
	c_0	c_1	c_2	c_3	c_4	c_5	c_6	c_7	c_8
0	0.798								
1	0.605	-0.251							
2	0.609	-0.240	0.032						
3	0.599	-0.239	0.054	0.050					
4	0.606	-0.235	0.052	0.026	-0.063				
5	0.606	-0.237	0.049	0.030	-0.048	0.032			
6	0.607	-0.237	0.048	0.031	-0.048	0.026	-0.016		
7	0.607	-0.237	0.049	0.030	-0.049	0.026	-0.013	0.007	
8	0.605	-0.237	0.050	0.030	-0.048	0.028	-0.013	0.003	-0.012



TEXT-FIG. 8. Original outline of a shell overlain by the outline reproduced using 5 terms (a, b) and 8 terms (c, d). The independent variable is θ (a, c) and $\cos \theta$ (b, d).

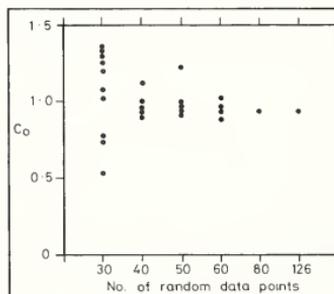
The outline was recreated from the coefficients of the polynomial, the polar coordinates of the fitted points being calculated using the NAG Library routine EO2AEF. When $v = \theta$ the outline is somewhat more circular than the original (text-fig. 8a, c) whereas the ends of the outline are somewhat more inaccurate when $v = \cos \theta$ (text-fig. 8b, d). This is an unavoidable consequence of using $\cos \theta$; the calculated curve must meet the hinge at an angle of 90° when $\theta = 0$ or 180° . $\cos \theta$ is preferred as the independent variable because an accurate portrayal of the ends of the outline is considered of less importance than the general shape which is recreated more accurately when $v = \cos \theta$. For this reason and because of the behaviour of the R.M.S. and the stability properties of the coefficients noted above, it was decided to adopt $\cos \theta$ as the independent variable, rather than θ .

Inspection of the residuals suggests that the five coefficients, c_0 - c_4 , are sufficient to give a good approximation (text-fig. 8a, b). However, it was found that the outlines recreated using the eight coefficients, c_0 - c_7 , look much more like *Naiaidites* (text-fig. 8c, d). The three coefficients, c_5 - c_7 , although small in value and accounting for little of the residual error, improve the detailed representation of the outline.

NUMBER OF DATA POINTS

About 100 data points were recorded on the generating curve of one shell. A random set of thirty of these 100 points were used to calculate the coefficients of the Tchebychev polynomial to degree 8. This was done ten times for each of 30, 40, 50, 60, and 80 data points. The variability of c_0 is shown in text-fig. 9, the value of the coefficient being plotted against the number of data points used. It is seen that when thirty data points are used the value of the coefficient varies from 0.5 to 1.34 and is 0.94 when the full data set is used. About 100 data points yield a stable value of 0.94 for c_0 .

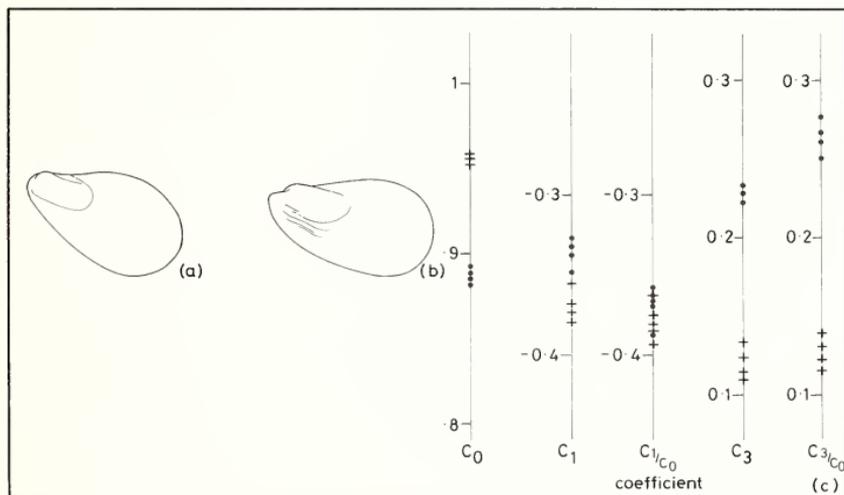
The same outline drawn and digitized by two further people gave values for c_0 ranging from 0.89 to 0.94 when about 100 data points were recorded. An error of about 5% was considered satisfactory, particularly considering that either the material or the technique was unfamiliar to the participants.



TEXT-FIG. 9. Value of c_0 plotted against number of random data points selected from a set of about 100 digitized on an outline. In each case coefficients were calculated to degree 8. When forty or more data points are used, the ten values of c_0 cannot be recorded separately at this scale.

THE EFFICIENCY OF THE COEFFICIENTS AS DISCRIMINATORS OF SHAPE

Two rather different shells (text-fig. 10) were selected, and drawn and digitized by different operators. The coefficients were calculated to degree eight for each digitized outline. When the value of the coefficients is plotted (text-fig. 10c), it is seen that certain coefficients (c_0 and c_3) have distinctly different values for the two shells, whereas other coefficients (c_1) are approximately the same for both shells. These two shells are of similar size, and the zeroth coefficient is a measure of size; it is the radius of the semicircle which fits the outline giving the smallest root mean square residual. Using this criterion as a measure of size, c_0 can be used to standardize the remaining coefficients. Plots of the standardized coefficients (c_1/c_0 , c_3/c_0) (text-fig. 10c) show that the first coefficient cannot be used to distinguish the two shells, but c_3 becomes more effective as a discriminator. This result is expected, because c_1 is a crude measure of asymmetry which is refined by successive odd-numbered coefficients. Negative values of c_1 indicate that the shells are asymmetric; that is, the posterior lobe is larger than the anterior lobe. These results indicate that shapes of *Naiadites* shells of any size may be discriminated using at most seven coefficients.



TEXT-FIG. 10. (a) and (b) two shells digitized and drawn by three different people. (c) value of the coefficients c_0 - c_3 and the ratios c_1/c_0 and c_3/c_0 ● = shell a. + = shell b.

EFFECTS OF POOR PRESERVATION

As noted earlier, the origin of growth is often obscured in fossil material. However, provided the umbo is not very large, the tests made above suggest that different operators will choose approximately the same origin. A more serious problem is the fact that the anterior lobe is often distorted, and thus its outline cannot be digitized with confidence. Although in *Naiadites* the anterior lobe is small, it was found that very different interpretations of the anterior outline gave rise to markedly different coefficients. Sometimes the distortion brings the anterior lobe below the level of the hinge, thus it is not possible to measure the radial length when $\theta = 180^\circ$. It was found that provided $v = \cos \theta$ and θ ranged from 0 to about 170° the coefficients obtained were similar to

those obtained when θ ranged from 0 to 180°. In reasonably well-preserved specimens of *Naiadites* it is usually possible to use a range of θ of 0–170°.

In *Curvirimula* it was found that the hinge rarely extended beyond the umbo, and often the maximum value of θ was 120°. As noted earlier, it is impossible to compare the coefficients of two curves if the ranges to which they fit are very different.

Further, not only should the range of θ be the same, but the morphologic structures described should be the same if the coefficients are to be used as discriminators. Thus, if the range of θ chosen is 0 to 120°, the coefficients calculated for one shell (text-fig. 11a) describe the whole of the generating curve, whereas those for a second shell (text-fig. 11b) fail to describe the anterior lobe, and the two sets of coefficients cannot be used to compare the generating curve of the two shells. In the genera studied the umbo and the hinge are the only structures on the outline which are homologous. However, the anterior lobe contains the anterior adductor muscles, part of the foot and its associated musculature, and the size of the anterior lobe is a good indicator of the mode of life of the organism. A suitable way of comparing these shells may be to describe the posterior lobe in terms of the coefficients which define its outline, and to describe the anterior lobe in terms of area, a parameter which can easily be calculated from the digitized points. Such a description would still be economical, and a comparison of shells described in this way would be justified on theoretical grounds. This method has not yet been tested.



TEXT-FIG. 11. Two specimens of *Curvirimula* having very different maximum value of θ .

SUMMARY AND CONCLUSION

The shape of the generating curve of those shells (including *Naiadites*) which have a straight hinge extending beyond the umbo may be described economically using the coefficients of a polynomial of the Tchebychev series of the eighth degree. Such descriptors are very stable provided that about 100 data points are used and that $\cos\theta$ is used as the independent variable. C_0 is a measure of size, and tests indicate that if it is used to standardize the coefficients of higher degree, the first five scaled coefficients can be used as shape discriminators.

Describing shells in this way has the further advantage that, because the whole of the generating curve can be reproduced, any other features of the shell such as the longest radial length can be calculated from these nine coefficients. If θ ranges from 0 to 180°, other features such as the area can be calculated directly from the coefficients.

When the hinge is not straight, or does not extend beyond the umbo, the shape can still be described, but it is difficult to specify the range of the independent variable in such a way that different species can be compared. In the case of *Curvirimula* the hinge rarely extends beyond the umbo. For this genus it is suggested that the coefficients of a very restricted portion of the generating curve, together with a further parameter, the area of the anterior lobe, which has functional significance, may be used in order to compare shells. For shells which lack a straight hinge it is possible that a periodic function may be more appropriate as a shape discriminator. The umbo could be retained for the purpose of orientation, but it may be necessary to define a geometric origin.

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REWORKED ACRITARCHS FROM THE TYPE SECTION OF THE ORDOVICIAN CARADOC SERIES, SHROPSHIRE

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ABSTRACT. Thirty-seven acritarch species in the type Caradoc rocks of south Shropshire are recognized as reworked from strata of Tremadoc and Arenig/Llanvirn age, their distribution reflecting an inverted stratigraphy. These microfossils yield valuable palaeoenvironmental data, their excellent preservation indicating a source on, or adjacent to, the Midland Platform; erosion of the relatively unconsolidated parent sediments occurred in a marine environment. Acritarchs were eroded and redeposited as discrete particles and wave and current action are considered the most likely erosive agents. The rate of release of microfossils is linked to a shallowing of the water-body; this resulted in a shift to a high energy environment with storm surges influencing the erosion and redeposition of sedimentary particles.

REWORKING of palynomorphs, the erosion and redeposition of the microfossils within younger sediments, is a problem familiar to most palynologists (Funkhauser 1969; Richardson and Rasul 1978, 1979) and has been discussed by Wilson (1964). Palynomorphs are prone to reworking because of their small size, abundance, and the durable nature of their complex wall. This paper attempts to show that although reworking may present a problem in biostratigraphical studies, it can provide a valuable insight into the depositional environment of the enclosing sediments. Murchison (1839) introduced the term Caradoc to geology when he applied the name 'Caradoc Sandstone' to a group of strata cropping out in the county of Shropshire. The clearest section was said by Murchison (p. 216) to occur in the valley of the River Onny near Horderley. Usage of the term Caradoc has been much restricted by subsequent workers and was given status as a Series by Lapworth (1916) who subdivided it into Groups based on lithology and faunal content. The exposures along the valley of the River Onny are accepted as the type section on historical grounds and these still comprise the best exposed and most complete succession of Caradoc rocks in the district. Since the recent works on the A489 road adjacent to the river, exposure is continuous through much of the sequence and access is better than it has been for many years. Extensive researches have been carried out on the macrofaunas and biostratigraphy of these sediments, a comprehensive review of these works being provided by Hurst (1979c). Palaeontological studies have concentrated on the rich shelly faunas, but Jenkins (1967) published some of the earliest microfossil data with his detailed examination of the chitinozoa. Twenty samples were collected from the Onny Valley as part of a larger study of Llandeilo and Caradoc acritarchs from the British Isles. A further thirteen samples were obtained for comparative purposes from north Shropshire in the vicinity of Chatwall Farm (SO 5137 9745, text-fig. 2). All samples were treated with standard laboratory techniques for the recovery of palynomorphs and most yielded abundant, diverse, and well-preserved acritarchs. The majority of samples examined contain numerous acritarchs of undoubted Caradoc age (text-fig. 5); these form the bulk of the acritarch assemblages recovered and will be described elsewhere.

All figured specimens are registered and held in the MPK series of the palynological collections at the Institute of Geological Sciences, Leeds.

AGE OF THE REWORKED MATERIAL

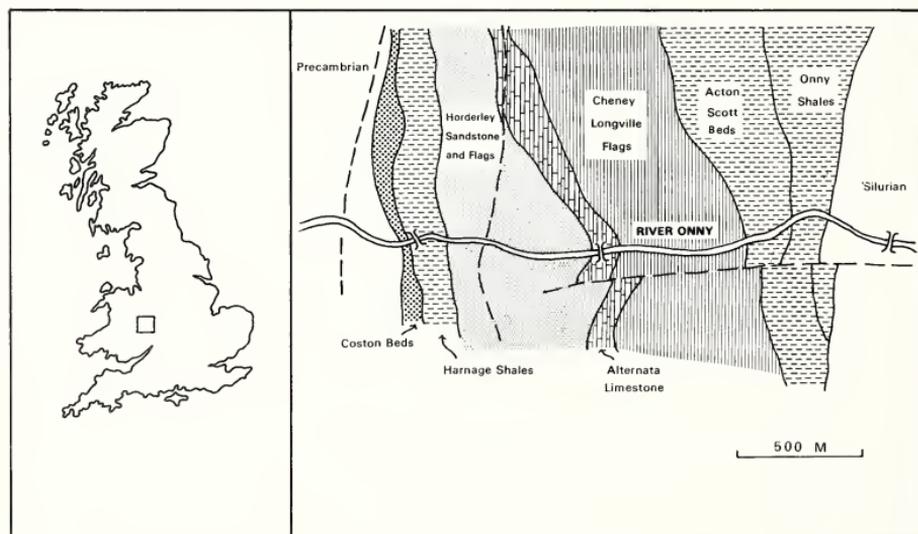
Samples from the Onny Valley contain reworked acritarchs that evidently originated from different sources since, on an age-basis, they fall into three broad categories.

Category 1. Acritarchs of Tremadoc age

Some species recovered can be identified as Tremadoc forms because their known stratigraphical ranges are restricted to strata of this age. Their occurrences here cannot be interpreted as extensions of their ranges because the species concerned remain unknown in strata of Arenig to Llandeilo age (see text-figs. 3, 4).

Category 2. Acritarchs of probable Tremadoc age

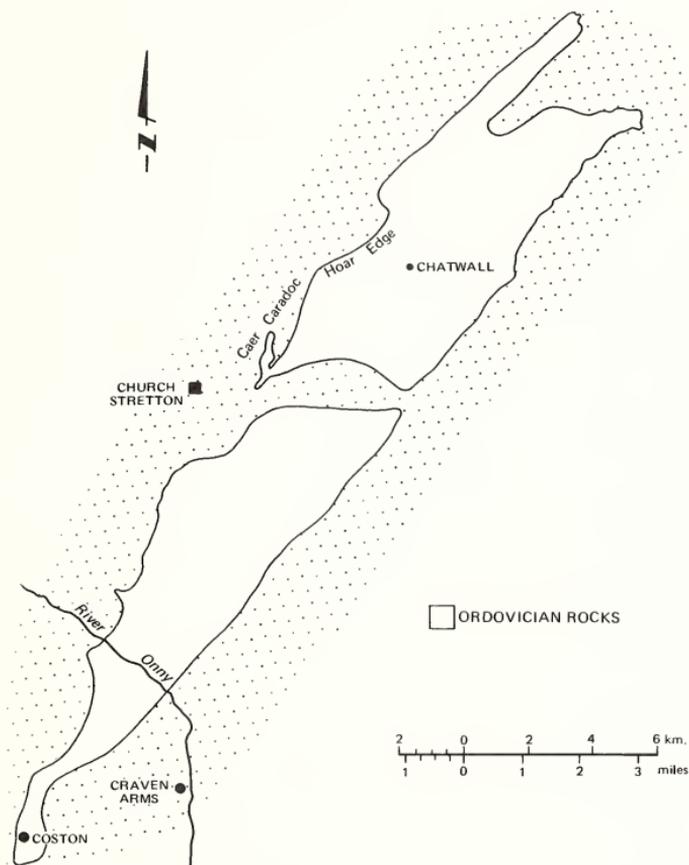
This category consists of taxa that are known both from the Tremadoc and the Arenig/Llanvirn but which, other than this occurrence, have not been recorded from younger strata in the British Isles, or elsewhere (text-figs. 3, 4). That these forms are reworked seems certain, but it is not possible to assign to them a precise stratigraphical age. Despite this, although an Arenig/Llanvirn age is accepted as possible for some of these individuals, it is probable that the majority were derived from rocks of Tremadoc age. This is indicated by the large numbers involved (see text-fig. 3) which suggest derivation from particularly rich pre-existing acritarch assemblages. It is known that parts of the Tremadoc sequence in Great Britain yield abnormally abundant acritarch populations; a rough calculation suggested a figure of 100,000 individuals per gram of rock, for a sample from the *Shumardia pusilla* Zone of the Shineton Shales of Shropshire (Downie 1958, p. 332). These profuse numbers are reflected in the periodic reworking of Tremadoc acritarchs into other parts of the geological column; for example, reworked Tremadoc assemblages have been identified in Devonian rocks in Oxfordshire (Richardson and Rasul 1979) and are known from Llanvirn sediments in north-west England (author's unpublished data). Strata of Tremadoc age are unquestionably the commonest recognized source of reworked acritarchs in the British Isles. In contrast, the work of Booth 1979 (unpublished Ph.D. thesis) and the present author's own unpublished data suggest that in Britain the Arenig/Llanvirn was a period of substantially lower phytoplankton productivity. Thus most of the acritarchs in this group were probably redeposited from sediments of Tremadoc age.



TEXT-FIG. 1. Location and geological setting of the Caradoc type section.

Category 3. Acritarchs of Arenig/Llanvirn age

The species placed in this category have stratigraphical ranges restricted to strata of this age. They are not present in the type Llandeilo of South Wales nor have they been recorded from Llandeilo or younger rocks elsewhere in the world.



TEXT-FIG. 2. Sketch-map of the outcrop of Ordovician rocks around Church Stretton, Shropshire, and the relative positions of exposures at Chatwall and the River Onny.

	SPECIES	SAMPLE NUMBERS															
		OV/D/1	OV/D/2	OV/D/4	OV/AS/1	OV/AS/2	OV/UCL/1	OV/LCL/1	OV/LCL/2	OV/A/2	OV/A/1	OV/UHS/1	OV/MHS/1	OV/LHS/2	OV/LHS/1	OV/HS/2	OV/HS/1
TREMADOC FORMS	<i>Archaeohystrichosphaeridium zaleskyi</i>							1									4
	<i>Cymatogalea cristata</i>						1	6	2	2							
	<i>Cymatogalea velifera</i>							1	4	2	7						1
	<i>Dasydiacrodium palmatibolum</i>										1	2					
	<i>Impluviculus cf. lenticularis</i>	1															
	<i>Saharidia fragile</i>							3	5	2	2						2
	<i>Stelliferidium cortinulum</i>								7	6	5	4	3				
	<i>Stelliferidium stalligerum</i>						1		11	4	4	3	3				
	<i>Tamofevia phosphoritica</i>																1
	<i>Trichosphaeridium annolovaense</i>								1	1	1	2					2
PROBABLE TREMADOC FORMS	<i>Acanthodiacrodium/Actinotodiscus</i>							27	41	21	55	19	1	1	1	19	
	<i>Michystridium diornamentum</i>						1										
	<i>Polygonium</i> 'sp.	2					11	55	82	95	102	45	54	1	2		
	<i>Priscaecia distincta</i>									1							
	<i>Vulcanisphaera africana</i>								2		2						
	<i>Vulcanisphaera cirrita</i>								4								
ARENIG/LLANVIRN FORMS	<i>Arkonia tenata</i>															3	
	<i>Arkonia virgata</i>							2		1	1	1					
	<i>Coryphidium australe</i>					1				1		5	2	1			
	<i>Coryphidium bohemicum</i>			1									1	3	2		
	<i>Coryphidium elegans</i>		1					1									
	<i>Dicrodiacrodium normale</i>															2	
	<i>Dictyotidium ? dentatum</i>					1											
	<i>Frankea breviscula</i>													1			
	<i>Frankea hamata</i>											3					
	<i>Frankea hamulata</i>															1	
	<i>Frankea longivacuola</i>													1			
	<i>Frankea sartbernardense</i>													2		1	
	<i>Marrocanium simplex</i>													1	1	2	
	<i>Multiplicisphaeridium maroquense</i>											1					
	<i>Multiplicisphaeridium multiraciale</i>	3	1		1				3	1		3	3			2	2
	<i>Multiplicisphaeridium rayii</i>																2
	<i>Striatotheca frequens</i>						1	1			1	2		1			
	<i>Striatotheca principalis</i>														2		2
	<i>Striatotheca principalis parva</i>															3	1
	<i>Striatotheca quies</i>		2								1	2	3		4	1	2
<i>?Tunsisphaeridium elgismusum</i>											1						
% Reworked Arenig/LLanvirn species	1.5	2	0.5	1	1	1	—	2.5	2	3.5	11	11	20	8	7	2	
% Reworked Tremadoc species	0.5	—	—	—	—	1	6	14	9.5	11	13	6	—	—	0.5	4.5	
% Reworked probable Tremadoc species	—	1	—	—	—	6	82	64.5	58.5	79.5	64	55	1	3	0.5	11.5	
% Total of reworked species	2	3	0.5	1	1	8	88	81	70	94	88	72	21	11	8	16	
Total number of acritarchs counted	200	200	200	200	200	200	100	200	200	200	100	100	100	100	200	200	

TEXT-FIG. 3. The distribution and numerical abundance of reworked acritarchs in samples from the Caradoc type section. The figure for each category of reworked acritarchs identified in every sample is given as a percentage based on a count of 200 specimens, or 100 specimens where acritarchs were sparse.

PREVIOUS OCCURRENCES SPECIES	CAMBRIAN		TREMADOC										ARENIG										ARENIG LLANVIRN			LLANVIRN			LLANDEILO		CARADOC				
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	
<i>Archaeohystrichosphaeridium zaleskyi</i>	•	•																																	
<i>Cymatogalea cristata</i>		•	•		•		•																												
<i>Cymatogalea velifera</i>		•	•	•	•									•																					
<i>Dasydicrodium palmatolobum</i>		•	•																																
<i>Impluviculus cf. fenticularis</i>						•																													
<i>Saharsia fragile</i>		•	•				•	•	•																										
<i>Stelliferidium cortinulum</i>					•			•	•																										
<i>Stelliferidium stelligerum</i>													•																						
<i>Timofeevia phosphoritica</i>	•																																		
<i>Trichoephaeridium annokoense</i>			•																																
<i>Acanthodicrodium Actinotodiazis</i> sp.	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Micrhystridium diornamentum</i>																	•																		
<i>Polygonum</i> spp.			•														•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Pracopalea distincta</i>		•																																	
<i>Vulcanisphaera africana</i>		•																																	
<i>Vulcanisphaera cirrata</i>																																			
<i>Arkonia tenuata</i>																																			
<i>Arkonia virgata</i>																																			
<i>Corysphaidium australe</i>																																			
<i>Corysphaidium bohemicum</i>																•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
<i>Corysphaidium elegans</i>																																			
<i>Dicrodicrodium normale</i>																																			
<i>Diktyotidium dentatum</i>																																			
<i>Frankes breviuscula</i>																																			
<i>Frankes hamata</i>																																			
<i>Frankes hamulata</i>																																			
<i>Frankes longiuscula</i>																																			
<i>Frankes sarbernardense</i>																																			
<i>Marrocanum simplex</i>																																			
<i>Multiplicisphaeridium maroqueense</i>																																			
<i>Multiplicisphaeridium multiradiale</i>																																			
<i>Multiplicisphaeridium rayii</i>																																			
<i>Stratototheca frequens</i>																																			
<i>Stratototheca principalis</i>																																			
<i>Stratototheca principalis parva</i>																																			
<i>Stratototheca queta</i>																																			
<i>?Tunaphaeridium elgimosum</i>																																			

TEXT-FIG. 4. Previous records of the reworked taxa identified in the type Caradoc. Locality numbers indicate the following references. 1. Vanguetaine 1978; 2. Timofeev 1959; 3. Rasul and Downie 1974; 4. Downie 1958; 5. Rasul 1974; 6. Martin 1977; 7. Rasul 1979; 8. Combaz 1967; 9. Martin 1973; 10. Deunff 1961; 11. Görka 1967; 12. Timofeev 1966; 13. Martin 1969; 14. Rauscher 1974; 15. Rasul 1976; 16. Vavrdová 1972; 17. Vavrdová 1973; 18. Booth 1979; 19. Cramer and Diez 1977; 20. Dean and Martin 1978; 21. Vavrdová 1966; 22. Vavrdová 1977; 23. Vavrdová 1976; 24. Turner and Wadge 1979; 25. Burmann 1970; 26. unpublished data; 27. Cramer and Diez 1976; 28. Cramer, Allam, Kanes, and Diez 1974; 29. Cramer, Kanes *et al.* 1974; 30. Downie and Soper 1972; 31. Burmann 1968; 32. Paris and Deunff 1970; 33. Loeblich and Tappan 1978.

DESCRIPTIVE PALAEOLOGY

Group ACRITARCHA Evitt 1963

The system of informal 'subgroups' proposed by Downie, Evitt, and Sarjeant (1963) has no status under the provisions of the International Code of Botanical Nomenclature (I.C.B.N.). As indicated by Wicander 1974 (p. 11), the introduction of new subgroups which reflect generic names (Staplin, Jansonius, and Pocock, 1965) poses substantial nomenclatural problems. For these reasons it is preferred here not to organize the acritarcha into a suprageneric classification but to simply list them in alphabetical order.

Genus ACANTHODIACRODIUM (Timofeev 1958) Deflandre and Deflandre-Rigaud 1961

The status in the literature of the 'diacrodians' is confused, a situation created when many of the early species described were assigned to invalid genera by Timofeev (1959). The resultant taxonomic confusion was exacerbated by Deflandre and Deflandre-Rigaud (1961) who revised and restricted most of Timofeev's original genera; unfortunately many of their emendations are either invalid or illegitimate under various provisions of the I.C.B.N. and must be rejected. Leoblich and Tappan 1978, discussed this problem (pp. 1236-1238) and created a new genus, *Actinotodissus*. This appears to be differentiated from *Acanthodiacrodium* on minor variations in morphology and has yet to be widely accepted. Considerable numbers of individuals attributable to *Acanthodiacrodium* or possibly to *Actinotodissus* were recorded here but no attempt was made to speciate them. Although the stratigraphical distribution of the 'diacrodians' is not wholly understood, it is clear that in the Tremadoc rocks of Great Britain such forms occur in abundance, while in Arenig and younger rocks they are relatively rare.

Acanthodiacrodium/*Actinotodissus* spp.

Plate 16, fig. 3

Description. Central vesicle varying in outline from ovate with rounded poles to elongate-subovate. Opposite poles bear similar processes which may be hollow or solid; the central portion of the vesicle is always without processes. Both vesicle and process wall are usually smooth, rarely granulate; the equatorial zone may bear longitudinal striae. No exocystment structure recorded.

Genus ARCHAEOHYSTRICHOSPHAERIDIUM Timofeev 1959 ex Leoblich and Tappan 1976

The genus *Archaeohystrichosphaeridium* is technically invalid (see Leoblich and Tappan 1976, p. 303) but many forms originally described under this name have not yet been transferred to other genera. The name is retained here pending transfer of included species to other genera.

Archaeohystrichosphaeridium zaleskyi Timofeev 1959

Description. Central vesicle spherical, smooth, bearing a moderate number (15-25) of smooth, simple, hollow, homomorphic processes which have wide bases tapering to an acuminate distal termination. The process interior communicates freely with the vesicle cavity. No exocystment structure recorded. Vesicle diameter 24-33 μm ; process length 5-10 μm . Four specimens measured.

Remarks. The spherical forms described here probably belong to the genus *Solisphaeridium* Staplin, Jansonius and Pocock (1965), but transfer should await the examination of *in situ* material.

Genus ARKONIA Burmann 1970

Arkonia tenuata Burmann 1970

Description. Central vesicle hollow, triangular in outline, compressed with each angle bearing a long, hollow, smooth, simple process tapering gradually to an acuminate distal termination. Processes communicate freely with the vesicle cavity and all lie in the same plane as the compression of the central body. The vesicle wall is

ornamented with fine, closely spaced striae which are approximately parallel to the vesicle sides; these striae do not extend on to the process wall which is smooth. No excystment structure recorded. Vesicle height 27–32 μm ; process length 33–36 μm . Three specimens measured.

Remarks. *A. tenuata* differs from *A. virgata* Burmann 1970 by having more numerous, more closely spaced, and finer striae ornamenting the vesicle wall.

Arkonion virgata Burmann 1970

Description. Similar to *A. tenuata* in over-all morphology but the vesicle wall is ornamented with fewer, coarse, widely spaced striae. No excystment structure recorded. Vesicle height 28–31 μm ; process length 34–39 μm . Four specimens measured.

Genus CORYPHIDIUM Vavrdová 1972

Coryphidium australe Cramer and Diez 1976

Plate 17, fig. 4

Description. Central vesicle hollow, quadrate in outline with rounded corners, strongly compressed. The vesicle wall bears numerous (more than fifty) short, relatively thick processes but is otherwise smooth. Processes tend to be more closely spaced towards the corners of the vesicle and sparse on the central portions. Processes are hollow, smooth, and communicate freely with the vesicle cavity; distal terminations may be capitate, bifurcate, or irregularly bulbous. No excystment structure recorded. Vesicle width 39–42 μm ; process length 6–8 μm . Eight specimens measured.

Coryphidium bohemicum Vavrdová 1972

Description. Central vesicle hollow, quadrate in outline with rounded corners, strongly compressed, the sides of the central body may be almost straight or concave. The vesicle wall bears numerous (30–60), short, relatively thick processes which are concentrated towards the corners, with few or none on the central portions of the vesicle. These processes are hollow, smooth, and communicate freely with the vesicle cavity; distal terminations may be flat-topped, bifurcate, multifurcate, capitate, or irregularly bulbous. The vesicle wall also bears well-developed striae which are mostly restricted to those central areas having few processes; these striae are approximately parallel to the vesicle sides around the margins but towards the centre may become strongly concave. No excystment structure recorded. Vesicle width 22–27 μm ; process length 3–6 μm . Five specimens measured.

Remarks. Probable occurrences of this species, recorded as 'Indéterminé forme A' in the Caradoc of Ombret, Belgium (Martin, Michot, and Vanguetaine, 1970) are here interpreted as reworked (see also Martin 1977, fig. 14).

Coryphidium elegans Cramer, Allam *et al.* 1974

Description. Central vesicle hollow, quadrate in outline with rounded corners, strongly compressed. The vesicle wall bears numerous (30–60), short, slender processes which tend to be concentrated towards the corners with few or none on the central portions. Processes are smooth, apparently solid, and the distal terminations may be rounded or capitate. The vesicle wall also bears well-developed striae which are most prominent on the central portions but may extend into the corners; these striae are approximately parallel to the vesicle sides but tend to become concave towards the centre. No excystment structure recorded. Vesicle width 20–21 μm ; process length 3–5 μm . Two specimens measured.

Genus CYMATIOGALEA (Deunff 1961) Deunff, Górka, and Rauscher 1974

Cymatigalea cristata (Downie 1958) Deunff, Górka, and Rauscher 1974

Plate 15, fig. 2

Description. Central vesicle spherical to sub-spherical; wall granular, divided into polygonal fields by low sutural ridges which bear smooth, apparently solid processes dividing distally into two to four simple lateral branches; the polygonal areas between sutural ridges lack processes. Excystment is by the development of a large round to

sub-polygonal polar opening, the periphery of which also bears processes. The operculum, which is commonly preserved inside the vesicle, is devoid of processes but has a coarse granular ornament. Vesicle diameter 25–31 μm ; excystment opening 27–30 μm ; process length 15–28 μm . Eight specimens measured.

Cymatiogalea velifera (Downie 1958) Martin 1969

Plate 15, fig. 1

Description. Central vesicle spherical to sub-spherical; wall ornamented with irregular grana and divided into polygonal fields by low sutural ridges that bear processes supporting thin membranes. The processes are smooth, slender, hollow with a solid proximal plug separating the process interior from the vesicle cavity; distally the processes divide into two or four simple lateral branches. Membranes are delicate and transparent although sometimes faint striations or thickenings may be seen. Polygonal areas between sutural ridges lack processes. Excystment is by the development of a large sub-polygonal polar opening the periphery of which also bears processes supporting membranes. The operculum which commonly is preserved inside the vesicle lacks both processes and membranes but has a coarse granular ornament. Vesicle diameter 30–40 μm ; excystment opening 26–35 μm ; process length 7–12 μm . Ten specimens measured.

Genus *DASYDIACRODIUM* (Timofeev 1959) Deflandre and Deflandre-Rigaud 1961

Dasydiacrodium palmatilobum Timofeev 1959

Plate 15, fig. 4

Description. Central vesicle ellipsoidal, smooth with rounded poles, one pole bears approximately fifteen simple, smooth, hollow, homomorphic processes which have wide bases and taper rapidly to an acuminate distal termination. The opposite pole bears a larger number (about twenty-five) of much shorter but otherwise similar processes. The intervening equatorial portion of the vesicle is without ornament. The interiors of all processes communicate freely with the vesicle cavity. No excystment structure recorded. Length of long axis 31–33 μm ; short axis 26–28 μm ; long processes 27–30 μm ; short processes 11–14 μm . Three specimens measured.

Genus *DICRODIACRODIUM* Burmann 1968

Dicrodiacrodium normale Burmann 1968

Plate 17, fig. 5

Description. Central vesicle is heteropolar, approximately oval in outline with a broadly rounded antapical pole and a more sharply rounded apical pole. The apical pole bears a single, smooth, hollow, cylindrical process which has a solid proximal plug separating the process interior from the vesicle cavity. Distally this process terminates in five to six short, simple, acuminate branches giving a grapnel-like appearance. The antapical pole bears a dense anastomosing network of fine threadlike processes. The vesicle wall is ornamented with widely spaced longitudinal striae. No excystment structure recorded. Vesicle height 58 μm ; vesicle width 33 μm ; length of apical process 25 μm . One specimen measured.

EXPLANATION OF PLATE 15

Selected acritarchs of Tremadoc age

All figures $\times 1200$

Fig. 1. *Cymatiogalea velifera* (Downie) Martin. OV/A/2b–5, MPK 2732, Onny Valley, Alternata Limestone. 2. *C. cristata* (Downie) Deunff, Görka and Rauscher. OV/A/2b–1, MPK 2733, Onny Valley, Alternata Limestone. 3. *Stelliferidium stelligerum* Deunff, Görka and Rauscher. OV/A/1a–1, MPK 2734, Onny Valley, Alternata Limestone. 4. *Dasydiacrodium palmatilobum* Timofeev. OV/UHS/1–2, MPK 2735, Onny Valley, Horderley Sandstone. 5. *Trichosphaeridium annolovaense* Timofeev. OV/A/1a–1, MPK 2736, Onny Valley, Alternata Limestone. 6. *Saharidia fragile* (Downie) Combaz. OV/HS/1–1, MPK 2737, Onny Valley, Harnage Shales, phase-contrast.



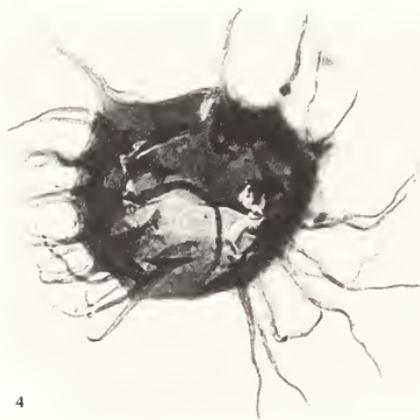
1



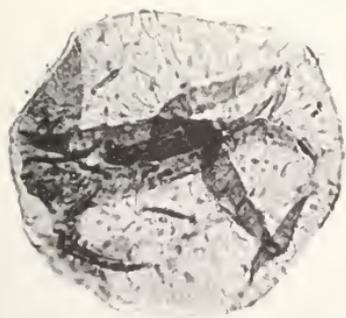
2



3



4



5



6

Genus *Dictyotidium* (Eisenack 1955) Staplin 1961
Dictyotidium? dentatum (Vavrdová 1976) Dean and Martin 1978

Description. Central vesicle hollow, sub-polygonal in outline. The vesicle surface is divided into a small number of polygonal fields (nine in the one individual recorded) delineated by prominent, smooth, transparent membranes the outer edges of which carry a row of short, capitate, often flat-topped denticles. No excystment structure recorded. Vesicle diameter 45 μm . One specimen measured.

Genus *Frankea* Burmann 1970
Frankea breviscula Burmann 1970

Description. Central vesicle hollow, smooth, triangular in outline, strongly compressed. Each angle bears a single slender, smooth process of moderate length (up to 70% of vesicle height) that tapers gradually towards the distal end; here it divides into five or six short, simple, acuminate lateral branches that arise in a single plane normal to the compression of the vesicle. The hollow processes all lie in the plane of the central body and communicate freely with the vesicle cavity. No excystment structure recorded. Vesicle height 28 μm ; process length 15 μm . One specimen measured.

Frankea hamata Burmann 1970

Description. Similar to *F. breviscula* in over-all morphology but differing in having shorter processes that always divide distally into two long, smooth, simple, strongly recurved lateral branches with acuminate terminations; these bifurcations occupy the same plane as the compression of the vesicle. No excystment structure recorded. Vesicle height 24–26 μm ; process length 13–15 μm ; length of lateral branches 11–14 μm . Three specimens measured.

Frankea hamulata Burmann 1970

Description. Similar to *F. breviscula* in over-all morphology but differing in having short slender processes. No excystment structure recorded. Vesicle height 29 μm ; process length 9 μm ; length of lateral branches 1–2 μm . One specimen measured.

Frankea longiuscula Burmann 1970

Description. Similar to *F. breviscula* in over-all morphology but with very long (up to 150% of vesicle height) slender processes. No excystment structure recorded. Vesicle height 41 μm ; process length 63 μm ; length of lateral branches 5 μm . One specimen measured.

Frankea sartbernardense (Martin 1966) Burmann 1970

Description. Similar to *F. breviscula* in over-all morphology but with very short stout processes. No excystment structure recorded. Vesicle height 21–24 μm ; process length 3–4 μm ; length of lateral branches 2–3 μm . Three specimens measured.

Remarks. Records of this species in the Silurian of Belgium (Martin 1969) are interpreted as reworked by the present author.

Genus *Impluviculus* (Loeblich and Tappan 1969) Martin 1977
Impluviculus cf. lenticularis Martin 1977

Plate 16, fig. 2

Description. Central vesicle hollow, compressed, polygonal in outline, apparently smooth. Each angle bears a slender, flagelliform process which tapers gradually to a closed distal termination; these processes are hollow proximally and communicate freely with the vesicle cavity but may become solid distally. Sometimes two processes may be closely located forming a pair. All processes arise around the margins of the central body and lie in the plane of compression. Vesicle diameter 9 μm ; process length 24–28 μm . One specimen measured.

Remarks. Assignment to *I. lenticularis* is not certain since the processes are much longer than those in the type material from the Tremadoc of Brabant, described by Martin (1977).

Genus *MARROCANIUM* Cramer, Kanes *et al.* 1974
Marrocanium simplex Cramer, Kanes *et al.* 1974

Plate 17, fig. 1

Description. Central vesicle hollow, smooth, quadrate in outline, strongly compressed. Each angle bears a single, smooth, simple process which tapers to a slightly rounded distal termination. The hollow processes lie in the same plane as the central body and communicate freely with the vesicle cavity. Thin, transparent membranes are suspended between the processes; those in a lateral position are wide, stretching out to the process tips while the apical and antipical membranes are seen only immediately adjacent to the vesicle. The membranes appear to be smooth and are fragile. No excystment structure recorded. Vesicle length 30 μm ; process length 25 μm . Three specimens measured.

Remarks. The transparent membranes recorded here possibly envelop the entire central body, thus forming a delicate periderm rather than being simple, single-layer structures as described by Cramer, Kanes, Diez and Christopher (1974). More data are required to determine this point.

Genus *MICRHYSTRIDIUM* (Deflandre 1937) Downie and Sarjeant 1963
Micrhystridium diornamentum Rasul 1979

Description. Central vesicle spherical, bearing two types of process. Some processes are long, hollow, relatively few (5-10), simple, smooth, and taper gradually to a simple acuminate distal termination. The remaining processes are much more numerous (probably more than 50), short, closely spaced, smooth, apparently solid and hair-like. No excystment structure recorded. Vesicle diameter 16 μm ; process length 13 μm and 3 μm . One specimen measured.

Remarks. This species, originally described from the Tremadoc of England has subsequently been recorded from the Arenig/Llanvirn of North Wales (Booth 1979, p. 127; as *M. robustum* in part).

Genus *MULTIPLICISPHAERIDIUM* (Staplin 1961) Eisenack, Cramer, and Diez 1976
Multiplicisphaeridium maroquense Cramer, Allam *et al.* 1974

Description. Central vesicle hollow, smooth, polygonal in outline, formed from the merging of process bases. Processes are long, smooth, broad, and widen rapidly proximally; they divide distally in a characteristic manner with first- and second-order lateral branches the tips of which recurve sharply to give a loosely coiled appearance. Processes are hollow and communicate freely with the vesicle cavity. No excystment structure recorded. Vesicle diameter 29 μm ; process length 22 μm . One specimen measured.

Multiplicisphaeridium multiradiale (Burmam 1970) Eisenack, Cramer, and Diez 1976

Plate 17, fig. 2

Description. Central vesicle hollow, smooth, polygonal in outline, formed from the merging of process bases. The processes are long, smooth, broad, and widen rapidly proximally; they divide distally by simple bifurcation up to the third order, forming slender acuminate lateral branches. The processes, varying in number from five to seven, are hollow and communicate freely with the vesicle cavity. No excystment structure recorded. Vesicle diameter 22-27 μm ; process length 14-17 μm . Ten specimens measured.

Remarks. This species resembles *M. maroquense* but is distinguished by the third-order branching and the lack of sharply recurved distal tips to the process branches.

Multiplicisphaeridium rayii Cramer, Allam *et al.* 1974

Description. Central vesicle hollow, smooth, polygonal in outline, formed from the merging of process bases. The processes are long, smooth, broad and widen rapidly proximally; they divide distally into four or five digitate, generally straight, dagger-like branches with rare second-order branching. Processes are hollow and communicate freely with the vesicle cavity. No excystment structure recorded. Vesicle diameter 38 μm ; process length 44 μm . One specimen measured.

Genus *POLYGONIUM* Vavrdová 1966
'*Polygonium*' spp.

Plate 16, figs. 5, 6

Description. Central vesicle hollow, polygonal to sub-polygonal, bearing numerous, long, hollow, simple processes which communicate freely with the vesicle cavity and have acuminate distal terminations. Processes may have a consistent concentric arrangement or may be apparently distributed at random. Vesicle wall smooth, process wall smooth or rarely granular. Processes always have wide bases which thin rapidly to a slender stem, tapering gradually to the distal tip. No excystment structure recorded. Vesicle diameter 26–35 μm ; process length 15–20 μm . Fifty specimens measured.

Remarks. The acritarchs included here under the name '*Polygonium*' embrace a wider variety of forms than is circumscribed by the genus *Polygonium* Vavrdová 1966. This taxon was considered by its author to be distinguished by always having processes arranged in a consistent concentric manner (Vavrdová 1966, p. 413). Some individuals showing this feature were recorded here (Pl. 16, fig. 6) but most specimens, otherwise indistinguishable, exhibit an apparently random process arrangement (Pl. 16, fig. 5). These forms constitute a taxonomic problem since, although they are abundant in Tremadoc to Llanvirn strata, no valid generic name has yet been proposed for them. The term '*Polygonium*' is used here to denote forms with both concentrically and non-concentrically arranged processes.

Genus *PRISCOGALEA* Deunff 1961
Priscogalea distincta Rasul 1974

Plate 16, fig. 4

Description. Central vesicle spherical to sub-spherical, bearing about fifty processes which appear to be distributed irregularly over the surface. Processes are smooth, solid, and taper towards the distal ends where they are usually multifurcate; a few bifurcate or simple processes may be present. The vesicle wall is ornamented with faint striae which radiate out from each process base. Excystment is by the development of a large polygonal to sub-polygonal polar opening, the periphery of which also bears processes. The operculum is smooth and without processes. Vesicle diameter 30–33 μm ; excystment opening 15–16 μm ; process length 6–8 μm . Two specimens measured.

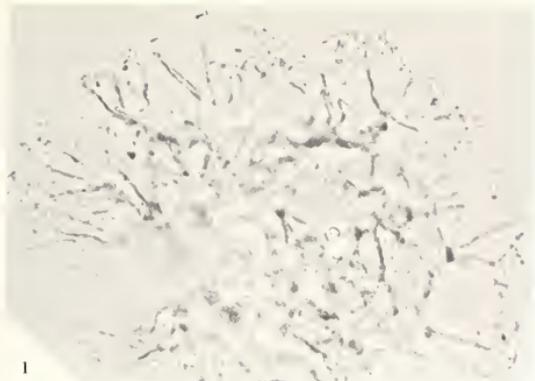
Remarks. The striate vesicle wall justifies the transfer of this species to the genus *Stelliferidium*, but this should await examination of *in situ* material. This species, previously known only from the Tremadoc, has been recorded from the Arenig and Llanvirn of Britain (Booth 1979, pp. 173, 322).

EXPLANATION OF PLATE 16

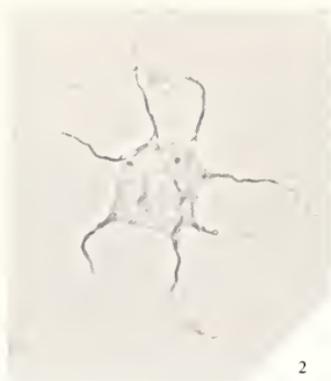
Selected acritarchs of probable Tremadoc age

All figures $\times 1200$

Fig. 1. *Vulcanisphaera cirrita* Rasul. OV/HS/1–1, MPK 2738, Onny Valley, Harnage Shales, phase-contrast. 2. *Impliviculus* cf. *lenticularis* Martin. OV/O/1–7, MPK 2739, Onny Valley, Onny Shales, phase-contrast. 3. *Acanthodiacrodium/Actinotodissus* sp. OV/UHS/1–1, MPK 2740, Onny Valley, Horderley Sandstone. 4. *Priscogalea distincta* Rasul. OV/A/2b–5, MPK 2741, Onny Valley, Alternata Limestone. 5–6. '*Polygonium*' spp. 5. OV/A/1a–1, MPK 2742. 6. OV/A/1a–1, MPK 2743, both from the Alternata Limestone of the Onny Valley.



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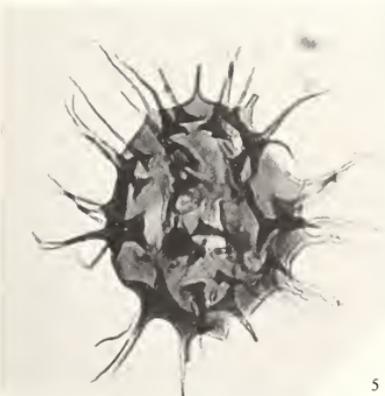
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6

TURNER, probable Tremadoc acritarchs

Genus SAHARDIA Combaz 1967
Sahardia fragile (Downie 1958) Combaz 1967

Plate 15, fig. 6

Description. Central vesicle circular in outline, wall thin ($< 0.5 \mu\text{m}$), fragile, and ornamented with irregularly sized and spaced grana. Concentric folds are developed in the wall adjacent to the periphery. Excystment is by the development of a small central pylome but often such openings are not apparent. Vesicle diameter $35\text{--}70 \mu\text{m}$; pylome diameter $9\text{--}15 \mu\text{m}$. Ten specimens measured.

Genus STELLIFERIDIUM Deunff, Górká, and Rauscher 1974
Stelliferidium cortinulum (Deunff 1961) Deunff, Górká, and Rauscher 1974

Description. Central vesicle spherical to sub-spherical; the wall is thick ($1\text{--}2 \mu\text{m}$) and bears $15\text{--}20$ smooth processes which appear to be distributed irregularly over the vesicle; these processes are hollow with a solid proximal plug separating the process interior from the vesicle cavity; from the base they taper gradually to a bifurcate or multifurcate distal termination. The vesicle wall is ornamented with faint striae which radiate out from the base of each process. Excystment is by the development of a large circular to sub-polygonal polar opening, the periphery of which always lacks processes. The operculum is smooth and is also without processes. Vesicle diameter $29\text{--}36 \mu\text{m}$; excystment opening $15\text{--}23 \mu\text{m}$; process length $5\text{--}9 \mu\text{m}$. Fifteen specimens measured.

Stelliferidium stelligerum Deunff, Górká, and Rauscher 1974

Plate 15, fig. 3

Description. Central vesicle spherical to sub-spherical, thick-walled ($1\text{--}2 \mu\text{m}$), and bears about sixty processes which appear to be distributed irregularly over the surface. Processes are hollow with a solid proximal plug separating the process interior from the vesicle cavity; they are smooth and taper gradually to a simple acuminate or bifurcate distal termination. Processes tend to be longest at the antapex becoming progressively shorter towards the polar opening. Excystment is by the development of a large, circular to sub-circular opening, the periphery of which bears short, generally bifurcating processes. The operculum, which is commonly preserved *in situ*, is granular and without processes. The vesicle wall is ornamented with thick prominent striae that radiate out from each process base. Vesicle diameter $31\text{--}37 \mu\text{m}$; excystment opening $18\text{--}21 \mu\text{m}$; process length $11\text{--}15 \mu\text{m}$. Fifteen specimens measured.

Genus STRIATOTHECA Burmann 1970
Striatotheca frequens Burmann 1970

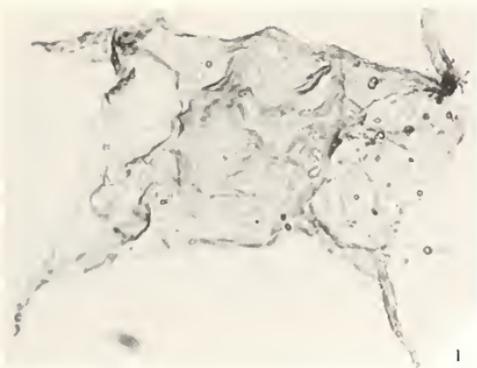
Description. Central vesicle hollow, quadrate in outline, strongly compressed. Each angle bears a single long, broad, simple process which tapers gradually to a generally rounded distal termination. The hollow processes lie in the same plane as the central body and are in free communication with the vesicle cavity. The vesicle wall is ornamented with fine striae that are approximately parallel to the vesicle margins around the periphery but become concave towards the centre; these striae pass on to the processes but die away distally. No excystment structure recorded. Dimensions of central vesicle $33\text{--}37 \mu\text{m} \times 31\text{--}36 \mu\text{m}$; process length $10\text{--}16 \mu\text{m}$. Five specimens measured.

EXPLANATION OF PLATE 17

Selected acritarchs of Arenig/Llanvirn age

All figures $\times 1200$

Fig. 1. *Marrocanium simplex* Cramer, Kanes *et al.* NS/4-4, MPK 2744, Chatwall, Harnage Shales. 2. *Multiplicisphaeridium multiradiale* (Burmann) Eisenack *et al.* OV/A/2b-5, MPK 2745, Onny Valley, Alternata Limestone. 3. *Striatotheca quieta* (Martin) Rauscher. NS/4-4, MPK 2746, Chatwall, Harnage Shales. 4. *Coryphidium australe* Cramer and Diez. OV/MHS/1-3, MPK 2747, Onny Valley, Horderley Sandstone. 5. *Dicrodiacrodium normale* Burmann. NS/4-1, MPK 2748, Chatwall, Harnage Shales. 6. *Tunisphaeridium elimosum* Vavrdová? OV/A/1b-1, MPK 2749, Onny Valley, Alternata Limestone.



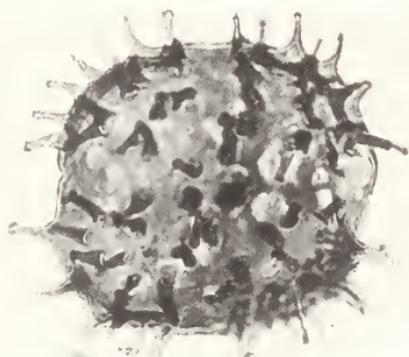
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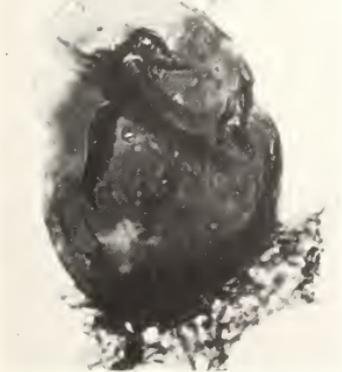
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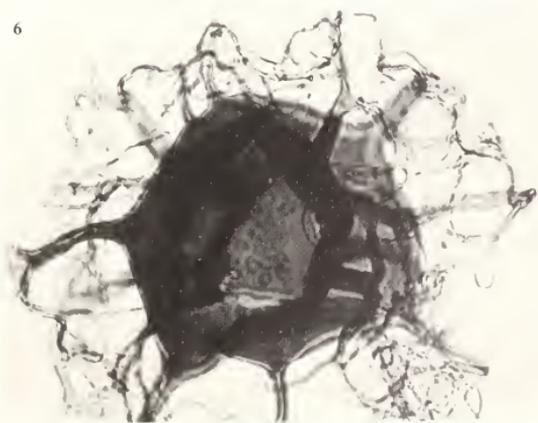
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Striatotheca principalis Burmann 1970

Description. Similar to *S. frequens* in over-all morphology but is larger, has long, slender processes with acuminate distal terminations and bears a vesicle ornament of coarse, widely spaced striae. No excystment structure recorded. Vesicle dimensions $40\text{--}44\ \mu\text{m} \times 36\text{--}38\ \mu\text{m}$; process length $20\text{--}31\ \mu\text{m}$. Four specimens measured.

Striatotheca principalis var. *parva* Burmann 1970

Description. Similar to *S. principalis* in over-all morphology, this variety is distinguished by its much smaller size. It differs from *S. frequens* in having slender processes with acuminate distal terminations, and a vesicle ornament of coarse, widely spaced striae. No excystment structure recorded. Vesicle dimensions $27\text{--}31\ \mu\text{m} \times 20\text{--}23\ \mu\text{m}$; process length $15\text{--}20\ \mu\text{m}$. Five specimens measured.

Striatotheca quieta (Martin 1969) Rauscher 1974

Plate 17, fig. 3

Description. Central vesicle hollow, quadrate in outline, strongly compressed; each angle bears an extremely short, simple process which tapers to a rounded distal termination. The hollow processes lie in the same plane as the central body and communicate freely with the vesicle cavity. The vesicle wall is ornamented with fine, closely spaced striae which are approximately parallel to the vesicle margins around the periphery but become concave towards the centre; these striations continue on to the process wall almost out to the distal tip. No excystment structure recorded. Vesicle dimensions $29\text{--}32\ \mu\text{m} \times 33\text{--}35\ \mu\text{m}$; process length $3\text{--}5\ \mu\text{m}$. Twelve specimens measured.

Remarks. Records of this species (as *Veryhachium quietum*) from the Silurian of Belgium (Martin 1969) are interpreted by the present author as reworked.

Genus TIMOFEEVIA Vanguetaine 1978

Timofeevia phosphoritica Vanguetaine 1978

Description. Central vesicle spherical to sub-spherical, wall smooth, divided by raised ridges into about twenty polygonal fields; the junctions of the ridges bear smooth processes which taper gently to a bifurcate or multifurcate distal termination. No excystment structure recorded. Vesicle diameter $32\ \mu\text{m}$; process length $9\text{--}11\ \mu\text{m}$; diameter of polygonal fields $9\text{--}11\ \mu\text{m}$. One specimen measured.

Genus TRICHOSPHAERIDIUM Timofeev 1966

Trichosphaeridium annolovaense Timofeev 1966

Plate 15, fig. 5

Description. Central vesicle spherical to sub-spherical but always compressed, wall smooth, moderately thick (about $1\ \mu\text{m}$) with compression folds developed. The vesicle bears more than 100 short, solid, smooth, simple hairlike processes whose distal terminations may be evexate or acuminate. No excystment structure recorded. Vesicle diameter $42\text{--}49\ \mu\text{m}$; process length $3\text{--}4\ \mu\text{m}$. Six specimens measured.

Genus TUNISPHAERIDIUM Deunff and Evitt 1968

Tunisphaeridium elimosum Vavrdová? 1973

Plate 17, fig. 6

Description. Central vesicle hollow, sub-polygonal in outline, wall smooth, bearing $15\text{--}20$, long, cylindrical, smooth processes which widen proximally and divide distally by means of simple bifurcation up to the fifth order; the distal terminations of these branches are long, slender, curved, and sometimes appear to join those of adjacent processes forming an anastomosing network of fine filaments. Processes are hollow and communicate freely with the vesicle cavity. No excystment structure recorded. Vesicle diameter $36\ \mu\text{m}$; process length $28\ \mu\text{m}$. One specimen measured.

Remarks. The specific assignment is not certain since the branching pattern of *T. elimosum* is described by Vavrdová as palmate rather than bifurcate as recorded here.

Genus *VULCANISPHAERA* (Deunff 1961) Rasul 1976*Vulcanisphaera africana* Deunff 1961

Description. Central vesicle spherical to sub-spherical, wall smooth or granular, bearing 50–100 processes which arise from hollow conical projections having a solid tip; normally three processes arise from a common base in this way, more rarely two or four. Processes are slender and taper gradually to a bifurcate distal termination. No exocystment structure recorded. Vesicle diameter 32–49 μm , process length 10–14 μm . Three specimens measured.

Remarks. The distal bifurcations are extremely fine and delicate and are often broken off giving the appearance of a simple acuminate termination. Published records of this species are restricted to strata of Tremadoc age; the present author has identified the taxon in assemblages from Britain which on their palynological content are of probable Arenig age (unpublished data). It is thus possible that this form ranges above the top of the Tremadoc.

Vulcanisphaera cirrita Rasul 1976

Plate 16, fig. 1

Description. Central vesicle spherical to sub-spherical with 50–100 processes arising from hollow projections which have a solid tip. The number of processes sharing a common base in this way varies from two to five. Processes are slender and taper only slightly towards the distal tip where they branch into numerous delicate thread-like branches. The branches of adjacent process groups may unite to form a complex anastomosing network of fine filaments. No exocystment structure recorded. Vesicle diameter 37–48 μm ; process length 9–11 μm . Three specimens measured.

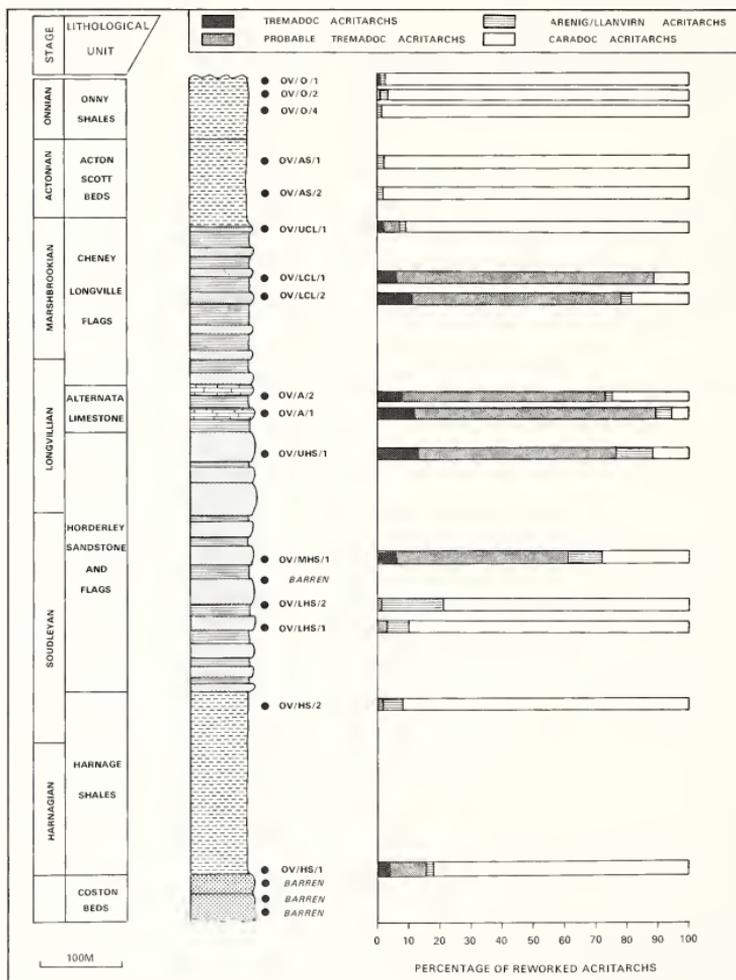
Remarks. Originally described from the Tremadoc of Shropshire, this species has been subsequently recorded from the Arenig/Lower Llanvirn of North Wales (Booth 1979, p. 190).

DISTRIBUTION OF THE REWORKED MATERIAL

The over-all pattern of reworking within the Onny Valley section is shown in text-fig. 5. Reworked acritarchs first appear in the Harnage Shales which represent the onset of fine-grained sedimentation. These acritarchs include species of both Tremadoc and Arenig/Llanvirn age, indicating that strata of both ages were being eroded to supply sediment to the shelf during early Caradoc time. Towards the top of the Harnage Shales and in the lower Horderley Sandstones, Arenig/Llanvirn forms dominate the reworked portions of the assemblages; only minor elements of probable Tremadoc age are present. A possible explanation of this is that widespread erosion of Arenig/Llanvirn sediments was occurring but that only a small area of Tremadoc rock was exposed. From the base of the Harnage Shales up to the middle Horderley Sandstone, reworked acritarchs consistently comprise 10–20% of the total assemblages. Above this level the proportion of reworked specimens in the sediments increases greatly to as much as 70%. This large and sudden increase in reworking is associated with an increase in the percentages of both Tremadoc and probable Tremadoc forms present. The simultaneous increase in the abundance of these two Categories tends to substantiate the Tremadoc age suggested for most individuals placed in Category 2. A high percentage of reworked acritarchs is evident until the upper part of the Cheney Longville Flags, always with taxa of Tremadoc and probable Tremadoc age predominating. The maximum level of reworking occurs in the Alternata Limestone, where up to 94% of the acritarchs are derived, the contemporaneous Caradoc forms being swamped out. The percentage of Arenig/Llanvirn forms fluctuates throughout the middle of the Caradoc sequence but is always small (text-fig. 5). The large numbers of reworked acritarchs of Categories 1 and 2 that are present from the middle Horderley Sandstone through to the upper Cheney Longville Flags suggest that an acritarch-rich source rock of Tremadoc age was extensively breached and continued to be eroded over a substantial period of time.

In the lower Acton Scott Beds reworked acritarchs constitute a mere 1 or 2% of the total assemblage and remain at this much-reduced level up to the top of the succession. This reduction in reworking coincides with a return to a low-energy mudstone environment.

If the majority of individuals placed in Category 2 are accepted as having originated in the Tremadoc then an interesting pattern to the reworking emerges (text-fig. 5). The distribution of taxa is essentially inverted, reflecting successive erosion of progressively older source sediments during Caradoc time. It should be noted that this pattern is modified by the relative abundance of Tremadoc forms at the base of the Harnage Shales. As discussed above, this clearly indicates early erosion of a Tremadoc source rock; however, the paucity of Tremadoc acritarchs in the overlying Harnage Shales



TEXT-FIG. 5. Showing the stratigraphical distribution of samples from the Caradoc type section together with the ages and percentages of the reworked acritarchs recorded from each horizon.

and Horderley Sandstone shows that reworking from this source was subsequently suppressed although not eliminated. Any explanation of this diminution in erosion of Tremadoc sediments would be purely conjectural at present. An inversion of this type, with younger material redeposited in the lower horizons and older forms appearing in the overlying strata, would be expected where relatively undisturbed sediments were being eroded and quickly laid down again. It may be assumed that the rocks discussed here would have been little altered by Caradoc time since the Ordovician was a period of tectonic quiescence in this region (Earp and Hains 1971, p. 89).

Samples from the lower Caradoc of the Chatwall district (text-fig. 2) contain abundant reworked acritarchs of Arenig/Llanvirn age with rare Tremadoc and probable Tremadoc forms, a distribution similar to that in the type section. Since the Caradoc sequence is much less complete at Chatwall and acritarchs are rare above the Harnage Shales, these occurrences are not discussed in detail here but they demonstrate that the reworking is not a local phenomenon restricted to the Onny Valley.

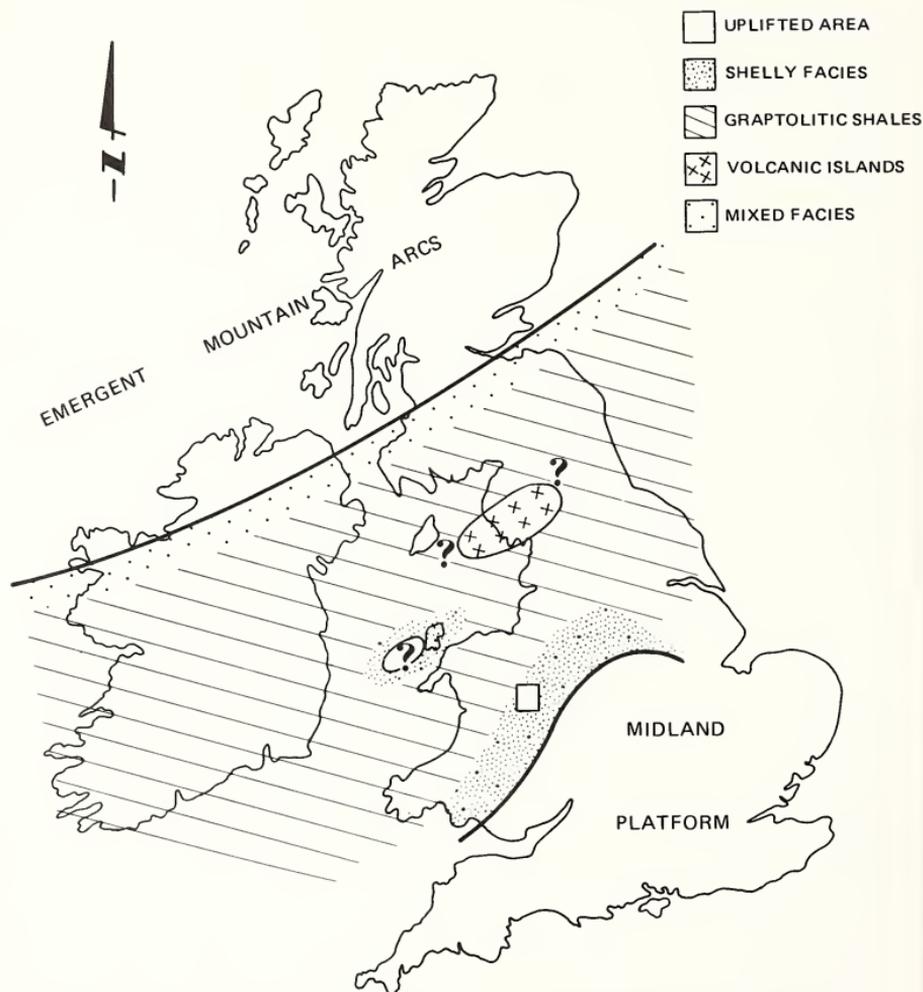
PROVENANCE OF THE REWORKED MATERIAL

The Tremadoc and Arenig/Llanvirn acritarchs encountered in the Caradoc type section are extremely well preserved suggesting that individuals were transported only short distances and underwent rapid reburial. Possible source rocks must therefore have been located close to the site of redeposition. It is unlikely that the reworked material was derived from the west since this was itself an area of deposition in Caradoc time. To the east and south, the Midland Platform formed a stable block during the Palaeozoic (text-fig. 6); Tremadoc rocks are widespread over this platform although Arenig/Llanvirn strata are practically unknown (Richardson and Rasul 1978, p. 37). To the south-east of Shropshire, probably close to the ancient margin of the Midland Platform, great thicknesses of Tremadoc sediments exist. Rocks of Arenig/Llanvirn age were possibly deposited in such peripheral areas but no traces have yet been found. Acritarch bearing Tremadoc and Arenig/Llanvirn strata are known from North Wales (Booth 1979; author's own unpublished data) and from the north of England (Booth 1979; Downie and Soper 1972), but the distances involved here are considerable and a closer source is considered more likely. No sedimentological evidence exists to indicate the direction of transport, but it appears probable that the reworked acritarchs were derived from the Midland Platform to the east or south-east. This is consistent with the available information on early Caradoc palaeocurrents (Williams 1969, p. 259, fig. 8).

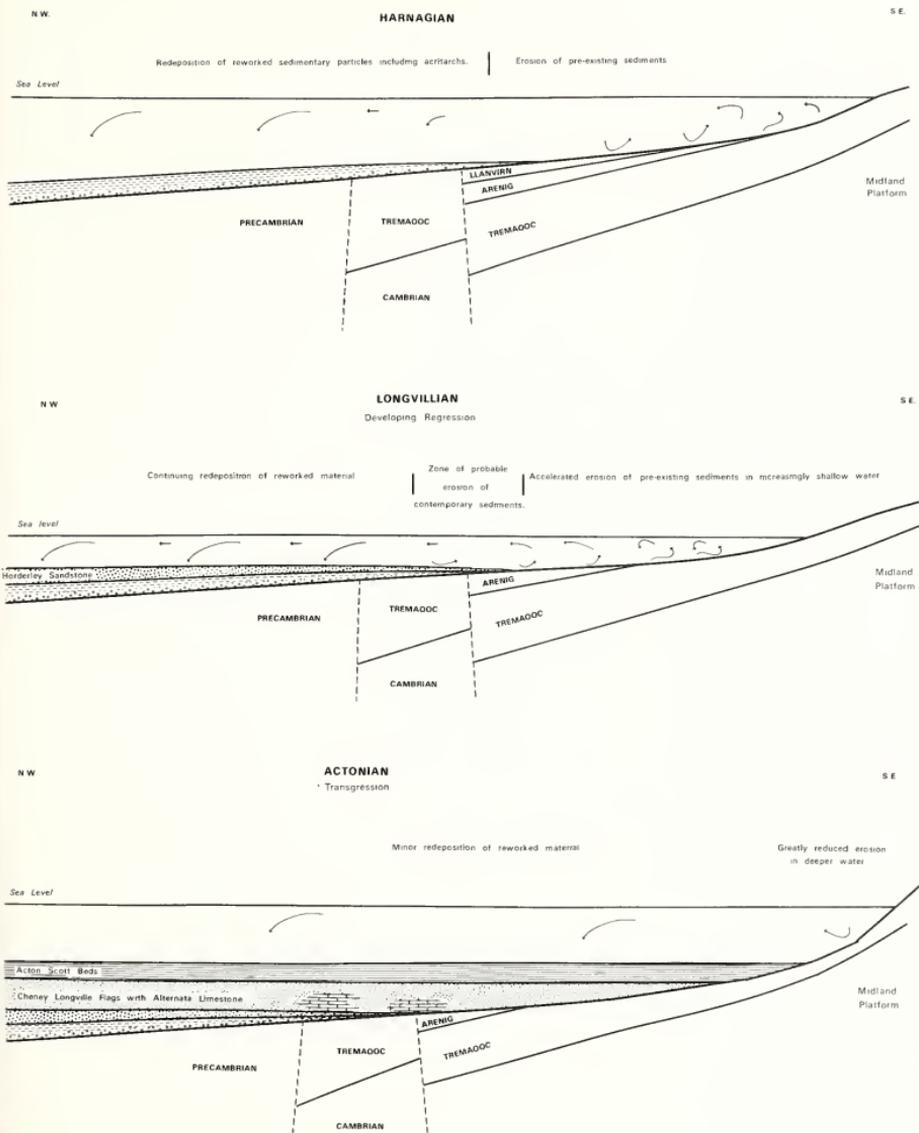
MECHANISM OF REWORKING

A widely accepted explanation of the mechanism for reworking of palynomorphs is that they were eroded and transported while encapsulated within particles of pre-existing sediments and so were protected from damage. If such recycled rock particles are present in a sediment they should be visible under microscopic examination (Richardson and Rasul 1978, p. 37). In the Onny Valley, lithologically diverse sediments such as the Harnage Shales, Horderley Sandstone, and Alternata Limestone all contain numerous reworked acritarchs. Thin-sections of samples from these formations were prepared and examined to see if such lithoclasts could be recognized but none was observed, the sediments presenting a more or less uniformly fine-grained appearance; the dimensions of sediment grains are between 5 and 100 μm with the vast majority being between 30 and 60 μm . Thus the grains are at most only slightly larger than reworked acritarchs recovered from the same samples. In addition, although no acritarchs were recognized in thin section, the sediments are clearly organic-rich and the abundant organic matter visible is trapped in the interstices. These factors make it unlikely that acritarchs were reworked in an encapsulated state, the evidence suggesting rather that they were eroded and redeposited as discrete sedimentary particles. This hypothesis is supported by the distribution pattern of the reworking which is unaffected by changes in the type of sediment being deposited (text-fig. 5). Similar reworked acritarchs are found in comparable numbers in sandstones, limestones, and flaggy micaceous siltstones. This alone suggests that the acritarchs were being introduced into the sediment/water-body system independently of the non-organic sediment particles.

If it is true that the reworked acritarchs were transported as individual particles then further conclusions can be drawn. Considering the excellent state of preservation of most reworked specimens, it is probable that dissolution of the parent rock was both easy and rapid. Since an indurated sediment would resist erosion, the Tremadoc and Arenig/Llanvirn rocks being eroded were probably at most only partly lithified. The retention of the most delicate morphological features on many reworked specimens suggests that erosion and transport were not only rapid but did not take place in a sub-aerial environment. Structures such as fine distal terminations of processes in



TEXT-FIG. 6. A suggested palaeogeographic reconstruction of the British Isles during Caradoc time (simplified, after Williams 1969).



TEXT-FIG. 7. Hypothetical diagrammatic cross-section through southern Shropshire in Caradoc time showing the postulated sequence of events. The Caradoc succession is simplified for the sake of clarity.

Vulcanisphaera cirrita (Pl. 16, fig. 1) and the delicate membranes of *Marrocanium simplex* (Pl. 17, fig. 1) would have been unlikely to survive long in turbulent conditions without the protection provided by encapsulation. Even if mechanical damage had been avoided, such features would have suffered rapid oxidation and disintegration. It is therefore postulated that erosion and redeposition of these pre-existing rocks took place in a shallow marine environment; wave and current action are considered the most likely agents for eroding and dispersing the unconsolidated sediments involved. Under these circumstances the enclosed acritarchs would be released directly into the sea, affording them the means both of protection and rapid dispersal and reburial (text-fig. 7). This agrees with the limited sedimentological evidence available which suggests that the Caradoc rocks were deposited in a shallow marine environment, possibly with off-shore barriers but with no estuaries present to have provided a potential source of reworked acritarchs from aerially exposed sediments (Hurst 1979a, p. 36). Hurst (op. cit., 1979b) has shown that in the Onny Valley the sequence from the upper part of the Horderley Sandstone to the basal Acton Scott Beds represents a regressive phase, and that the deposits of this interval were greatly affected by storm surge activity. The shallowing of the water body would have led to an increasingly high-energy regime, while individual surges would have resulted in mass sediment movement with rapid redeposition on the cessation of these geologically ephemeral events (text-fig. 7). Text-fig. 5 shows that the high-energy environment which resulted in the deposition of the upper Horderley Sandstone, Alternata Limestone, and Cheney Longville Flags, coincided with the period of greatest acritarch reworking. Above the base of the Actonian the percentage of reworked acritarchs is drastically reduced and it was at this time that storm swells ceased to exert any significant effect (Hurst 1979b, p. 196, Table 1). Unfortunately Hurst's studies do not extend down into the Soudleyan so it is uncertain how close the correlation is between the increasing energy levels and the first appearance of high levels of reworking. None the less there is clearly a link between the high-energy regime and abundant reworking, supporting the view that un lithified Tremadoc and Arenig/Llanvirn sediments were being eroded in a shallow marine environment.

Much has been written in recent years on the effects of storm surges on contemporaneous marine sediments (Brenner and Davis 1973; Reineck and Singh 1972, 1973), but there appear to be few data available on the effects of such events on soft pre-existing sediments at the water/substrate interface. Although little consideration has been given in the literature to the possibility of reworking from such sediments, the situation visualized here is not unique. For example, Quaternary clays in the Moray Firth, Scotland, contain extensive assemblages of reworked late Jurassic and early Cretaceous microfossils, particularly organic-walled microplankton (Owens and Marshall, 1978, pp. 24-26). This unoxidized material is well preserved and is clearly derived from unconsolidated Jurassic and Cretaceous shales and clays upon which the Quaternary rests in this area (Dr. R. Harland, pers. comm.). The physical state of these Mesozoic sediments suggests that reworking within lithic clasts would have been unlikely and redeposition of the microfossils as discrete particles is considered probable.

CONCLUSIONS

The type Caradoc rocks of Shropshire yield abundant acritarch assemblages which contain Caradoc species admixed with reworked Tremadoc and Arenig/Llanvirn taxa.

The vertical distribution of reworked forms reveals essentially an inverted stratigraphy with Arenig/Llanvirn acritarchs predominating in the lower horizons while the older Tremadoc species become the most abundant forms in the middle part of the sequence.

The lack of visible lithoclasts in thin sections of these rocks suggests that the microfossils were introduced into the sediment body as individuals and were not encapsulated in redeposited fragments of pre-existing rocks; this is substantiated by the fact that the presence and abundance of reworked acritarchs appears to be entirely independent of lithotype.

The excellent state of preservation of the reworked acritarchs indicates that they underwent little transportation before reburial. It also suggests that the parent sediments were relatively

unconsolidated and that their erosion was caused by marine action in a shallow-water environment.

The high percentages of reworking in the middle part of the section are partly related to the increasing erosion of particularly acritarch-rich Tremadoc rocks. In addition, this sequence represents a regressive phase with storm surges having profound effects on the shallowing water body. Such high-energy events would have greatly increased the erosion rate of the un lithified sediments exposed at the sea bed. A state of continuous low-level erosion and acritarch reworking is envisaged, punctuated by periodic intense turbidity associated with an upsurge in the rate of release of pre-existing microfossils.

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LOWER CARBONIFEROUS CONODONT FAUNAS FROM RAVENSTONEDALE, CUMBRIA

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ABSTRACT. Conodont faunas from the Lower Carboniferous, Courceyan-Holkerian Stages, of Ravenstonedale are described. Three zones, the *Taphrognathus*, *Cloghergnathus*, and *Cavusgnathus* Zones, are recognized in the Chadian-Holkerian strata and one fauna, Fauna A, in the mid-Courceyan. These zones and the Fauna are correlated with the standard British Stages and with the American classic sections. The faunas are typical of the shallow water facies of the Lower Carboniferous and are dominated by the genera *Taphrognathus*, *Clydagnathus*, *Cloghergnathus*, and *Cavusgnathus*, which characteristically occur in intertidal and shallow subtidal environments. These shallow-water faunas are joined by deeper-water immigrants only in the Arundian but, even at this level, they are the dominant elements, indicating only a slight water depth increase. The absence of the deeper-water genera *Gnathodus* and *Siphonodella* adds difficulty to the correlation of this succession with goniatite-bearing sequences, but correlation with the Avon Gorge and with shallow-water facies in the north of England is possible. Three species, *Apatognathus asymmetricus*, *A. scandalensis*, and *Cloghergnathus carinatus* are proposed as new taxa.

THIS account of the conodont faunas of the Lower Carboniferous succession of Ravenstonedale is a documentation of one aspect of a succession which in recent years has become increasingly important to the stratigraphy of the Carboniferous period as a whole. The special significance of Ravenstonedale is, however, long standing, since it falls within the area designated by Garwood (1913, p. 451) as his type area for the Lower Carboniferous of the north of England. Garwood (1907, 1913) had produced a zonation, based primarily upon corals and brachiopods, which was a complement to the slightly earlier and very influential work of Vaughan (1905) in the Bristol area. Vaughan had designated the Lower Carboniferous as 'Avonian' in view of 'the completeness of the sequence in the Avon section' (1905, p. 264) and had further produced the well-known and much used zonal scheme based, he supposed, upon the evolutionary lineages of corals and brachiopods. Garwood (1913) recognized the great importance of Vaughan's paper and consequently included a correlation of his zones with those of Vaughan (Garwood 1913, p. 452).

This faunal zoning proved to be outstandingly successful. Indeed, in the opinion of Ramsbottom (1973, p. 568) the advance of Carboniferous stratigraphy was for some time ironically hampered by this very fact, since it appears to have induced a period when very little attention was paid to the many other aspects of the Lower Carboniferous sequence, in particular to details of lithology and their interpretation. Vaughan's zonal scheme along with Garwood's correlation for the north of England, was the foundation upon which Dinantian stratigraphy was based for sixty years, until it was superseded by a series of divisions based upon major cycles of deposition (Ramsbottom 1973). These cycles coincide very closely with the six new stages proposed by George, Johnston, Mitchell, Ramsbottom, Sevastopulo, and Wilson (1976) which are designed to be applied throughout Britain.

One consequence of the re-examination of the Dinantian rocks was that Ramsbottom (1973) was able to show that, far from being complete, the Avon Gorge succession contains four major non-sequences, and as a result large parts of the succession of the north of England are not able to be directly correlated with Vaughan's type area or zonal scheme. In addition, other biozonations based upon the Avon Gorge succession must necessarily be as incomplete as the coral/brachiopod zonation. One such scheme is that of Rhodes, Austin, and Druce (1969) in which they established fourteen conodont assemblage zones, the three highest of which were actually based upon the

north crop of the South Wales coalfield rather than upon the Avon Gorge. Substantial revision of this zonal scheme has, however, since (Austin 1973) been necessary, with the result that whilst the Brigantian (part of three conodont assemblage zones) and Courceyan (six assemblage zones plus a non-sequence) are usefully subdivided, the whole of the interval from just below the top of the Asbian down to a horizon within the Chadian is occupied by the *Cavusgnathus/Apatognathus* assemblage zone, non-sequences, or horizons with no conodonts (see George *et al.* 1976, Table 1).

The present study in Ravenstonedale was initiated in an attempt to provide a Dinantian conodont sequence from an area in which the succession has been demonstrated to be much more complete than that of the Avon Gorge (Ramsbottom 1973, p. 595).

STRATIGRAPHY

At its outset the Carboniferous period presented in the North-west Province a landscape of probably some considerable relief, dominated by rocks of Ordovician and Silurian age. During Dinantian times this landscape was gradually overwhelmed by a major transgression, evidence for which can be seen in the progressive overlap of Carboniferous strata on to Lower Palaeozoic and thereby giving rise to an increasing hiatus at the base of the Carboniferous succession. Complete submergence was not achieved until Asbian times, and as a result, within the North-west Province the local base of the Carboniferous succession varies in age from Courceyan to Asbian.

Deposition of the relatively thick (approx. 1500 m) Dinantian succession of Ravenstonedale began with local subsidence in a region known as the Stainmore Trough or Gulf, which opened to the east and was bounded to the north, west, and south by the positive massifs of the northern Pennines and the Lake District. Subsidence appears to have begun earlier in this trough than elsewhere and to have continued throughout Dinantian times. The Ravenstonedale area thus provides the most complete Dinantian succession within the North-west Province, with what appears to be an almost continuous record of sedimentation from Courceyan to Namurian. Readers are referred to Johnson and Marshall (1971) for further details on the regional setting of the Ravenstonedale area.

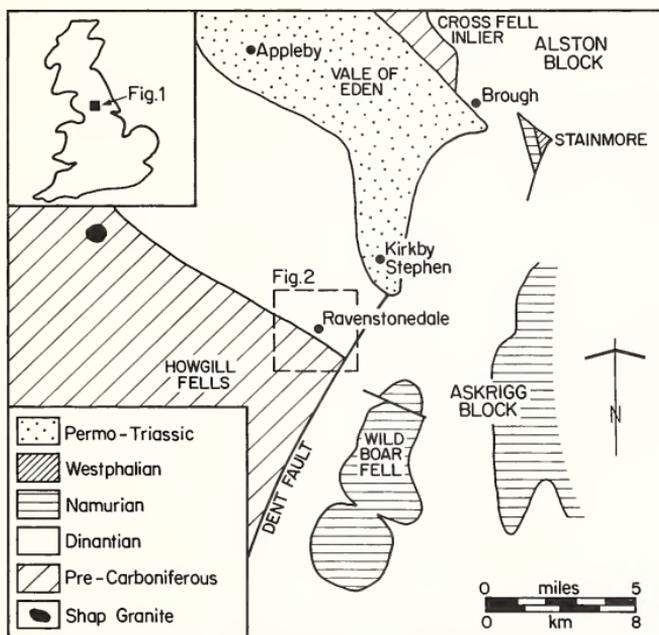
The present outcrop of this succession strikes north-westwards from the Dent Fault near Ravenstonedale, towards Penrith (text-fig. 1) on the southern side of the Vale of Eden. The regional structure is relatively simple, with gentle dips predominantly in a north to north-easterly direction. Natural stream exposure is generally good, and when combined with other natural exposures, road-cuttings, and the numerous small quarries, provides an almost complete record of the succession, except near its base, where much of the detail is obscured by an extensive deposit of glacial drift. The problems associated with the lower part of the succession were amply outlined by Holliday, Neves, and Owens (1979) in their account of a shallow borehole programme undertaken near Ravenstonedale over the period 1975 to 1978.

Working in collaboration with Holliday *et al.* the present authors have recently described the conodont faunas from the exposed part of the Pinsky Gill Beds (Varker and Higgins 1979) which form the lowest unit of the succession. These beds, which lie unconformably upon steeply inclined Silurian Bannisdale Slates and beneath the felspathic conglomerate, were shown by Holliday *et al.* (1976) to be 45–50 m in total thickness, of which only approximately 15 m near the base are exposed. The conodont faunas indicate an age of mid-Courceyan, i.e. late K or Z on the coral/brachiopod scheme, for the base of the Dinantian succession in Ravenstonedale.

The overlying felspathic conglomerate, which is also poorly exposed, was calculated by Johnson and Marshall (1971, p. 267) to be 36.4 m in thickness in Thackthwaite Gill. However, since neither of the boundaries of the horizon are well exposed and Holliday *et al.* (1976, p. 349) have shown them to be gradational with no major breaks in deposition, calculations of thickness can only be approximate. Holliday *et al.* (1976, p. 348) estimated the cumulative thickness from their borehole evidence to be around 42 m and interpreted the felspathic conglomerate as a continental interlude between the marine Pinsky Gill Beds and the overlying marine Stone Gill Beds. Capewell (1955) considered both the Pinsky Gill Beds and the felspathic conglomerate to be the lateral equivalents of the much-thicker basal beds which occur to the north-west, where they reach 274 m in thickness in the Lowther Valley area.

Above the felspathic conglomerate there are the Stone Gill Beds, which consist predominantly of limestone but also include thin (usually less than 1 m) siltstone and shale/mudstone horizons, which are usually calcareous. The lower part of this sequence and its junction with the conglomerate is not exposed but Holliday *et al.*

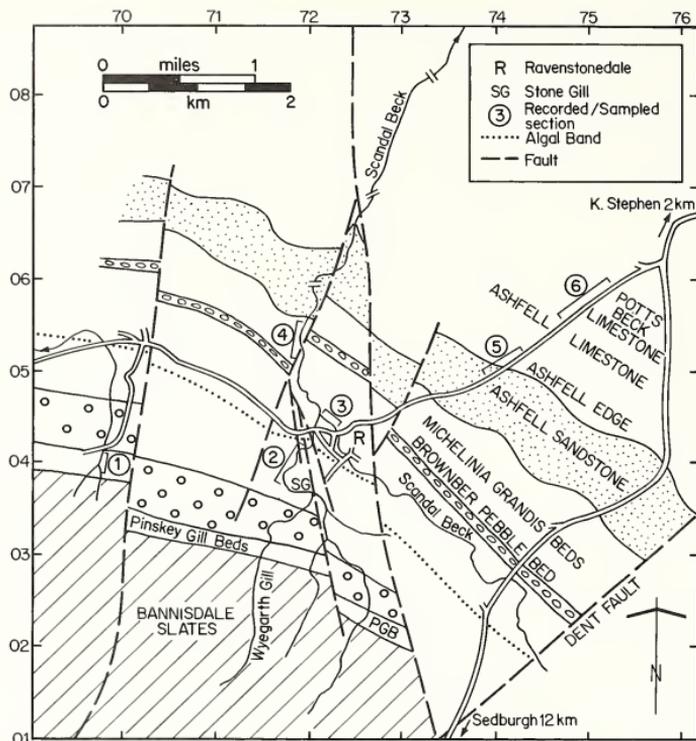
(1976, pp. 349, 350) estimated the thickness of the unexposed beds to be only slightly in excess of 42 m from borehole evidence. Virtually all of the remaining part of the Stone Gill Beds is exposed in Stone Gill itself, where they have been recorded and sampled, at intervals not exceeding 3 m, by the present authors (section 2, text-figs. 2, 3). The sequence includes a great variety of limestone lithologies, although calcite mudstones predominate and large parts of the succession have suffered some dolomitization. This part of the Dinantian succession also includes several of the marker bands described by Garwood (1913), in particular the *Vaughania* Band and the *Palaeochinus* Bed, both of which occur near the base of the exposed succession.



TEXT-FIG. 1. Location of the Ravenstonedale Area.

The overlying Coldbeck Beds begin at the *Spongiostroma* Band of Turner (1950) and extend up to a nodular algal band which outcrops beneath Coldbeck bridge at Ravenstonedale (NY 7209 0435). These beds, which are also predominantly fine grained limestones, may be distinguished from the Stone Gill Beds by their sparser fauna and the occurrence of several nodular algal layers. The algal layer described by Turner (1950) may be one of these, since it appears to be slightly lower stratigraphically than the band taken by Ramsbottom (1974, p. 52) to mark the top of the unit. Exposure of the Coldbeck Beds in Stone Gill is almost complete and once again conodont samples were taken at intervals not exceeding three metres (section 2, figs. 2, 3). It is, however, likely that these samples do not fully represent the Coldbeck sequence since Turner (1950, pp. 30, 35) presented evidence which suggested that approximately 30-35 m of beds had been removed from this stream section by faulting.

The Stone Gill Beds and the Coldbeck Beds were considered by Ramsbottom (1973, p. 574) to represent the transgressive and regressive phases of his first major cycle of the Dinantian, and they were both consequently included in the Courceyan Stage by George *et al.* (1976). An inconsistency was, however, noted by the latter authors (1976, p. 38) in that foraminifera from the Stone Gill Beds included forms typical of the V_{1a} of Belgium, i.e. Chadian, not Courceyan. Holliday *et al.* (1979, p. 354) considered the then available

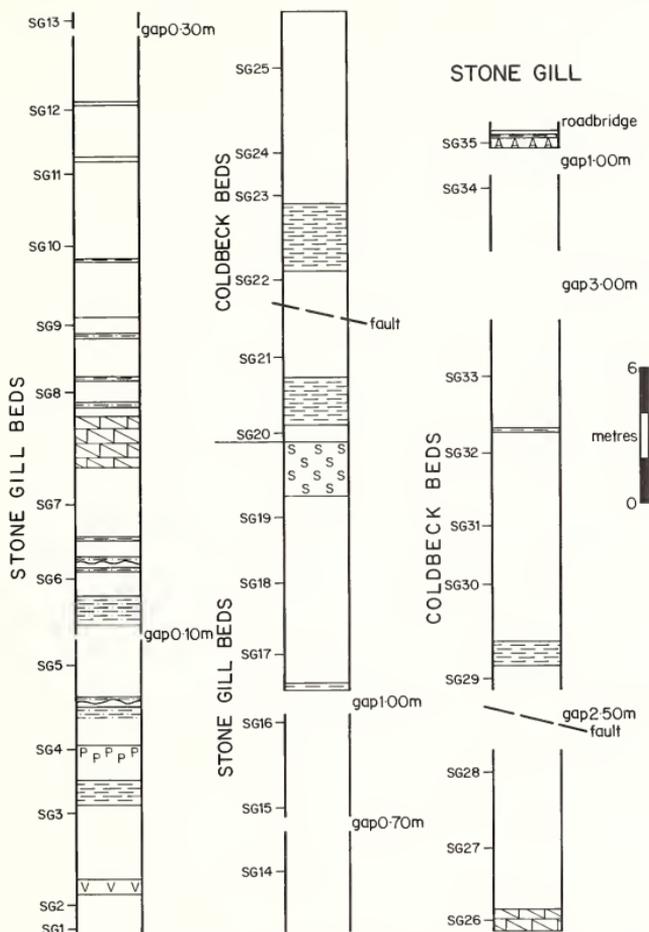


TEXT-FIG. 2. Geological map of the Ravenstonedale area showing the location of the sampled sections (Based with permission upon one inch GEOLOGICAL SURVEY SHEET No. 40)

palaeontological evidence for the position of the Chadian/Courceyan boundary to be inconclusive but concluded on sedimentological grounds that the boundary should be lower than indicated by George *et al.* and placed it, with reservation, high in the felspathic (Shap) conglomerate. On this basis, the whole of the Stone Gill/Coldbeck succession would be of Chadian age.

The succession continues with the Scandal Beck Limestone, which was considered by George *et al.* (1976, p. 38) to represent the whole of the Chadian Stage. These authors placed the top boundary of the unit, and stage, in an unexposed part of the sequence some 15 m below the Brownber Pebble Bed and indicated a total thickness for the unit of approximately 100 m. Johnson and Marshall (1971, p. 265) considered the same interval to be closer to 125 m in thickness. The Scandal Beck Limestone was sampled for conodonts only from approximately 10 m of partly dolomitized bioclastic limestone and calcite mudstone which occur near the base of the unit. It is this sequence which outcrops at the confluence of Stone Gill and Scandal Beck (section 3, text-fig. 2), which is represented in text-fig. 4.

The Brownber Pebble Bed, which forms a useful marker horizon in the region as an approximation for the base of the Arundian Stage, is 4 to 6 m in thickness and consists of calcareous sandstone with quartz pebbles, particularly in its upper part. Above the pebble bed the Arundian succession of Ravenstonedale may be conveniently divided into two parts, the *Michelinia grandis* Beds and the overlying Ashfell Sandstone. There are considerable variations in the published thicknesses attributed to these units. Turner (1950, p. 33) described the *M. grandis* Zone as consisting of 'nearly 150 feet (c. 46 m) of well bedded, somewhat iron-stained



TEXT-FIG. 3. Section in Stone Gill of the Stone Gill and Coldbeck Beds. For legend see text-fig. 4.

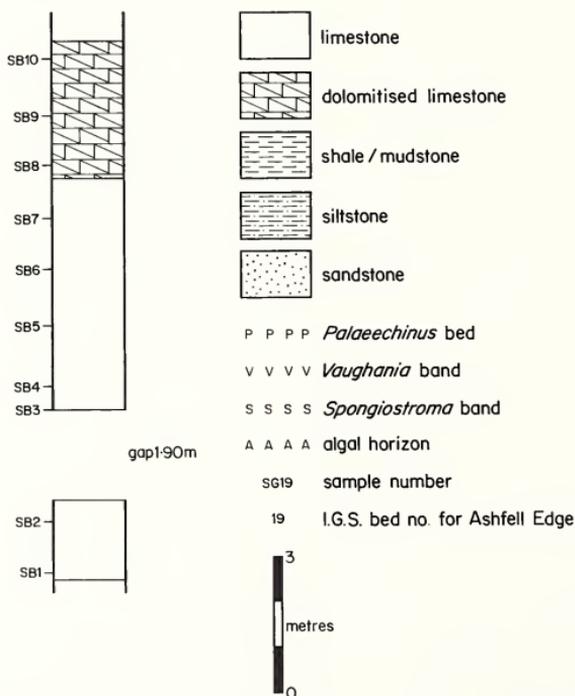
limestones with a horizon of chert nodules 30 feet above the base'. Johnson and Marshall (1971, p. 265), however, allocated 110 m to the *M. grandis* Zone and approximately 145 m to the whole interval between the Brownber Pebble Bed and the base of the Ashfell Sandstone. Ramsbottom (1974, p. 55) indicated that the beds of this same interval, which represent the transgressive phase of his third major cycle, reach about 240 m in the Ravenstonedale district. Finally, George *et al.* (1976, p. 38, fig. 11) allocated a thickness of about 130 m. The ten conodont samples collected by the present authors (section 4, text-fig. 2) were collected at regular intervals through the succession as exposed in Scandal Beck.

The Ashfell Sandstone is reported to reach 170 m in thickness in the Ravenstonedale area (Ramsbottom 1974, p. 57) but it does thin rapidly southwards. Only the top 13.25 m have been examined in the present

study at the well-known roadside exposures of the Ravenstonedale/Kirkby Stephen road, Ashfell Edge (section 5, text-fig. 2). At this locality the Ashfell Sandstone is represented by massive, false-bedded sandstone with slump structures, soft purple and green mudstones, and thin, sometimes lenticular, limestones, several of which are highly fossiliferous, containing large, *in situ*, dendritic coral colonies (text-fig. 5). Turner (1950, p. 34) considered these latter beds, the *Lithostrotion martini* horizon of Garwood (1913) to be confined to the immediate vicinity of the Ashfell Edge locality.

The Arundian/Holkerian boundary is well exposed at this locality and is marked by the incoming of the predominantly limestone sequence known as the Ashfell Limestone, which represents the whole of the Holkerian Stage. The lowest 60 m of this unit was almost continuously exposed in the road section on Ashfell Edge where, along with the upper part of the Ashfell Sandstone, it was measured and recorded by Dr. I. C. Burgess, Mr. M. Mitchell, and Dr. W. H. C. Ramsbottom (Institute of Geological Sciences) in September 1972. The sequence represented in text-fig. 5 is based upon their measured section (with their kind permission), but unfortunately recent civil engineering work has obscured some of the higher horizons. A total of thirteen conodont samples were taken from the horizons indicated (text-fig. 5). The upper part of the Ashfell Limestone sequence is not continuously exposed although exposures, both natural and in quarries, are frequent enough to allow conodont samples to be taken at fairly regular intervals. The total thickness of the Holkerian succession on Ravenstonedale Common approaches 200 m.

SCANDAL BECK



TEXT-FIG. 4. Section of Scandal Beck Limestones seen in Scandal Beck and Legend for text-figs. 3-5.

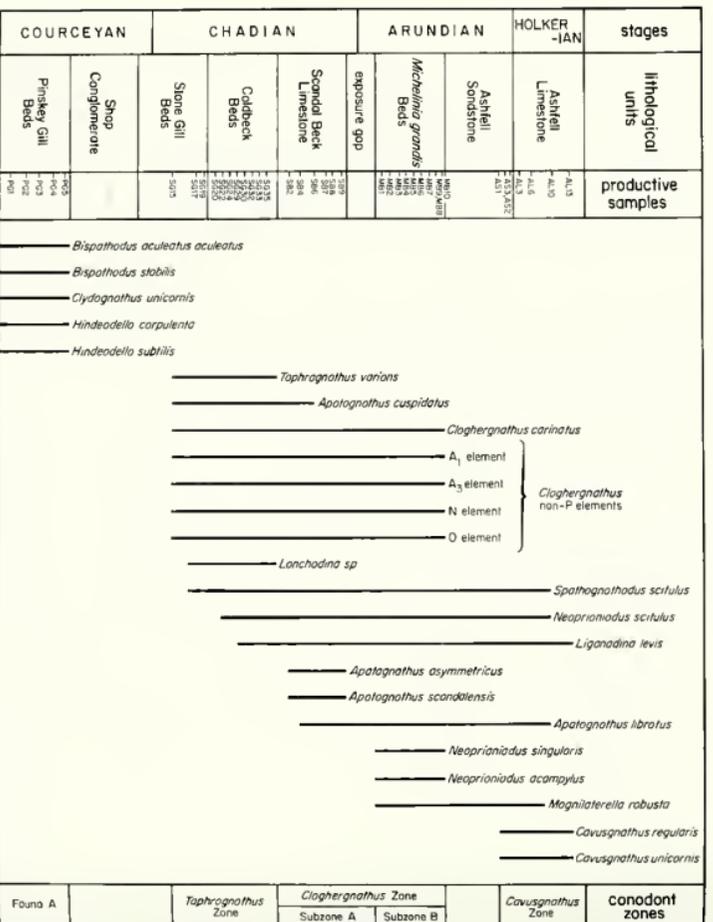
CONODONT FAUNAS

A sequence of four conodont faunas is recognizable in the Ravenstonedale succession. However, because the element ranges of the lowest fauna are incompletely known this is not named as a formal zone. The upper three zones are from an almost completely exposed and continuous sequence and are named and defined with a greater degree of certainty (see text-fig. 6).

Fauna A

The elements of Fauna A have recently been described by Varker and Higgins (1979). They occur in the outcrop section of Pinskye Gill and a series of dolomites and dolomitic limestones in the Pinskye Gill Borehole at depths between 33 and 36 m. The fauna probably typifies the whole of the Pinskye Gill Beds, but is so impoverished in both species and abundance that the full range of the elements is not known.

The fauna is dominated by *Bispathodus aculeatus aculeatus* (Branson and Mehl) and *Clydograthus unicornis* Rhodes, Austin and Druce together with hindeeodulids and ozarkodinites. The association of these forms led Varker and Higgins to conclude that the fauna was mid-Courceyan in age belonging to late K or early Z Zones of the Avon Gorge and South Wales, and correlating with the *costatus costatus* (*gnathodus delicatus* Zone of Rhodes, Austin, and Druce (1969)). Sevastopulo and Johnston (personal communication) would place the fauna firmly in the Z-Zone in terms of the Irish sequence.



Taphrognathus Zone

This is a partial range zone occurring in the upper part of the Stone Gill Beds and in the Coldbeck Beds. The Shap Conglomerate sequence above the Pinskey Gill Beds and the lowest part of the Stone Gill Beds do not contain conodonts. Faunas first appear some 40 m above the base of the exposed section in Stone Gill and continue up to the top of the Coldbeck Beds at Coldbeck Bridge.

The fauna remains impoverished in species, but is somewhat richer in abundance than that of the Pinskey Gill Beds. It is characterized by *Taphrognathus varians* Branson and Mehl, *Cloghergnathus carinatus* sp. nov., *Spathognathodus scitulus* (Hinde), *Apatognathus cuspidatus* Varker, and a variety of non-platform elements. *T. varians* is probably the best-known species for it has a very wide distribution. In the Upper Mississippi Valley and Missouri (Collinson, Rexroad, and Thompson 1972) it characterizes the middle part of the Valmeyeran Series (Upper Osage/Lower Meramec) ranging from the Keokuk to the lower part of the Upper St. Louis Formations. It is also known from Australia (Jenkins 1974) in strata which Jenkins concluded were of early Viséan age. *Taphrognathus* has also been recorded from Britain in the Main Algal Limestone of Roxburghshire (Rhodes *et al.* 1969), where it is of early Viséan age. Finally it occurs in Ireland (Austin and Mitchell 1975) again in the early Viséan. *Cloghergnathus* also occurs with *Taphrognathus* in Ireland as does *Spathognathodus scitulus*. *S. scitulus* is characteristic of the St. Louis Formation, Upper Valmeyeran in the Upper Mississippi Valley, where it overlaps the range of *Taphrognathus* although the closely related species *S. coalescens* occurs earlier and coexists with the greater part of the range of *Taphrognathus* (fig. 7).

The *Taphrognathus* Zone correlates broadly with the *Bactrognathus-Taphrognathus* Zone which occurs in the upper part of the Burlington Formation of the Upper Mississippi Valley. In Europe this fauna is uncommon but does occur in Ireland (Austin and Mitchell 1975) with the characteristic early Viséan *Mestognathus beckmani* and it was given a lower Viséan age. George *et al.* (1976) referred the Stone Gill Beds and the Coldbeck Beds to the late Courceyan, but the presence of V_{1a} foraminifera (Ramsbottom 1977) clearly indicates an early Viséan age for these sediments, and they are now referred to the Chadian (Ramsbottom 1977).

UPPER MISSISSIPPI VALLEY Collinson, Rexroad + Thompson 1972		S. W. MISSOURI Thompson + Fellows 1970	BELGIUM	BRITAIN George <i>et al.</i> 1976	RAVENSTONEDALE	
formations	conodont zones	conodont zones	assise	stages	formations	conodont zones
St. Louis	<i>Apat scalenus</i> - <i>Cavusgnathus</i>		V_3^b V_3^0 V_2^b	Asbion Holkerian	Ashfell Limestone	<i>Cavusgnathus</i>
	Warsaw - Salem	<i>Taph varians</i> <i>Apatognathus</i>		V_2^0 V_4^b		
Keokuk		<i>Gnathodus texanus-Taphrognathus</i> - <i>G. bulbosus</i>		V_4^0	Chodion	Scandal Beck Limestones
	Burlington	<i>Bactrognathus</i> - <i>Taphrognathus</i>	<i>B. distortus</i> - <i>G. cuneiformis</i>			Coldbeck Beds
Fern Glen		<i>Bactrognathus</i> - <i>P. communis</i>	<i>Bactrognathus</i> - <i>Ps. multistriatus</i>	Tn_3	Courceyan	Stone Gill Beds
	Meppen	<i>G. semiglaber</i> - <i>Ps. multistriatus</i>	<i>G. semiglaber</i> <i>P. comm. carina</i>			Shap Conglomerate
Chouteau		<i>S. isostriata</i> - <i>S. cooperi</i>	<i>S. cooperi hassi</i> <i>G. punctatus</i> <i>G. delicatus</i> <i>S. cooperi cooperi</i>	Tn_2		Pinskey Gill Beds

TEXT-FIG. 7. Correlation of the Ravenstonedale conodont and sedimentary sequence with the Belgian Assises and the North American conodont sequences.

Taphrognathus sp. also occurs in the Lower Windsor Group of Nova Scotia (von Bitter 1976) although its occurrence with *Cavusgnathus* spp. probably indicates a younger age than the *Taphrognathus* Zone of Ravenstonedale.

Cloghergnathus Zone

This assemblage zone occurs in the Scandal Beck Limestone and the *Michelinia grandis* Beds. Every sample has yielded a fauna although none of them are abundant.

The characteristic species present are *Cloghergnathus carinatus*, *Spathognathodus scitulus*, *Apatognathus asymmetricus*, and *A. scandalensis*. The appearance of *Magnilaterella robusta* and *Neoprioniodus singularis* at the base of the *Michelinia grandis* Beds allows the subdivision of this zone into two subzones: a lower one with *Cloghergnathus*, *Apatognathus asymmetricus*, and *A. scandalensis*, and an upper one with *Neoprioniodus singularis* and *Magnilaterella robusta*. Both of the latter species are known to have longer ranges elsewhere and their appearance within the zone may well be due to environmental change at the base of the *Michelinia grandis* Beds. The fauna of the zone is not distinctive and is merely an interregnum between the disappearance of *Taphrognathus* and the appearance of *Cavusgnathus*.

This interval compares closely to the *Taphrognathus varians*-*Apatognathus* interval in the Upper Mississippi Valley (Collinson *et al.* 1972) which occupies the Warsaw, Salem, and lower St. Louis Formations. In Ireland (Austin and Mitchell 1975) there is a broad zone between the top of the Lower Carboniferous Shale (C₂S₁) with *T. varians*, and the upper Calp Limestone (D₁), with *Cavusgnathus* sp., of which the lower part would correspond to the *Cloghergnathus* Zone.

George *et al.* (1976) dated the Scandal Beck Limestone (Subzone A) as Chadian and the *Michelinia grandis* Beds (Subzone B) as Arundian. According to George *et al.* (1976) this part of the sequence is largely missing in the Avon Gorge or is represented by non-conodont bearing strata (Austin 1973).

Cavusgnathus Zone

The *Cavusgnathus* Zone includes the highest beds of the Ashfell Sandstone and at least the lowest beds of the Ashfell Limestone. The fauna includes *Cavusgnathus regularis* and *C. unicornis*, *Neoprioniodus scitulus*, *Spathognathodus scitulus*, *Magnilaterella robusta*, and *Apatognathus libratius*.

This fauna correlates with that of the *Apatognathus scalenus*-*Cavusgnathus* Zone of the Upper Mississippi Valley (Collinson *et al.* 1972) which occurs in the Upper St. Louis Formation. However, as Austin (in Austin and Mitchell 1975) has pointed out, there is a breccia between the Upper and Lower St. Louis Formation with some condensation of faunas. This may account for the absence of the major gap between the disappearance of *Taphrognathus* and the appearance of *Cavusgnathus* which occurs in the Ravenstonedale sequence. This zone compares well with the lower part of the *Cavusgnathus*-*Apatognathus* Zone of the Avon Gorge (Austin 1973) (text-fig. 8).

The Ashfell Sandstone is included in the upper part of the Arundian and the Ashfell Limestone in the Holkerian by George *et al.* (1976).

Influence of environment on the conodont faunas

The influence of the depositional environment on the conodont animal in the Palaeozoic generally is readily apparent from a perusal of the symposium volume on conodont palaeoecology (Barnes 1976), and in the Lower Carboniferous in particular from the work of Austin (1976) and von Bitter (1976). There is a clear distinction between extremely shallow-water faunas seen in the Windsor Group of Nova Scotia (Globensky 1967; von Bitter 1976) and Ravenstonedale and the basinal faunas of the same age in Spain (Higgins and Wagner Gentis, in press) and in Germany (Bischoff 1957; Voges 1959). Other faunas show mixing of both shallow-water and basinal types, and Austin (1976) has attempted to show typical associations of this type. Although these differences are normally ascribed to a depth control on the conodont animal, there may be also an element of provincialism as suggested by Austin (1976), for the type of fauna seen in Ravenstonedale appears to have a restricted geographical distribution. In view of the growing evidence of environmental control of the conodont animal it is important to know whether the faunal changes in the Ravenstonedale sequence reflect evolutionary or environmental changes, or both.

Clydagnathus, occurring in dolomites and dolomitic limestones in Pinsky Gill is, according to Austin (1976), found in dolomites and oolites in littoral/deltaic and offshore neritic facies only,

STAGES George et al 1976	AVON GORGE		RAVENSTONEDALE conodont zones this paper	
	George et al 1976 Kellaway & Welch 1955	Rhodes, Austin & Druce 1969 Austin 1973		
Holkерian	Upper Clifton Down Limestone	<i>Cavusgnathus</i> - <i>Apatognathus</i>	<i>Cavusgnathus</i>	
Arundian	Lower Clifton Down Limestone	<i>Cavusgnathus</i> - <i>Apatognathus</i>	<i>Cloghergnathus</i>	B
	Upper Clifton Down Mudstone Goblin Coombe Oolite	no conodonts		
Chadian	Lower Clifton Down Mudstone	no conodonts	A	
	Gully Oolite Sub-Oolite Bed	<i>Mestognathus beckmanni</i> - <i>Polygnathus bischoffi</i>		
			<i>Taphrognathus</i>	
Courceyan	Black Rock Limestone	<i>G. antetexanus</i> <i>P. lacinatus</i>	Found A	
		<i>P. lacinatus</i> - <i>Ps. longiposticus</i>		
		<i>Bispathodus costatus costatus</i> - <i>G. delicatus</i>		
	Lower Limestone Shale	poor exposure <i>S. cf. robustus</i> <i>B. aculeatus</i>		
		<i>Siphonadella</i> - <i>P. inornatus</i>		
	Shirehampton Beds	<i>Pa. variabilis</i> - <i>P. inornatus</i>		

TEXT-FIG. 8. Comparison of the conodont zonation of Ravenstonedale with that of the Avon Gorge.

and is typically supratidal. Sandberg (1976), in his study of late Devonian biofacies, concluded that *Clydagnathus* is abundant in offshore banks and lagoons of shallow brackish to normally saline banks commonly occurring with algae.

Taphrognathus, according to Austin has a similar distribution to that of *Clydagnathus*, and von Bitter (1976) came to a similar conclusion in relating *Taphrognathus* to his Biofacies II which occurred in inner shelf and reefoid environments.

Apatognathus and *Spathognathodus scitulus* generally occur together and were suggested by Austin (1976) to be an association which occurred in the littoral/delta front, offshore neritic, and back reef lagoonal facies. Von Bitter grouped these two with his Biofacies II association.

Cavusgnathus has a similar shallow-water origin to *Taphrognathus* according to Austin (1976), von Bitter (1972, 1976), and Merrill and Martin (1976).

Cloghergnathus is a relatively new genus and its distribution is poorly known, but it does occur

in the Windsor Group of Nova Scotia (Globensky 1967; von Bitter 1976) where it would probably be placed in von Bitter's biofacies II, and it also occurs in Ireland (Austin and Mitchell 1975) where it occurs in association with *Taphrognathus*.

The majority of the platform conodonts in these faunas are asymmetric: *Clydagnathus unicornis* and all species of *Cavusgnathus* are right-sided whereas *Cloghergnathus carinatus* is both left and right sided and *Taphrognathus varians* often shows a tendency towards asymmetry. The asymmetry appears to be associated with shallow-water environments, but is not restricted to these environments. *Cavusgnathus*, for example, may occur in basinal environments (Higgins 1975), and so may *Apatognathus* but in small numbers only. They are only dominant in shallow-water faunas. Similarly, the basinal faunas of this age, dominated by the symmetrical or highly ornamented platform elements, may occur on the margins of the shallow-water zones mixed with asymmetric elements. Von Bitter recorded the presence of simple gnathodids in his biofacies II, and more complex gnathodids occur with *cavusgnathids* and *apatognathids* in his deep-water biofacies III. In the Ravenstonedale sequence such mixing occurs rarely, indicating the extreme shallowness of the water. *Neoprioniodus singularis*, which is a common basinal species, occurs as an uncommon component of the *Michelinia grandis* Beds but its origin is known to be earlier in basinal sequences and it must be regarded as a deeper-water immigrant into a dominantly shallow-water environment.

Thus *Clydagnathus*, *Cloghergnathus*, *Taphrognathus*, *Cavusgnathus*, and *Apatognathus* are environmentally controlled to a high degree, occurring typically in littoral and lagoonal facies but ranging into offshore infratidal facies. The faunas in which they occur are restricted in both variety and abundance. Their persistent occurrence throughout the Ravenstonedale sequence is a reflection of the persistence of this facies in the area, and has enabled us to study the development of these unusual faunas through a long sequence. The proposed zones, although fundamentally environmentally controlled, are of biostratigraphic usage within this type of environment.

Neoprioniodus singularis, on the other hand, is clearly of only local value as a stratigraphic marker and merely reflects the major transgression which occurred at the base of the *Michelinia grandis* Beds (see also Leeder in discussion of George 1978) and brought with it immigrant faunas into the area.

In broad outline the changes in the conodont faunas occur both at stage boundaries and at the cycle boundaries of Ramsbottom (1973, 1977), although the two do not exactly coincide. The boundary between the *Taphrognathus-Cloghergnathus* Zones is coincident with the algal horizon at the top of the Coldbeck Beds which, according to Ramsbottom (1973, 1977), is the boundary between two cycles. Similarly the boundary between Subzones A and B of the *Cloghergnathus* Zone coincides with the Chadian-Arundian boundary although the exact horizon of the boundary is thought to be unexposed (George *et al.* 1976). The beginning of the *Cavusgnathus* Zone coincides with the appearance of the first limestone above the sandstone beds of the Ashfell Sandstone. These occur in a few metres of shales immediately below the base of the Ashfell Limestone which is taken as the boundary between the Arundian and Holkerian Stages, and the boundary between cycles 3 and 4 of Ramsbottom (1973).

With the exception of the Subzone B fauna, all the conodont faunas are of a shallow-water type and they occur throughout the cycles in the Chadian, through the lower part of the Arundian, and reappear at the top of the Arundian. The general distribution of the faunas supports the attribution of the beds to the stages of George *et al.* (1976), but the similarity between the faunas is probably due to the position of the Ravenstonedale area during Lower Carboniferous times at the head of a shallow gulf where a change of sea level to bring in sandstone or algal horizons led to the absence of conodonts rather than a change in the type of fauna.

SYSTEMATIC DESCRIPTIONS

All type and figured material has been lodged in the micropalaeontological collection, Department of Geology, University of Sheffield.

Genus *Apatognathus* Branson and Mehl

Type species. Apatognathus varians Branson and Mehl, 1934

Apatognathus asymmetricus sp. nov.

Plate 19, figs. 7, 9

Holotype. Pl. 19, fig. 7. R21.

Horizon. Scandal Beck Limestone, sample SB9.

Diagnosis. Anterior process, laterally thickened, half the height of the posterior process which is thin. Denticles on posterior process fused and twice the height of those on the anterior process.

Description. Processes unequal, diverging at about 40°. Strongly inwardly curved. Anterior process low, laterally thickened with a shelf on the upper edge, and maintaining its height to the extremity. Up to ten denticles on the oral surface whose inclination increases towards the cusp. The denticles are small, laterally compressed, and are incurved. They are discrete for about half their length.

Posterior process thin, but high, up to twice the height of the anterior process and the inner face is strongly convex. The denticles are twice as high as those of the anterior process and are fused for most of their length. They are strongly laterally compressed and decrease in height towards the extremity of the process. The denticles are slightly incurved.

Cusp is twice the height and width of the posterior bar denticles. The adjacent posterior bar denticle is fused to its posterior edge, but it is largely free on its anterior edge due to the small size of the anterior process denticles.

The cavity is triangular and is situated on the inner face of unit below the cusp. The processes are grooved on the aboral side.

Comparison. This species most closely resembles *Apatognathus cuspidatus* from which it differs in lacking lateral thickening on the posterior process and having more strongly fused denticles. It differs from *A. scandalensis* in having lateral thickening on the anterior process.

Apatognathus libratus Varker

Plate 19, fig. 12

1967 *Apatognathus? libratus* Varker pp. 134, 135, pl. 18 figs. 3, 6, 8, 9, 12, 13.

Remarks. This is an extremely large specimen, but its major characteristics conform to the diagnosis of *Apatognathus libratus*. The main difference lies in the width of the process beneath the cusp which is twice as broad as in other figured specimens of this species.

Apatognathus scandalensis sp. nov.

Plate 19, fig. 10

Holotype. Pl. 19, fig. 10, R18.

Horizon. Scandal Beck Limestone, sample SB8.

Diagnosis. A wide angled, almost symmetric, *Apatognathus* with thin processes and denticles on the anterior process which are highest near, but not at, the cusp. The denticles on the anterior process are twice the height of those on the posterior process.

Description. The processes diverge at about 50° and are strongly inwardly curved. The unit is slender and thickening of the processes only occurs close to the cusp, where a slight shelf is formed.

The anterior limb is slightly longer than the posterior and is strongly curved inwardly. It is higher than the posterior limb and bears up to thirteen laterally compressed denticles which rise to a point about one-third from the cusp. The denticles are sharply pointed and are flatter on the outer than the inner side and are discrete for more than half their length. The posterior process is about two-thirds the length of the anterior process and is inwardly curved about the same amount. Only slight thickening occurs near the cusp. Up to ten denticles occur on its oral surface and these are only half the height of the largest anterior process denticles and are subequal.

The cusp is twice the height and width of the largest denticle on the processes, and is laterally compressed more strongly on the outer than the inner side. It is discrete for more than half its length and is sharply pointed. It is slightly curved inwards.

A shallow triangular pit occurs at the base of the cusp and is situated on the inner face rather than aborally. It is continued along the processes as barely discernible grooves.

Comparison. *Apatognathus scandalensis* most closely resembles *A. cuspidatus* but differs in having a less strongly inclined and a smaller cusp and a larger angle between the processes.

Genus *Cavusgnathus* Harris and Hollingworth, 1933

Type species. *Cavusgnathus altus* Harris and Hollingworth, 1933

Cavusgnathus regularis Youngquist and Miller

Plate 18, figs. 12, 13

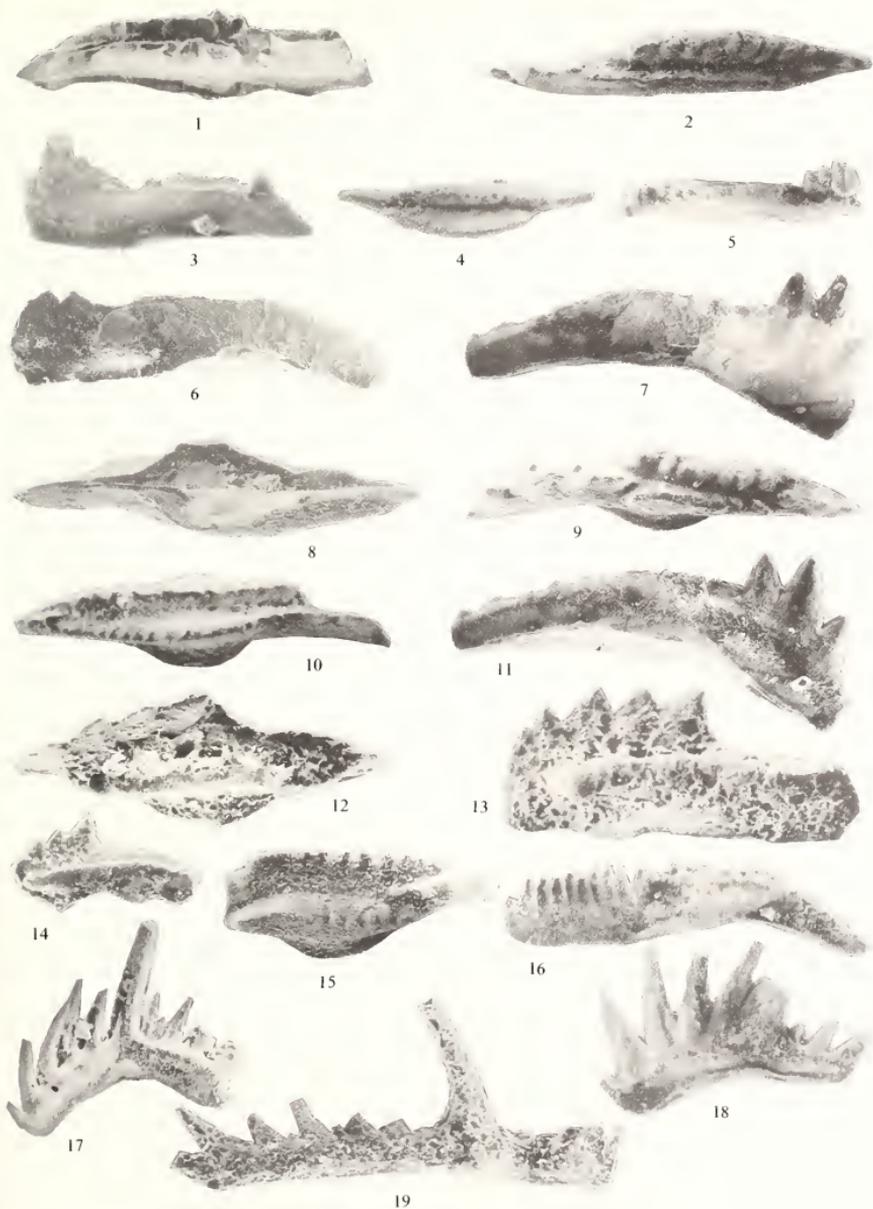
1949 *Cavusgnathus regularis* Youngquist and Miller, p. 169, pl. 101, figs. 24, 25.

Remarks. The generally short and compact form and the regular denticulation of the blade of this species are present in the Ravenstonedale specimens, but there are some differences from previously described examples. The principal difference is the length of the fixed blade which extends up to half the length of the platform and is larger than that normally found on specimens of this species.

EXPLANATION OF PLATE 18

All figures × 60

- Figs. 1-11. *Cloghergnathus carinatus*. P. element. 1, oral view of specimen from the Stone Gill Beds, sample SG19, specimen R29, transitional to *Taphrognathus varians*. 2, 7, oral and outer lateral views of holotype, specimen from the Scandal Beck Limestone, sample SB2, specimen R30. 3, inner lateral view of a specimen from the Stone Gill Beds, sample SG19, specimen R32. 4, oral view of a young specimen from the Coldbeck Beds, sample SG32, specimen R31. 5, outer lateral view of a young specimen from the *Michelinia grandis* Beds, sample MB10, specimen R35. 6, 10, outer lateral and oral views of a specimen from the Scandal Beck Limestone, sample SB9, specimen R33. 8, 9, 11, aboral, outer lateral and oral views of a specimen from the Coldbeck Beds, sample SG32, specimen R34, specimen transitional to *Taphrognathus varians*.
- Figs. 12, 13. *Cavusgnathus regularis*. Oral and inner lateral views of a specimen from the Ashfell Sandstone, sample AS1, specimen R36.
- Fig. 14. *Cavusgnathus unicornis*. Inner lateral view of a specimen from the Ashfell Sandstone, sample AS1, specimen R38.
- Figs. 15, 16. *Taphrognathus varians*. Oral and inner lateral views of specimens from the Stone Gill Beds, sample SG19, specimens R37, R39.
- Fig. 17. *Lonchodina* sp. Inner lateral view of specimens from the Coldbeck Beds, sample SG33, specimen R27.
- Fig. 18. O element of *Cloghergnathus carinatus*. Inner lateral view of a specimen from the Coldbeck Beds, sample SG32, specimen R14.
- Fig. 19. A₁ element of *Cloghergnathus carinatus*. Inner lateral view of a specimen from the Coldbeck Beds, sample SG31, specimen R3.



HIGGINS and VARKAR, Lower Carboniferous conodonts

Cavusgnathus unicornis Youngquist and Miller

Plate 18, fig. 14

1949 *Cavusgnathus unicornis* Youngquist and Miller, p. 619, pl. 101, figs. 18-23.

Remarks. The median carina developed only in the posterior part of the platform is prominent only in large specimens and is often completely absent in small specimens.

Genus *Cloghergnathus* Austin and Mitchell

Type species. *Cloghergnathus globenskii* Austin and Mitchell, 1975.

Remarks. *Cloghergnathus* was named by Austin (in Austin and Mitchell 1975) for specimens with a lateral blade which does not extend on to the platform as a high, crested structure as in *Cavusgnathus*. The blade may occupy a sub-median position whilst remaining connected to one of the platform sides and such forms are probably transitional to *Taphrognathus*. Its characteristics are those of *Clydagnathus* Rhodes, Austin, and Druce an early Courceyan genus but a considerable stratigraphic gap occurs between the last occurrence of *Clydagnathus* and the first appearance of *Cloghergnathus* in the Chadian.

Cloghergnathus carinatus sp. nov.

P element

Plate 18, figs. 1-11

Holotype. Pl. 18, figs. 2, 7. R30.

Horizon. Scandal Beck Limestone, sample SB 2.

Diagnosis. A right- and left-sided element with the anterior blade developed on the inner side of the unit. A central trough runs the length of the platform but is occupied by a short carina in the posterior quarter. The blade is short, one-quarter to one-third the length of the platform, and does not extend on to the platform. It is extended above the platform and is convexly curved. The unit is arched.

Description. The anterior blade consists of up to five denticles of which the largest is in the centre giving the blade a convex outline. The denticles are free for about half their length. The platform is straight to strongly curved and bears a deep median trough which is occupied by a carina for up to the last third of the platform. The carina is very prominent in small specimens. The inner parapet is curved and commonly does not reach the posterior end of the unit and is continued anteriorly as the blade, although the curvature of some specimens is difficult to determine because the blade may be outwardly curved. In a few specimens the blade is slightly offset and, whilst it originates from the inner side of the platform, it occupies a sub-central position on both right and left forms. The oral surface of the platform is covered by nodes or transverse ridges. The platform is widest near midlength and commonly the inner side is wider than the outer. The unit is arched in lateral view both the oral and aboral surfaces of the platform being curved and the aboral surface of the blade being strongly downturned. The curvature is less marked in young specimens which may be almost straight. The cavity occupies the whole of the aboral surface of the platform and is widest slightly anterior to its mid-point tapering to both the anterior and the posterior.

Comparisons. *Cloghergnathus carinatus* differs from *C. globenskii* Austin and Mitchell by its arched aboral and oral surfaces, its convex blade, which originates from the inner side, and the presence of the posterior carina. *C. rhodesi* is left-sided, does not possess a carina, and its blade shape is unknown.

Remarks. There is a tendency for the blade of *C. carinatus* to be median in position and it may include some of the *Taphrognathus-Cavusgnathus* transition forms of Rexroad and Collinson (1963; especially fig. 24, p. 111). Austin (in Austin and Mitchell 1975) has argued that *Cloghergnathus* is

not intermediate between *Taphrognathus* and *Cavusgnathus* but is an offshoot of the former genus in which the blade, although lateral, does not extend on to the platform. In this respect *Cloghergnathus* mirrors *Adetognathus* which is probably a younger homeomorph, or which may prove to be the same genus when its full range is known. All figured specimens of *Cloghergnathus* have a low blade or one which rises gradually as in *C. carinatus* none of them have the typical cavusgnathoid blade. In addition, all known species of *Cloghergnathus* are either right- and left-sided or only left-sided, whereas *Cavusgnathus* species are all right-sided. *C. carinatus* is also similar to *Clydagnathus darensis* but differs in having a larger basal cavity.

Cloghergnathus non-platform Elements

O element

Plate 18, fig. 18; Plate 19, fig. 4

1957 *Ozarkodina compressa* Rexroad, p. 36, pl. 2, figs. 1, 2.

Remarks. The Ravenstonedale specimens have the prominent apical denticle of the paratype but have a smaller number of denticles on the processes than is usual in this element. However, it is thought to fall within the variability of the element.

N element

Plate 19, fig. 18

1941 *Prioniodus varians* Branson and Mehl, p. 174, pl. 5, figs. 7, 8.

1957 *Prioniodina varians* (Branson and Mehl), Bischoff, p. 49, pl. 5, fig. 35.

1957 *Neoprioniodus varians* (Branson and Mehl), Rexroad, p. 35, pl. 2, fig. 10.

Remarks. Von Bitter (1976) named *Neoprioniodus camurus* Rexroad as the Ne element in his multi-element reconstruction of *Cavusgnathus windsorensis*. He also figured a similar form in his reconstruction of the non-P elements of *Cavusgnathus* sp. from the Pennsylvanian (1972, pl. 9, fig. 5). Baesemann (1973) figured a similar neoprioniodontid in his reconstruction of *Adetognathus* (pl. 2, figs. 26, 35). No form comparable to *N. camurus* occurs in the Ravenstonedale samples where the only neoprioniodontids are *N. varians*, *N. acampylus*, and *N. scitulus*.

A₁ element

Plate 18, fig. 19; Plate 19, fig. 20

1953 *Hindeodella ensis* Hass, p. 81, pl. 16, figs. 19-21.

1960 *Hindeodella tenuis* Clarke, p. 8, pl. 1, figs. 10, 11.

Remarks. There are two variants in this element. One is typified by *Hindeodella tenuis* and *H. ensis* and is the more common of the two. This has a long posterior process with alternating denticles and a long, often inwardly curved anterior bar commonly with non-alternating denticles which are as large as the large posterior bar denticles. The other variant is shorter and arched with a cusp which is as long as the posterior process, and has non-alternating denticles of which the posterior process denticles increase in size posteriorly.

A₃ element

Plate 19, figs. 5, 6, 8

Description. A robust unit consisting of two massive lateral processes, a large cusp, and a slender posterior process. The cusp is large, slightly curved posteriorly, and has a triangular cross-section with sharp posterior and lateral edges. Its surface is covered with fine discontinuous striations. The posterior bar is incomplete, appears to be narrow, and has an oval cross-section.

The lateral processes are massive, bar-like with a square cross-section, and almost in the same plane. They

are as long as the main cusp and slightly inclined downwards. The denticles on the oral surface, up to five in number, are large, increasing in size towards the extremities of the processes, and are flattened in an antero-posterior direction. The largest denticle is approximately half the size of the cusp.

The aboral side of the unit is grooved, and the grooves meet forming a small triangular pit beneath the cusp.

Remarks. This form most closely resembles *Hibbardella ortha* Rexroad, the primary difference being the shallow angle between the processes. It is also much more massive than *H. ortha* but this is a characteristic shared by specimens of all species in the Ravenstonedale faunas and is most likely due to the shallow-water environments in which the fauna occurs.

Genus *Magnilaterella* Rexroad and Collinson

Type species. *Magnilaterella robusta* Rexroad and Collinson 1963.

Magnilaterella robusta Rexroad and Collinson

1940 *Lonchodina* sp. Branson and Mehl, p. 171, pl. 5, fig. 10 only.

1956 *Metalonchodina?* sp. Elias p. 124, pl. 4, fig. 3.

1963 *Magnilaterella robusta* Rexroad and Collinson, pp. 14-17, pl. 1, figs. 4, 5, 9.

Remarks. Typically *Magnilaterella robusta* has a prominent bevel on the inner side of the lateral process. However, Rexroad and Collinson (1965) did include specimens without the bevel which have the characteristic denticulation on the lateral process.

At the present time the multi-element species to which *M. robusta* belongs is unknown.

EXPLANATION OF PLATE 19

All figures $\times 60$

Figs. 1-3. *Lonchodina* sp. Inner lateral views of specimens from the Coldbeck Beds. Fig. 1 from sample SG33, specimen R1; fig. 2 from sample SG31, specimen R2; fig. 3 from sample SG33, specimen R40.

Fig. 4. O element of *Cloghergnathus carinatus*. Inner lateral view of a specimen from the Coldbeck Beds, sample 29, specimen R26.

Figs. 5, 6, 8. A₃ element of *Cloghergnathus carinatus*. Posterior views of specimens from the Coldbeck Beds, sample 29, specimens R9-11.

Figs. 7, 9. *Apatognathus asymmetricus*. 7, inner lateral view of holotype from the Scandal Beck Limestone, sample SB9, specimen R21. 9, inner lateral view of a specimen from the Scandal Beck Limestone, sample SB7, specimen R20.

Fig. 10. *Apatognathus scandalensis*. Inner lateral view of holotype from the Scandal Beck Limestone, sample SB8, specimen R18.

Figs. 11, 13, 19. *Apatognathus cuspidatus*. Inner lateral views of specimens from the Scandal Beck Limestone, fig. 11 (SB7), specimen R16 and fig. 19 (SB2), specimen R17, and Coldbeck Beds sample SG33, specimen R15.

Fig. 12. *Apatognathus libratus*. Inner lateral view of a specimen from the Ashfell Sandstone, sample AS1, specimen R19.

Fig. 14. *Spathognathodus scitulus*. Outer lateral view of a specimen from the Ashfell Sandstone, sample AS1, specimen R5.

Fig. 15. *Neoprioniodus singularis*. Inner lateral view of a specimen from the *Michelinia grandis* Beds, sample MB2, specimen R8.

Fig. 16. *Neoprioniodus* cf. *acampylus*. Inner lateral view of a specimen from the *Michelinia grandis* Beds, sample MB2, specimen R13.

Fig. 17. *Neoprioniodus* sp. Inner lateral view of a specimen from the Coldbeck Beds, sample SG29, specimen R7.

Fig. 18. N element of *Cloghergnathus carinatus*. Inner lateral view of a specimen from the Scandal Beck Limestone, sample SB9, specimen R12.

Fig. 20. A₁ element of *Cloghergnathus carinatus*. Inner lateral view of a specimen from the Coldbeck Beds, sample SG29, specimen R24.



HIGGINS and VARKAR, Lower Carboniferous conodonts

Genus *Neoprioniodus* Rhodes and Muller

Type species: *Prioniodus conjunctus* Gunnell 1931.

Neoprioniodus cf. *acampylus* Rexroad and Collinson

Plate 19, fig. 16

1965 *Neoprioniodus acampylus* Rexroad and Collinson, p. 11, pl. 1, figs. 25-27.

1968 *Neoprioniodus acampylus* Rexroad and Collinson, Thompson and Goebel, p. 37, pl. 3, fig. 2.

Remarks. This specimen conforms to the general outline and description of *Neoprioniodus acampylus* but differs in possessing a more robust posterior process which is laterally thickened, and it lacks the flaring inner lip of that species. It differs from *N. camurus* Rexroad in being unbowed. This species has been recorded only from the Warsaw and Salem Formations of the Upper Mississippi Valley (Rexroad and Collinson 1965) and the Meramacian of Indiana (Thompson and Goebel 1968). It occurs at a similar position in Ravenstonedale being confined to the *Michelinia grandis* Beds.

Neoprioniodus sp.

Plate 19, fig. 17

Description. Robust unit consisting of cusp and a short posterior bar. The posterior bar is laterally thickened, approximately square in cross-section, and is about half the length of the cusp, but is not complete. Its oral surface bears four denticles which are discrete for more than half their length and are laterally compressed but more strongly so on the inner side. They are incurved and of varying length, the highest being the penultimate one on the cusp. The bar is straight and is bevelled on the inner face.

The cusp is four times the length of the posterior process denticles and is strongly incurved and slightly curved posteriorly. Its outer side is convex but the inner side has a lip along both margins which continues down to the anticusp. The anticusp is short and appears to be pointed but the tip is broken. The aboral edge of the cusp is strongly bevelled but the bevelling does not continue down the anticusp.

The cavity is elliptical, small, and is continued as a faint groove beneath the posterior process.

Genus *Lonchodina* Ulrich and Bassler

Type species: *Lonchodina typicalis* Ulrich and Bassler 1926.

Lonchodina sp.

Plate 18, fig. 17; Plate 19, figs. 1-3

Description. The unit includes both right and left forms; it is bowed. The cusp is large, laterally flattened with sharp edges, strongly inwardly curved, and posteriorly inclined and curved. Typically the cusp narrows gently towards the oral tip but in some specimens the base is very wide. The processes are the same height and length and both are laterally thickened but the height is twice the thickness. The posterior process is almost at right angles to the cusp and its oral surface bears three to six laterally compressed denticles of variable size, but the two penultimate ones are the largest and one of them may be as large as the cusp. The denticles are inwardly curved and are in the same plane as the cusp, but are more strongly posteriorly inclined. The anterior process bears three to five denticles on its oral surface which are subequal in size and half the size of the cusp. They are more founded than the posterior process denticles and are posteriorly and inwardly curved. Both processes are strongly bevelled and striated on the inner side and inclined inwardly on the upper side, giving the processes a triangular cross-section. The inner bevelled side is markedly striated on the lower half. There is a small lip over the basal cavity. The aboral side is narrow with a small triangular pit beneath the cusp and a narrow groove beneath the processes.

Remarks. The multi-element apparatus to which this distinctive form belongs is unknown.

Genus *Spathognathus* Branson and Mehl

Type species: *Spathodus primus* Branson and Mehl 1941.

Spathognathodus scitulus (Hinde)

Plate 19, fig. 14

1900 *Polygnathus scitulus* Hinde (part), p. 343, pl. 9, figs. 9, 11 only.

1949 *Spathognathodus scitulus* (Hinde) Youngquist and Miller, p. 622, pl. 101, fig. 4.

Remarks. Austin and Rhodes recorded a fused cluster consisting of one specimen of *Spathognathodus scitulus* and four specimens of *Apatognathus* sp. from the Lower Carboniferous of the Avon Gorge. Undoubtedly the forms have a similar range and commonly occur in the same samples. Baesemann (1973) described a multi-element species, *Ozarkodina minuta* which includes a P element, *S. minutus* which is very similar to *S. scitulus*. Similarly, von Bitter (1976) suggested that *S. cristulus*, also morphologically similar to *S. scitulus*, could be the P element of his *Ellisonia* sp. apparatus. However, neither Baesemann's nor von Bitter's accompanying element are present in the Ravenstonedale sequence, and the Austin and Rhodes model may be the more likely for the *S. scitulus* apparatus.

Genus *Taphrognathus* Branson and Mehl

Type species: Taphrognathus varians Branson and Mehl 1941.

Taphrognathus varians Branson and Mehl

Plate 18, figs. 15, 16

1941 *Taphrognathus varians* Branson and Mehl p. 182, p. 6, figs. 27-33, 35-40.

Remarks. A short carina occurs in the posterior quarter of the median sulcus which occurs on a few but not the majority of previously figured specimens of this species. At the present time such specimens are included within *Taphrognathus varians*.

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SOMASTEROIDEA, ASTEROIDEA, AND THE AFFINITIES OF *LUIDIA* (*PLATASTERIAS*) *LATIRADIATA*

by DANIEL B. BLAKE

ABSTRACT. Important changes in the taxonomy and phylogenetic interpretation of stellate echinoderms were proposed during the 1960s by H. B. Fell; certain of this author's ideas are re-evaluated. Fell argued that the extant west American sea star *Platasterias latiradiata* Gray is a surviving member of the otherwise Palaeozoic Somasteroidea. The extant family Luidiidae was considered primitive among true asteroids and it was included with the Palaeozoic family Palasteriscidae in the order Platysterida. The skeletal arrangement of *Platasterias* and *Luidia* was interpreted as having been derived with relatively limited change from a currently unknown Cambrian crinoid ancestry. It is argued here that *Platasterias* is not a somasteroid but a subgenus of *Luidia*, and the Luidiidae is returned to the large living order Paxillosida. The origin of the morphology of *Luidia*, including *Platasterias*, is related to sea star behaviour and habitat rather than a crinoid ancestry. The Luidiidae is not considered to be of major importance in delineating asteroid phylogeny.

SEVERAL papers published during the 1960s by H. B. Fell (1962*a, b*; 1963 *a-c*; 1967) developed a series of stimulating and intriguing hypotheses on stellate echinoderm phylogeny that significantly altered viewpoints of the history of these organisms. Certain of these ideas are reconsidered in this paper.

Prior to Fell's work, three classes or subclasses were recognized among stellate echinoderms: the Asteroidea (sea stars or starfish), Ophiuroidea (brittle stars or serpent stars and basket stars), and the Somasteroidea, the last a taxon of primitive echinoderms then considered to be restricted to lower and middle Palaeozoic rocks. Relationships among the groups were unclear. Because of disparate early development, many biologists (e.g. Hyman 1955) believed the ophiuroids and asteroids had independent origins, and were only secondarily similar in certain features. These workers found (and still find) it undesirable to combine ophiuroids and asteroids in formal higher taxa below the phylum level, e.g. the class Stelleroidea and subphylum Asterozoa *sensu* Spencer and Wright 1966.

Other workers, stressing the fossil record, were of the opinion that the two living groups shared a common origin, and that their ancestors or near ancestors could be recognized among the fossil somasteroids. Further, Fell (e.g. 1948) considered that the developmental arguments for separating the asteroids from ophiuroids were unconvincing. These workers tend to believe that the two should be combined in a phylogenetically unified higher taxon below the phylum level (e.g. Spencer and Wright 1966).

In his work on phylogeny, Fell developed a number of interrelated topics: (1) the nature of the Somasteroidea; (2) the relationships among the extant sea stars *Platasterias*, *Luidia*, the remaining asteroids and the Palaeozoic Somasteroidea; (3) the relationship between the extant ophiuroid *Ophiocanops* and the Palaeozoic ophiuroids; and (4) the phylogenetic relationships among somasteroids, asteroids, and ophiuroids. Fell proposed a hypothesis for the origins of stelleroids from an inferred crinoid ancestry, suggested a sequence of evolutionary events leading from the Somasteroidea to the Ophiuroidea and Asteroidea, and transferred a number of living taxa to groups previously considered to be of exclusively Palaeozoic occurrence. These included the family Luidiidae from the Paxillosida to the Platysterida, both within the Asteroidea; the genus

Platasterias from the Asterozoa (Paxillosida) to the Somasteroidea; and the ophiuroid *Ophiocanops fugiens* to the Oegophiurida from the Phrynophiurida. Fell's re-evaluations were enthusiastically received by some workers, but a number of his ideas were challenged, including the arguments for the derivation of asterozoans from crinoids, by Philip (1965), answered by Fell (1965); the affinities of *Ophiocanops*, by Hotchkiss (1977); and the affinities of *Platasterias* by several workers (e.g. Madsen 1966; Blake 1967, 1972, 1973; Pearse 1969; Algor 1971).

A survey of textbooks and papers published during the later 1960s and 1970s shows a continuing uncertainty as to how *Platasterias latiradiata* should be treated, yet the question of affinities of the species is an important one. Not only is a living fossil intriguing simply as a survivor, but its existence raises questions on the nature of evolutionary processes. Further, once ranked as a 'living fossil', a species will become the basis for reconstruction of the biology of its presumed close fossil relatives, a fact illustrated by Fell's (1962b, p. 2) explanation of purpose for one of his papers: 'This contribution is limited to brief discussion of the major features of somasteroid anatomy, as illustrated by *Platasterias*.' *Platasterias* as a somasteroid clearly will strongly influence interpretations of stellate echinoderm biology and history.

The concern of this paper is primarily with the second of the four topics cited above, the nature of *Platasterias* and the Luidiidae. Other problems in the nature of relationships among stellate echinoderm groups are in need of restudy, but these ideas are beyond the purposes of this paper.

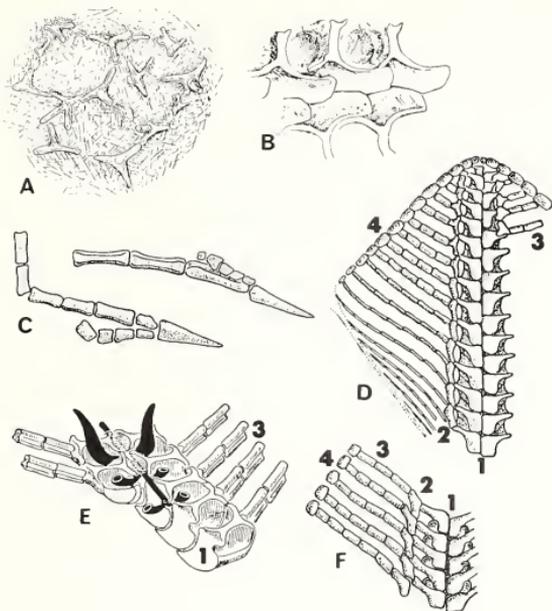
I will argue that *P. latiradiata* should be considered a subgenus of *Luidia*, itself a genus unequivocally included in the Asterozoa (rather than the Somasteroidea) by Fell (1963a). Assigning *Platasterias* as a subgenus of *Luidia* does not in itself challenge Fell's ideas on somasteroid/asteroid phylogeny; *Luidia* (including *Platasterias*) might still be the primitive extant asteroid with many features, as outlined by Fell, derived with little modification from the somasteroids. In re-evaluating the taxonomic and phylogenetic position of the monogeneric Luidiidae, I will next argue that there is no clear connection between Palaeozoic somasteroids and the luidiids (including *Platasterias*), and that the Luidiidae should be transferred from the order Platysterida to the order Paxillosida. A functional, rather than phylogenetic, hypothesis for the origin of luidiid morphology is proposed.

SOMASTEROIDEA

The concept of the Somasteroidea originated with Spencer (1951) and evolved with the work of Fell (1962a, b; 1963a-c; 1967), Spencer and Wright (1966), and McKnight (1975). In spite of this effort, the group is difficult to characterize and therefore comparisons between somasteroids and other organisms are difficult as well. Relevant fossils are in need of restudy and reillustration. I have based the following diagnosis on the literature (and not original study of the fossils), and I believe it represents the fossil somasteroids as pictured by those workers who include *Platasterias* in the taxon. In keeping with the arguments presented here, however, I have removed characters derived from *Platasterias* only. Although such a diagnosis logically follows arguments for transfer of *Platasterias*, a concept of the Somasteroidea is necessary for the comparisons that follow.

Subclass Somasteroidea Spencer, 1951

Asterozoans in which the axial skeleton consists of ambulacra in a double series, usually paired but apparently alternating in some species. Each ambulacra gives rise to a transverse series of ossicles; in apparently primitive species, these ossicles are similar and rod-like elements termed virgals, but in more advanced species the virgals are differentiated into adambulacra, marginals, and related ossicles. A permanent ambulacral furrow or groove is lacking so that the long axis of the ambulacra is approximately linear and horizontal, and the ossicles essentially lie in the plane of the remaining ossicles of the oral surface. The adambulacra (or first virgal) (different spellings of 'virgal' and its plural form have been used; I have followed Spencer and Wright 1966) generally abuts the lateral (abradial) margin of the ambulacra, or overlap is slight. In some species the ambulacra probably could be raised to form temporary ambulacral furrows. A large or small radial channel for the radial water canal is present along the oral margin of the line of juncture of pairs of ambulacra, or it is more or less enclosed by the ambulacra. The tube-feet are seated in broad basins which in some species communicate to the body cavity. Jaw ossicles are differentiated, but odontophores are lacking. Open



TEXT-FIG. 1. Morphology of the Somasteroidea, modified slightly after Spencer (1951) and Fell (1963a). A, abactinal arrangement of *Sturzaster marstoni* (Salter), morphology considered by Spencer to be close to that of *Chinianaster*; Spencer (1951, p. 95). B, ambulacrals of *Archegonaster pentagonus*; Spencer (1951, p. 104). C, metapinnules with cover plates, *Chinianaster levyi*; Fell (1963a, p. 394). D, interpretation of arm of *Ampullaster ubaghasi*, view of oral surface; Fell (1963a, p. 394). E, reconstruction of a part of the arm of *Chinianaster*, water vascular system darkened; Fell (1963a, p. 402). F, interpretation of arm, near tip, of *Villebrunaster thoralis*; Fell (1963a, p. 394). Key: 1, ambulacrals; 2, adambulacrals; 3, virgals; 4, marginals. Illustrations courtesy of H. Barraclough Fell and the Royal Society.

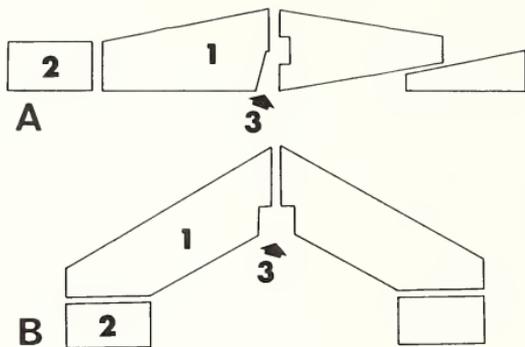
buccal slits might be present at the mouth frame in at least some species. Aboral ossicles are paxilliform, with delicate tetradiate bases. Encrusting ossicles or spinelets are present at least on some ossicles of the ventral surface. Over all, the skeleton beyond the ambulacrals is quite delicate (text-fig. 1).

Discussion. Most of these characters are also expressed among species assigned to the Asteroidea, but critical to the concept of the Somasteroidea is an ambulacral/adambulacral arrangement in which an ambulacral furrow or groove is lacking (text-fig. 2). Spencer (1951, p. 88) says in reference to somasteroids that '... these first stages show no sign of an ambulacral furrow', and Fell (1963a, p. 389) used the development of a furrow or groove as the basic character separating somasteroids from asteroids. The ambulacral groove or furrow is different from the ambulacral channel for the radial water canal; for further discussion, see under ambulacral column arrangement.

In somasteroids the abradial margin of the ambulacral either abuts the adradial side of the adambulacral (first virgal), or the ambulacral can overlap the adambulacral to a very limited extent (text-fig. 2). In his discussion of somasteroids, Fell (1963a, p. 393) says 'Each metapinnule arises from the abradial margin of one of the paired ambulacral (or brachial) elements . . .'. The long axis of the ambulacral is approximately horizontal and the basin for the tube-foot lies close to the plane of the oral surface.

In true asteroids the ambulacral rests on the aboral surface of the adambulacral, rather than laterally adjacent to it (text-fig. 2). In addition, the axis of the adradial end of the ambulacral is oblique to that of the general ambulacral/adambulacral articulation surfaces. These arrangements produce a permanent furrow with the basin for the tube-foot elevated.

McKnight (1975) argued that the lack of an odontophore is an important character unifying somasteroids. The odontophore is a small, unpaired typically T-shaped ossicle present between members of a jaw ossicle pair. It appears to brace and thus strengthen the jaw apparatus, and its phylogenetic development might reflect the changing food habits suggested by Spencer (1951), away from the small particle feeding inferred for somasteroids to the large particle feeding present in many living asteroids.



TEXT-FIG. 2. Stylized diagrams oriented transverse to arm axes, showing arrangement of 1, ambulacrals, and 2, adambulacrals in A, somasteroids (*Chinianaster* arrangement to left, *Ampullaster* to right), and B, asteroids. The overlap of the ambulacral on the adambulacral in *Ampullaster* is very small; compare to text-fig. 1D. 3, radial water channel. Based on work of Spencer (1951) and Fell (1963a), especially the latter's fig. 7, p. 395.

COMPARISONS BETWEEN *PLATASTERIAS*, FOSSIL SOMASTEROIDS AND TRUE ASTEROIDS

Platasterias is compared to fossil somasteroids and living asteroids, especially *Luidia* as traditionally recognized, in the following somewhat overlapping sequence: (1) over-all body form; (2) nature of the skeleton; (3) ambulacral column arrangement; (4) growth gradients; (5) other morphologic features; (6) feeding. Fell's view of *Platasterias* as a somasteroid was derived in large part from his evaluation of ambulacral column arrangement and growth gradients. A discussion of the taxonomic positions of *Platasterias* and *Luidia sensu* Fell therefore must wait until section 4. Each section begins with a summary of the ideas of Spencer (1951), Fell (1962a *et seq.*), and Spencer and Wright (1966) and continues with my comments. I have tried to include all major arguments on *Platasterias*, but the discussion is not comprehensive on other topics, such as the morphology

TABLE 1. Changes in the distribution of important characters in the inferred somasteroid/asteroid phylogeny, as envisaged by H. B. Fell. The diagram was prepared by the writer, based on his reading of Fell (1963a, pp. 389 ff.; 1963b) and it is intended as an aid to understanding Fell's ideas of the major events in his inferred phylogeny (represented by the sequence 1 through 6) rather than as an exact character distribution summary. Dotted lines mean a character is present in only some members of a division, and minor exceptions occur. For example, although the family is not entered separately, the Porcellanasteridae lack an anus and suctorial tube-feet, whereas other sea stars, such as certain *Astropecten* and *Asterias* species, have subpetaloid arms. Notes: (1) virgals similar in Division 1, dissimilar in Division 2; (2) development of actinals becomes stronger through the sequence; (3) no entry in Fell (1963a) for this division. The terminal is the unpaired ossicle at the distal tip of the arm.

Among somasteroids, the monogeneric Chinianasteridae was considered primitive, based largely on the presence of undifferentiated virgals and robust ambulacra, and the absence of communication pores between ambulacra for ampullae. Next in the sequence, but not separated from the Chinianasteridae in Fell 1963a, came the Villebrunasteridae, including *Villebrunaster* and *Ampullaster*. Here, virgals are differentiated and pores, inferred for internal ampullae, were present. *Platasterias* (Platasteriidae) was considered to have common features with both the Chinianasteridae and the Villebrunasteridae but appeared to be about at the villebrunasterid grade based on the inferred differentiation of the virgals, and the presence of internal ampullae (1963b, p. 144). The monogeneric Archegonasteridae, not included in the table, was considered to be an advanced somasteroid, specialized in body shape and lack of interradial slits, metapinnule reduction, and development of the robust marginals. True asteroids originated with development of a permanently erect ambulacral furrow.

SOMASTEROIDEA	Group 1								
	1. Chinianasteridae		complete transverse gradients	petaloid arms	virgals ¹				
	2. Platasteriidae							feeding fascioles	
	Group 2								
	3. Platanasteridae								
	4. Luidiidae	furrow erect			terminals	superambulacra	actinals		
ASTEROIDEA	Group 3								
	5. Astropectinidae						respiratory fascioles		
	6. Most other asteroids							non-suctorial tube feet	anus

of the fossils. Fell's (1963a, b) major ideas on somasteroid/asteroid phylogeny are summarized in Table 1.

McKnight (1975) modified the concept of the Somasteroidea and transferred five Palaeozoic genera to this taxon. His modification is included here, but I did not attempt to re-evaluate somasteroids in light of the transferred taxa because properties of these genera were not incorporated in, and do not appear to bear directly on, Fell's ideas on the position of *Platasterias* and *Luidia*.

1. Over-all body form

Spencer (1951, p. 91) described somasteroids as having a large central body in which the arms are parts of the oral surface, i.e. '... the arms are just beginning to be differentiated'. Fell (1963a) described somasteroids as extremely flattened but, more important, as asterozoans with petaloid arms. Fell (1963a, fig. 5) presented a sequence of diagrams illustrating the inferred transformation of arm shape beginning with the petaloid arm of a monoserial crinoid, and ending with the triangular

arm of the extant astropectinid *Plutonaster*. The petaloid arm of *Platasterias* was placed by Fell between the petaloid arms of a chiniansterid somasteroid and a somewhat weakly petaloid platanasterid asteroid. Petaloid arms thus were considered to be subdued in the most primitive of Asteroidea, the fossil *Platyasterida*, and they are absent from later groups.

Spencer (1951) did not consider the somasteroids to be flattened, rather he saw them as flexible, noting (p. 93): 'At one time the body is strongly compressed, at another the body of the same species is well rounded.'

Discussion. *P. latiradiata* is a relatively flat species, but such a body shape is not restricted to somasteroids, e.g. see such extremely flattened living asterinids as *Anseropoda* and *Stegnaster*.

Although the arms of *Platasterias* are strongly petaloid and the disc deeply notched interbrachially (Pl. 20, fig. 1), comparable shapes are known elsewhere, albeit more weakly developed. Examples include *Astropecten regalis* (Pl. 20, fig. 2) (Paxillosida) and *Asterias forbesi* (Forcipulatida) (Pl. 20, fig. 8). Inferomarginals in *Astropecten regalis*, like those in *Platasterias*, are transversely elongate (Blake 1973, pl. 14) and the body is flattened. These similarities among taxonomically widely separated species suggest convergence as an alternative hypothesis for origin of body shape, perhaps under conditions such as those suggested by Madsen (1966): 'I assume the petaloid arms in *Platasterias* (brought about by the transverse elongation of the adambulralia and inferomarginalia) to be secondary adjustment to a life on a shifting sandy bottom (and perhaps a primarily ciliary method of feeding).' Fell (1962a, p. 634) noted that the extreme narrowness of the ambulacral furrow in *Platasterias* is suggestive of the fossil somasteroids, although he observed that this could be secondary. Narrow furrows occur in other modern taxa, for example, the Ophidiasteridae (Valvatida) and the Echinasteridae (Spinulosida).

2. Nature of the skeleton

Spencer (1951) considered *Chinianaster* and *Villebrunaster* to be the primitive somasteroids. In these genera he recognized three types of ventral ossicles: the ambulacrals arranged in a double row, the mouth angle ossicles, and the rod-like intermarginals or virgals arranged in transverse series extending from each ambulacral ossicle. Fell used the term 'metapinnules' for the rows of virgals, after the inferred homologous pinnules of crinoids. In more advanced somasteroids the morphologically simple virgals became differentiated to form marginals, adambulacrals, and other ossicles.

EXPLANATION OF PLATE 20

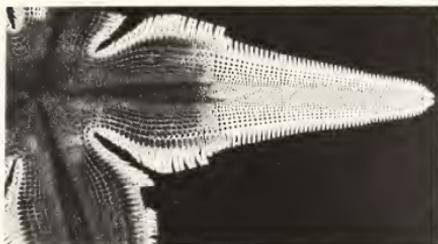
Figs. 1, 5, 6, 10, 12. *L. (Platasterias) latiradiata* (Gray). 1, over-all aboral view showing petaloid arms, alignment of abactinials, and similarity in marking to that of *L. clathrata*, see Pl. 22, $\times 1$. 5, lateral view of inferomarginal, furrow left, row of processes are articular facets linking successive inferomarginals, $\times 9$. 6, adambulacral, proximal view, furrow right; one muscle groove (upper, light arrow) and one articular facet (lower, dark arrow) marked; these and other structures correspond in positions with similar structures in *L. clathrata*, fig. 4 (see Blake 1972, 1973; Heddle 1967 for further discussion). 10, aboral view of cleared arm showing enlarged superomarginal row (arrow) arising at terminal, as in *L. clathrata*, see fig. 9, $\times 3$. 12, aboral view of uncleared arm showing abactinal ossicle and granule development, compare to *L. clathrata*, fig. 11, $\times 3$.

Fig. 2. *Astropecten regalis* Gray. Oral view showing petaloid arms and well defined marginal spines (arrow), $\times 1$.

Figs. 3, 4, 9, 11. *Luidia clathrata* (Say). 3, lateral view of inferomarginal, furrow left, $\times 9$. 4, adambulacral, inclined proximal view, furrow right, see discussion for fig. 6, above, $\times 9$. 9, inclined aboral view of cleared arm, see discussion for fig. 10, above, $\times 3$. 11, aboral view of uncleared arm, see discussion for fig. 12, above, $\times 3$.

Fig. 7. *Luidia neozelanica* Mortensen. Lateral view of inferomarginal, compare with figs. 3, 6; note outline and lack of articular facet row in this species; see text for further discussion, $\times 9$.

Fig. 8. *Asterias* sp. Aboral view showing petaloid arms in which an interbrachial notch (arrow) nearly reaches the madreporite, $\times \frac{1}{2}$.



1



2



3



4



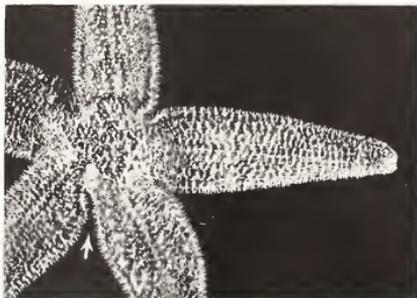
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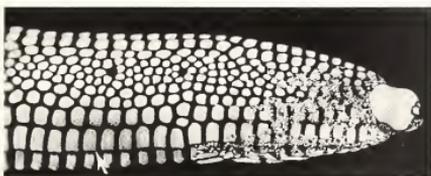
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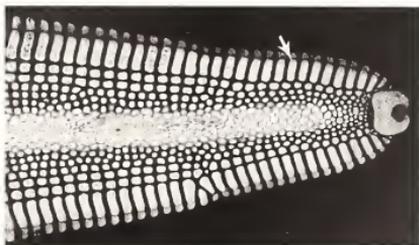
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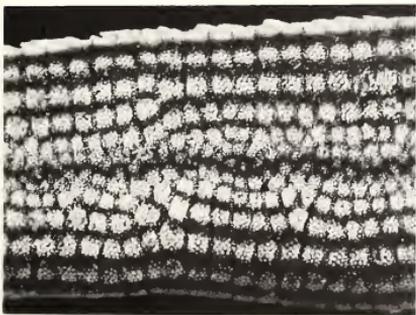
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9



10



11



12

The change in terminology marks this differentiation. Some virgals were partially (Archegonasteridae) or completely lost (Archophiactinidae) (Spencer 1951).

Spencer (1951) did not describe marginals in *Villebrunaster* from his relatively incomplete material, but Fell (1963*b*, p. 144) pointed out that these ossicles can be recognized in more complete specimens. Fell (1962*b*, p. 66; 1963*a*, p. 396) further noted that there are no adambulacrals, superambulacrals, or inferomarginals in *Chinianaster*. The metapinnules of *Chinianaster* terminate in a free radiole, as in *Villebrunaster* (Fell 1962*b*, p. 16). These patterns are important in interpreting *Chinianaster* as the primitive somasteroid, and *Villebrunaster* as a second step in somasteroid evolution.

The ambulacrals of somasteroids (text-fig. 1) were described as stout and block-like, or a lateral wing is developed; they form a sheath or channel for the radial water vessel. The virgals are rod-like and form the walls of channels separating successive metapinnules. The virgals of *Villebrunaster* were described (Fell 1962*b*, p. 16) as having a flattened base and a flanged keel (text-fig. 1*C*, *E*) and thus were seen as similar to those of *Platasterias*, but Fell (1963*a*, p. 422) cautioned that these ossicles proved morphologically plastic in later evolution.

The abactinal skeleton of fossil somasteroids (text-fig. 1*A*) consists of an open meshwork of paaxilliform ossicles, each consisting of a slender, vertically oriented axial stalk bearing a number of elongate basal flanges. Fell (1962*b*, p. 14) noted that *Chinianaster* abactinals are quite similar to those of *Platasterias* and *Luidia* but less similar to those of the astropectinids in that in the latter the base is disc-like and lacks basal projections, and the stalk is relatively stout.

In living sea stars, an unpaired ossicle termed the odontophore is found between members of an oral ossicle pair. In certain Palaeozoic asteroids, Spencer (1919 in 1914-1940) concluded that this ossicle was derived from an occluded inferomarginal, but because of the distribution of ossicles about the jaw region in *Chinianaster* and *Villebrunaster*, Fell (1963*a*, p. 401, fig. 8) suggested that in *Platasterias* an analogous T-shaped ossicle was derived from an occluded, non-metapinnular tegminal ossicle. McKnight (1975), however, argued that an odontophore (and, presumably, the analogous T-shaped ossicle as well) is lacking from adult somasteroids. Stressing the significance of the absence of this ossicle McKnight (1975) transferred the Helianthasteridae and three genera of the Taeniactinidae to the Somasteroidea from the Spinulosida *sensu* Spencer and Wright (1966). The somasteroid skeleton beyond the ambulacral column was described by Spencer (1951, p. 93) as 'slightly built'.

Discussion. The primary similarity between *Platasterias* and fossil somasteroid ossicle form seems to be in transverse elongation, and, perhaps, the development of keel- and flange-shaped ossicles, as in *Chinianaster* and, to some extent, *Platasterias*.

Virgals differentiated as marginals are absent from *Chinianaster*, the inferred primitive somasteroid (Fell, 1963*b*, p. 144). Those of *Villebrunaster* (text-fig. 1*F*), representing the inferred next phylogenetic step (Fell, 1963*b*), are rather simple cylinders elongate parallel to the arm axis. They are not transversely elongate as is the case in *Platasterias* (Pl. 20, fig. 5; Pl. 21, figs. 2, 5) and as presumably would be true in a primitive somasteroid under strong influence of transverse gradients (see below). Illustrated ambulacrals (Fell, 1963*a*, figs. 5, 6; text-fig. 1, herein) of fossil somasteroids are relatively robust with a broadened adradial head and an abradial wing deflected distally, whereas those of *Platasterias* (Pl. 21, fig. 2) are wide and short, lacking the broadened head. In over-all outline, the ambulacrals of *Platasterias* thus seem to be more primitive even than those of *Chinianaster* (although ambulacrals were not considered to be derived from virgals). *Chinianaster* lacks differentiated adambulacrals, whereas those of *Villebrunaster* (Fell 1963*a*, fig. 6; text-fig. 1, herein) apparently are simple ossicles elongate parallel to the arm axis, rather than transversely elongate as is the case in *Platasterias* (Pl. 20, fig. 5; Pl. 21, fig. 5). There are no known fossils of adambulacral shape similar to those of *Platasterias*.

In contrast, ossicle morphology of *Platasterias* is very close to that of *Luidia clathrata*, differing significantly only in degree of transverse elongation (Pl. 21, figs. 1, 2; text-fig. 3). The abactinals, marginals (Pl. 20, figs. 3, 5) and adambulacrals (Pl. 20, figs. 4, 6) are particularly similar. This is true not only of the form itself, but also of the complex articulation structure arrangement of the

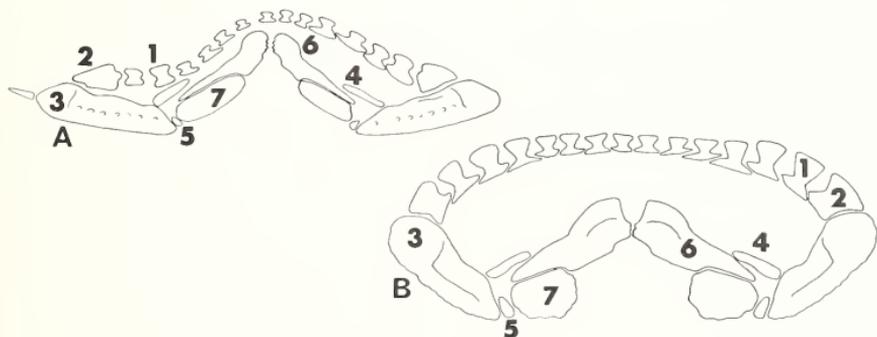
ambulacral column, involving both ambulacrals and adambulacrals (Blake 1972, 1973). The abactinal surface of the adradial end of the ambulacral is truncated in *Platasterias*, but the basic form of these ossicles is the same as in *Luidia*. Fell (1962b) stressed the presence of a Y-shaped groove on the actinal surface of the ambulacral of *Platasterias*, pointing out that the structure also occurs on fossil somasteroids, and he suggested that the associated muscle is used to temporarily elevate the ambulacral furrow. This muscle depression, however, occurs on all modern asteroids.

Fell (1962b, p. 7) also noted in *Platasterias* that the tube-feet emerge from a broad, basin-like depression. The transverse section of the middle of the long axis of the ambulacrals of most asteroid species (except, for example, the compressed ossicles of certain asteriids and asterinids and the delicate ossicles of the pterasterids) is cylindrical, hence a broad, basin-like depression is typical of most species.

Algor (1971) pointed out that *Platasterias* has the ambulacral system characteristic of modern asteroids, and he concluded that *Platasterias* is in no way primitive. Algor (1971) differentiated between ancient and modern asteroids on the basis of articulation structures across the furrow, arguing these muscles and facets were weakly developed in Palaeozoic taxa compared to the sturdy patterns seen in living species. Algor's sample of the Palaeozoic species was too small, for sturdy articulation structures comparable to that of modern species do occur, e.g. in *Promopalaester magnificus* (Miller) and *P. dyeri* Meek. Important, however, is that *Platasterias* is constructed in the same pattern as *Luidia*, rather than in the weakly articulated manner described for the somasteroids.

Superambulacrals are present in both *Platasterias* and *Luidia* but they have not been reported from fossil somasteroids. Inferomarginals of both *Platasterias latiradiata* and *L. clathrata* are step-shaped with overlapping, multifaceted contact points (Pl. 20, figs. 3, 5) (Blake 1973). The superomarginals are relatively large in *Platasterias* but their basic form is the same as those of *L. clathrata*. Arrangement and basic morphology of mouth frame ossicles are essentially the same between *P. latiradiata* and *L. clathrata*, although the odontophore is absent from fossil somasteroids (McKnight 1975). Distal arm ossicles, which are not transversely elongate, are essentially identical between *P. latiradiata* and *L. clathrata*, and much closer to each other than they are to those of species belonging to any other genus.

Fell (1962b, p. 15) suggested that the abactinals of *P. latiradiata* are similar to those of *L. neozelanica*, however, paxilliform abactinals occur in all of the living sea star orders except the Forcipulatida. A survey of the diagrams of Fisher (1911) shows that basal projections are present



TEXT-FIG. 3. Cross-sections of arms of A, *Luidia (Platasterias) latiradiata*; and B, *Luidia (Petalaster) clathrata*. In life, arms are flexible and ossicle orientations vary with behaviour; inferomarginals can be more steeply inclined to the horizontal than shown here or in Pl. 21, fig. 1. Key: 1, abactinals; 2, superomarginals; 3, inferomarginals; 4, superambulacrals; 5, actinals; 6, ambulacrals; 7, adambulacrals.

in abactinials of taxonomically diverse species and that the slender abactinials illustrated for several of the spinulosidan families (e.g. Solasteridae, Korethrasteridae, Pterasteridae) are closer to Spencer's somasteroid illustration (1951, fig. 5) than are those of *Platasterias* or *Luidia*. The abactinials of *P. latiradiata* and *L. clathrata* are very similar to each other, however.

Similarities extend to exterior morphology as well (Pl. 20, figs. 1, 11, 12; Pl. 22), as was demonstrated by Madsen (1966) for *P. latiradiata* and *L. marginata*.

I have argued on the basis of skeletal morphology that *P. latiradiata* clearly is very close to *L. clathrata*, but shows only relatively minor similarities to fossil somasteroids. Fell dissected specimens of *Luidia*; if the similarities are this strong, why was he not struck by them as well? I believe the answer lies in the species of *Luidia* available to Fell for dissection. For forty-three species of *Luidia*, Döderlein (1920) recognized ten subgenera and four supra-subgeneric taxa he termed 'groups', each group named for a representative species. Döderlein (1920, p. 223) presented a phylogenetic interpretation of *Luidia* in which he suggested that the Clathrata Group was primitive and gave rise to both the Quinaria and Alternata Groups; the Ciliaris Group was in turn derived from the Quinaria Group.

In external appearance, species of the four groups are superficially similar to one another, whereas the ossicle morphology of the members of the Ciliaris Group is quite distinct from that of the other three (Blake 1973); I suspect that if the external morphology of the Ciliaris Group were as distinct as the skeletal morphology, this group would be recognized as a separate genus.

In his discussions Fell placed little emphasis on the species available to him for study, but in an illustration of abactinials (1962*b*, p. 15) and an arm tip in cross-section (1963*a*, p. 386) he does note that his drawings were based on *L. neozelanica*. This species had not been described at the time of Döderlein (1920), but it has since been referred to the Ciliaris Group (Clark 1953; Fell 1963*a*, p. 433). Further, Fell's (1963*a*, p. 395) drawing of the cross-section of a *Luidia* arm shows a crescentic inferomarginal outline typical of the Ciliaris Group, rather than the step-shape typical of the marginals of the other three groups (Pl. 20, figs. 3, 5, 7). Madsen (1966) assigned *Platasterias* to *Petalaster*, a subgenus of the Clathrata Group; although I recognized *Platasterias* at the subgeneric level because of its distinctive shape, I agree with Madsen's inclusion of the species in the Clathrata Group.

Fell thus appears to have based his comparisons between *Luidia* and *Platasterias* on a species inferred to be well removed in phylogenetic position (Döderlein 1920) and distinct in ossicle morphology (Blake 1973) from those *Luidia* species which are suggested to be closest to *P. latiradiata* (Madsen 1966).

3. Ambulacral column arrangement

Although not in his diagnosis, Spencer (1951, p. 88) noted that '... these first stages ...' (in reference to somasteroids in general) '... show no sign of an ambulacral groove ...'. Spencer did describe a '... shallow channel ...' (p. 102) along the midradius of *Archegonaster*, and '... a deep channel ...' (p. 98) in *Chinianaster*. Spencer (1951) cited his 1914 paper for illustration of the channel. In a drawing of an asteroid arm in cross-section, Spencer (1914 in 1914-1940) showed that the ambulacral channel refers to the axial notch for the radial water canal. The channel is thus a structure distinct from the ambulacral furrow or groove. Although the ambulacral channel is deep in *Chinianaster*, the basins for the tube-feet are '... placed almost in the oral plane'. If an ambulacral furrow is present, as in asteroids, the ambulacrals are arched and the basins for the tube-feet are raised above the oral surface of the animal.

In Fell's discussions, whether or not the ambulacral furrow is at most temporarily erect (somasteroids) or permanently erect (asteroids) is essential to the notion of somasteroids and *Platasterias* as a somasteroid. The change from temporarily to permanently erect was selected as the point at which the pre-asteroid phase gave way to the asteroid phase (1963*a*, p. 391).

Fell described a well-developed 'lateral wing' on the ambulacral of *Platasterias*. This 'wing' provides attachment for the musculature extending to the first virgal (i.e. the adambulacral) that permits temporary erection of the ambulacral ossicle to form an inverted V-shaped groove considered homologous with the asteroid furrow. The ossicle arrangement in *Platasterias* was considered to be asteroid-like and leading toward the asteroid grade of organization (1962*b*, p. 10). Although recognizing that in *P. latiradiata*, the wing extends over the adambulacral in the manner found in asteroids, Fell (1963*a*, p. 393) considered '... the major [i.e. transverse] axis of the ambulacral

lies almost horizontally, in the same axis as the metapinnule which it bears, as in the Villebrunasteridae In asteroids, the adambulacrals are below the abradial end of the ambulacrals and the basins for the tube-feet permanently raised above the substrate.

The channel for the water canal in *Platasterias* was considered partially enclosed by the ambulacral ossicles, much as in the Palaeozoic fossils.

Discussion. Interpretation of the ambulacral ossicles is important to the idea of a temporarily erectable furrow (Pl. 21, figs. 1, 2; text-fig. 3). In *Platasterias*, the impression of a linear, nearly horizontal ambulacral ossicle is conveyed by the broad 'lateral wing' of the ambulacral, but important to the nature of the furrow is the angle between the axis of the ambulacral/adambulacral articulation and the axis of the adradial portion of the ossicle. The ambulacral/adambulacral articulation axis is approximately horizontal in the relaxed living sea star (although capable of broad adjustment; see Heddle 1967) and therefore the angle the adradial end of the ossicle makes to the articulation axis reflects the relaxed, permanent furrow development. From a number of medial arm ossicles of mature specimens that I measured on a binocular microscope stage, this angle is approximately 20° in *L. clathrata*, 30° in *P. latiradiata*. The size of the angle depends on the precise points selected for measurement, but the critical idea is that in *Platasterias*, as in *Luidia*, these two axes are not parallel; a permanent furrow is present in both. Fell's sketches (1963a, p. 395), although presumably not intended to be precise, do accurately reflect approximate relationships, and the presence of a furrow in both.

In a figure description, Fell (1962b, p. 13) suggested that the outer, oral surfaces of the adambulacrals, as seen in *Platasterias*, are erected into the furrow at the asteroid grade. Although these faces are pulled toward one another as any sea star closes the furrow, the surfaces are not erect in the furrow in asteroids and remain directed toward the substrate in the relaxed animal. As is true of other surface ossicles, the adambulacrals bear spines on their surficial faces. Both *Platasterias* and other sea stars have approximately vertically oriented adradial side faces on the adambulacrals.

Equally important to ambulacral ossicle orientation is the nature of the ambulacral/adambulacral articulation structures, for, as noted above, the same facets and muscle depressions, arranged in approximately the same proportions, can be recognized in both *Platasterias* and *Luidia* (Pl. 20, figs. 4, 6) (Blake 1972, 1973), as well as in other asteroids. Both sea stars must be capable of approximately the same movements; Heddle (1967) described how this musculature and articulation can be used in locomotion and digging, and in a different genus I (Blake 1981) have argued that these structures can be used in righting, interpretations that seem appropriate for *Platasterias* as well as *Luidia*. The broad lateral wing, as suggested by Madsen (1966) for the inferomarginals and adambulacrals, is a part of the morphology of *Platasterias* adapted to its habitat of a shifting, sandy bottom.

As noted by Fell (1962b, p. 7), the radial water canal in *Platasterias* occupies a channel along the arm axis (Pl. 21, fig. 1) much as in certain somasteroids. A similar channel, however, occurs in *L. clathrata* (Pl. 21, fig. 2) as well as in other asteroids (e.g. *Asterias*), hence the feature is not of taxonomic value among living sea stars.

4. Growth gradients

Spencer (1951, p. 91) described the interambulacrals, or virgals, as arranged in linear series at an angle to the ambulacral row with a single series arising at the abradial edge of each ambulacral. The development of virgals provided the basis for the families recognized by Spencer: in the Chinianasteridae, ossicles occupy the entire oral surface apart from the ambulacrals and mouth; in the Archegonasteridae, virgals occur only distally on the arms, and virgals are lacking from the Archophiactinidae.

Fell (1963a) developed his ideas of growth gradients in asterozoans about this transverse alignment of oral surface ossicles. Growth gradients were considered to be parallel or weakly convergent lines along which morphologic structures were aligned. Growth gradients were envisioned as

arranged in two series, one set parallel to the arm radius and a second, lateral set subperpendicular to the first. The ambulacral ossicles, nerve ganglia, and radial water vessel were aligned along the main longitudinal gradient, the adambulacrals along the first lateral gradient, and so on.

Each row of virgals was termed a metapinnule, and each represents a transverse gradient. The influence of either longitudinal or transverse gradients could be stronger; where transverse gradients dominated, metapinnule ossicles were aligned, whereas these ossicles were offset transversely but aligned longitudinally as the longitudinal gradients became dominant. The differentiation of the typical asteroid oral surface ossicles from the morphologically similar virgals was associated with the inferred declining influence of transverse gradients: the adambulacral from virgal 1, the superambulacral from virgal 2, the marginal from virgal 3, and the marginal radiole, from virgal 4 (Fell, 1963a, pp. 392, 405).

Transverse gradients dominate in primitive somasteroids (e.g. *Chinianaster*) but gradually lose their influence; longitudinal gradients dominated in *Astropecten* and phylogenetically later asteroids. The transverse gradients were ultimately derived from the inferred crinoid ancestor, hence the metapinnule from the crinoid pinnule.

Members of ambulacral pairs apparently alternate across the arm axis in certain fossil somasteroids (Spencer 1951, p. 102) much as the brachials alternate in biserial crinoids. This similarity of arrangement contributed to Fell's view of a close relationship between crinoids and stelleroids (Fell 1963a, p. 415). In *Platasterias* the transverse gradients were considered clearly recognizable (Pl. 21, fig. 5), although the ossicles are equally clearly equated with their inferred homologues in asteroids.

Ossicle alignment was the sole criterion provided for recognition of gradient type. Most post-Palaeozoic sea stars have few to many ossicles on the oral surface between the adambulacral and inferomarginal series: these are the so-called actinal intermediates of Fell's terminology, or more simply, actinals (text-fig. 3). Actinals typically form a more or less tightly packed mosaic, they are similar to one another in shape, and although a broad size range can be present, size changes are gradational across the surface. The ossicles thus are perceived as forming parallel rows of a single orientation, or, frequently, intersecting rows, one of which is oriented more or less parallel to the arm axis, the other radiating obliquely from the furrow toward the animal margin. Dominant orientation of rows can be consistent within taxa; Hotchkiss and Clark (1976) used the arrangement of these ossicles to separate the *Asteropseidae* from the *Poraniidae*.

EXPLANATION OF PLATE 21

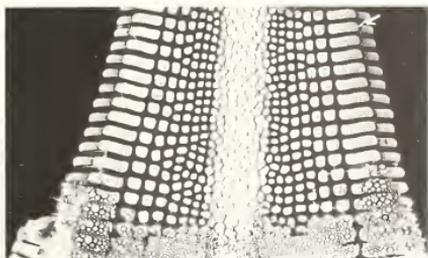
- Figs. 1, 4, 6. *Luidia clathrata* (Say). 1, transverse view of arm, ossicles identified in text-fig. 2; see note with text-fig. 2, $\times 3$. 4, inclined aboral view of arm showing alignment of lateral abactinals with superomarginal row (arrow); alignment is lost in midarm area; some spinelets are still in place, $\times 3$. 6, oral surface of arm showing alignment of inferomarginals (arrows), actinals, and adambulacrals. Tube-feet are visible along arm axis, $\times 3$.
- Figs. 2, 3, 5. *L. (Platasterias) latiradiata* (Gray). 2, transverse view of arm, ossicles identified in text-fig. 2, $\times 4$. 3, aboral view of arm showing alignment of lateral abactinals with superomarginal (arrow) row; alignment is lost toward midarm region, $\times 3$. 5, oral surface of arm showing alignment of ossicles, enlarged marginal radioles; arrow indicates inferomarginals, $\times 3$.
- Fig. 7. *Asterias* sp. Aboral view of interior of oral surface of arm showing alignment of ossicles in radial series, see discussion in text; arrows indicate ambulacrals, $\times 3$.
- Fig. 8. *Archaster typicus* Müller and Troschel. Oral surface of arm showing well-defined fascioles (arrow) between inferomarginals. Pits in some adambulacrals are for pedicellariae. Note similarity of lateral spines with those of *L. (P.) latiradiata* and *Astropecten regalis* (Pl. 20, fig. 2), $\times 3$.
- Fig. 9. *Dermasterias imbricata* (Grube). Oral surface of arm showing ambulacral spines (arrows) crossing over furrow axis, in function forming furrow cover plates, $\times 3$.



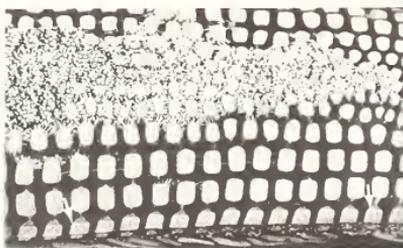
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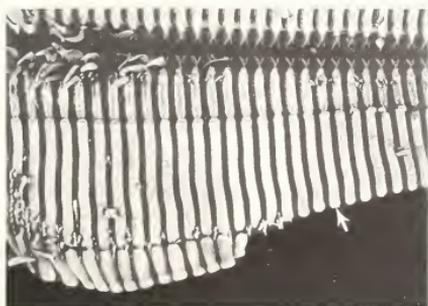
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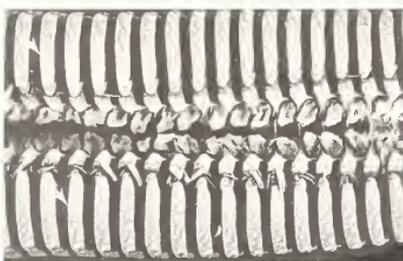
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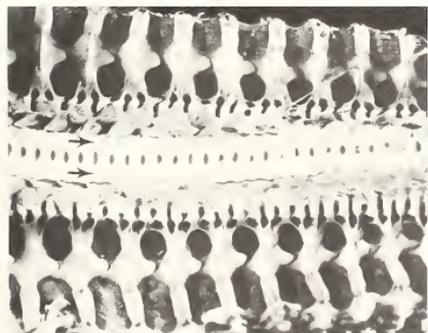
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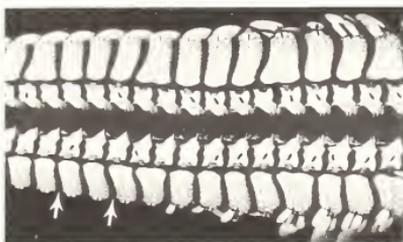
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Certain authors have interpreted the oblique arrangement of actinals in true asteroids as reflecting transverse growth gradients *sensu* Fell, but Fell himself equivocated on the origins and significance of these ossicles. In reference to the astropectinid and later stages of evolution, Fell (1963a, p. 389) said 'Actinal intermediate plates are usually present, and are arranged in longitudinal rows; they are sometimes also arranged in oblique series, but these latter are unrelated to the transverse gradients which produce the ambulacra and adambulacra.' The inferred phylogenetic history of these ossicles was described as well (Fell 1963a, p. 391): 'Actinal intermediate plates are lacking from division 1 (i.e. Chinianasteridae, see Table 1, herein), appear as minute and irregular rudiments in division 2 (i.e. Platasteriidae), persist as somewhat larger and more irregular elements in the luidiids, become progressively more conspicuous in various genera of the Astropectinidae, and extremely conspicuous in post-astropectinid groups.' In suggesting that actinals were absent at the chinianasterid grade but appeared at the platasterid grade, Fell implied that these ossicles are derived but appeared very early. In addition, Fell (1963b, p. 144) stated that the virgals in *Platasterias* had stabilized at four elements (identified above) not including actinals.

Fell (1963a, p. 387), however, also stated, 'Ossicles are differentiated along the transverse gradients in the following sequence, from within outwards: adambulacral, superambulacral (if present), actinal intermediate plates, marginals.' Elsewhere, Fell (1962a, p. 635) referred to actinals as 'accessory virgalia'; in the figure description (Fell 1962b, fig. 4a), the actinal was labeled 'intercalary virgalium (actinal intermediate)' and again (1963b, abstract) the metapinnule was referred to as differentiated into the actinal intermediate, as well as the other ossicle types. Although he apparently was uncertain as to how to treat these ossicles in *Platasterias* and *Luidia*, Fell's strongest statements seem to be that the actinals were secondary, and not derived from virgals.

In order to understand Fell's interpretation of *Platasterias* and the nature of the Somasteroidea, it is necessary to consider the several steps Fell (1963a) used to select the groups of extant sea stars he inferred to be primitive, and the phylogenetic sequence selected to connect fossil somasteroids to living species. Among living sea stars, Fell limited his search for the primitive group to the Luidiidae, Astropectinidae, and Porcellanasteridae because 'It has been generally agreed that the more primitive extant asteroids are the three families in which the tube-feet lack suckers' (1963a, p. 285). Of the three, the porcellanasterids were tentatively eliminated because they lack superambulacra, one of the ossicles inferred to be homologous with the virgals of somasteroids.

More important to Fell's (1963a, p. 385) phylogenetic ideas was the concept of growth gradients. Among living sea stars, transverse rows are most clearly defined in the Luidiidae, less so (because the two systems of gradients were seen as changing influence gradually) in the Astropectinidae and Porcellanasteridae. As Fell had recognized the strongly developed transverse gradients in the lower Paleozoic somasteroids, their development in the Luidiidae permitted recognition of this group as primitive among living families. The gradients are weaker but present in the Astropectinidae (Fell, 1963c, p. 467), which was then next in the phylogenetic sequence. The Porcellanasteridae is specialized in a number of features, and was therefore third in the sequence.

Isolation of *Platasterias* as a somasteroid began with the realization that this genus '... exhibits growth gradients identical with those of Ordovician somasteroids' (Fell, 1963a, p. 383). Fell then obtained specimens of *Platasterias* for dissections; this work led to the assignment of *Platasterias* to the Somasteroidea, as well as to the refinement of a phylogenetic sequence extending from somasteroids through several steps of asteroid evolution (see Table 1). The phylogenetic sequence was based on a variety of characters and emphasized morphology of the fossils but not their stratigraphic position because the fossils appeared through an interval of strata inferred to be too brief to permit recognition of phylogenetic sequence based on stratigraphic sequence (1963a, p. 385). Fell (1967, p. 580) pointed out, however, that his phylogeny is consistent with what is known of the stratigraphic sequence.

In summary, gradient recognition depends upon ossicle alignment. A continuing, gradual decline in transverse gradient influence and a concomitant increase in the influence of longitudinal gradients was suggested to have occurred during somasteroid/asteroid phylogeny.

Discussion. As pointed out by Fell, the ambulacra, adambulacra, superambulacra, and marginals are aligned in both *Platasterias* and *Luidia* (Pl. 21, figs. 5, 6). Although *Luidia* typically has a cluster of larger spines at the abradial ends of the marginals (Pl. 22, figs. 1, 9) rather than

a single larger radiole, as in *Platasterias* (Pl. 21, fig. 5), the positions of the spines on the marginals are the same. Although only a single large spine occurs on each *Platasterias* marginal, numerous smaller spines are present, and further, number of spines apparently is not important, as is shown by the variation found among *Luidia* species. Presence of a single marginal radiole in the petaloid species *Astropecten regalis* (Pl. 20, fig. 2) argues for the convergent evolution of marginal spine reduction. Because there is no difference in ossicle alignment between *Platasterias* and *Luidia*, this character cannot be used for taxonomic separation (although ossicle proportions do differ).

A more serious problem arises from the arrangement of the actinals and abactinals. These ossicles in *Luidia* and *Platasterias* are relatively stout, and the actinals and the lateral two to four rows of abactinals in *Platasterias* and the Clathrata Group species of *Luidia* are aligned with the four ossicles (Fell, 1963a, pp. 392, 405) of the transverse series (Pl. 20, figs. 1, 9-12; Pl. 21, figs. 3-6). Abactinal alignment with the marginals is weaker toward the middle of the abactinal surface and among the other *Luidia* groups (*sensu* Döderlein 1920) in general. A single row of actinals is present in most species of *Luidia*, including members of the apparently primitive Clathrata Group (Döderlein 1920), but extra series are present among the Alternata Group.

In some manner, the arrangement of the actinals and abactinals must be accommodated with ideas on transverse gradients because the alignment satisfies the criterion of transverse gradient recognition. Fell (1963a, p. 415) recognized the problem presented by the abactinals and noted that these ossicles were not aligned in the primitive Chiniasteridae. He suggested (p. 416) that in *Platasterias* the gradients would seem to be carried into the soft tissues in their path, and that caused '... the paxillae to differentiate as if they were virgalia'. The alignment was thus considered secondary. Fell also (1963a, p. 389) pointed out that actinal intermediates (i.e. actinals) are aligned in transverse series in various astropectinid and phylogenetically (*sensu* Fell 1963a) later sea stars.

For discussion purposes, I have accepted the following hypotheses from Spencer's and Fell's papers: (1) that asterozoans were derived from a crinoid ancestry, so that the primitive asterozoan had radial rows of virgals; (2) that somasteroids are the primitive asterozoans and gave rise to the asteroids; (3) that abactinals were present in the primitive somasteroid (because Spencer 1951, described them in the earliest known taxa). If (1) or (2), as now understood, were rejected, then the phylogenetic hypothesis using growth gradients could not be maintained. If (3) were rejected, then the fossil record is misleading and where it is misleading can be interpreted only using external criteria.

Beginning with these assumptions, abactinal alignment seen in *Platasterias* and *Luidia* can be considered either primitive and present in the first somasteroid, or derived and appearing after the first somasteroid grade. The actinals of *Platasterias* and *Luidia* can be considered either as primitive and homologous with virgals, or not. If primitive, then their alignment must be primitive, i.e. they are a part of the primitive transverse gradient. If secondary, their alignment must be secondary as well (i.e. their alignment could not be part of a primitive transverse gradient if the ossicles themselves did not occur in the primitive species). Where I treat the actinals as primitive, I will treat the specific actinal arrangement seen in *Platasterias* and *Luidia* (i.e. a single actinal row) as secondary because of the distribution of these ossicles in the accepted (see above) primitive somasteroid.

First, if we accept both abactinal arrangement and actinal ossicles as seen in *Luidia* as primitive, then the fossil record is incomplete and misleading. The abactinal pattern reported in somasteroids, including *Chiniaster*, the inferred primitive genus, is an open meshwork of light paxilliform ossicles (Spencer 1951, p. 91). If a hypothesis of declining influence of transverse gradients is to be followed, then the abactinal arrangement seen in *Platasterias* and *Luidia* must have been derived from some unknown pre-chiniasterid somasteroid, and retained while other characters (including ossicle differentiation) were evolving toward the asteroid grade. This means that known fossil somasteroids had to be off the main line of somasteroid evolution because their abactinal fields had already attained a derived, open meshwork state (text-fig. 1A; Pl. 21, fig. 3), a condition not reached in surviving asteroid evolution (*sensu* Fell) until after the level of the Paxillosida. Following the implications further because the abactinals of *Luidia* and *Platasterias* are sturdy, the primitive abactinal condition in somasteroids likely was sturdy as well, and the relatively fragile ossicles of known

fossils represent derived states. Thus, taxa with the relatively sturdy arrangement are unknown from the fossil record, whereas the relatively fragile ones were preserved. Finally, the fossil record itself becomes unreliable in that although most oral surface ossicle distributions in known fossils are considered to represent primitive conditions, the abactinal arrangement is considered secondary for reasons external to the fossils themselves.

As to the actinal surface ossicles, their reduction sequence in known somasteroids began with a full oral surface field (*Chinianasteridae*), continued through an intermediate step in which ossicles were present only distally on the arms (*Archegonasteridae*), and ended with complete elimination of these ossicles (*Archophiactinidae*) (Spencer 1951). Thus the presence in *Platasterias* and most *Luidia* of a single row extending the entire arm length must represent a lineage separate from known fossils because they match neither any known fossils, nor the known reduction sequence.

The second approach is to assume, as Fell did, that abactinal alignment and actinal ossicles are secondary. This path, however, also yields difficulties because it requires extension of the transverse gradients on to the aboral surface at the time the influence of these gradients is hypothesized to be declining and the longitudinal gradient influence increasing. Because the row of actinals also becomes aligned with adjacent adambulacrals and marginals, we must hypothesize alternating rows of increasing and decreasing influence of transverse gradients (i.e. adambulacrals, decreasing; actinals, increasing; marginals and marginal radioles, decreasing; abactinals, increasing). Even if we were to argue that abactinals represent an ossicle system separate from crinoids and not derived from them, and therefore not primitive in somasteroids, the problem of alignment is not resolved. Abactinals do occur in an open meshwork pattern in the known primitive somasteroid (*Chinianaster*), and *Platasterias* was considered to be approximately at the *Villebrunaster* level of organization, at a post-*Chinianaster* pre-*Archegonaster* somasteroid grade. Transverse gradients are hypothesized to be declining in influence during this sequence, yet in *Platasterias* these gradients had to be extending their influence on to a new area of the body.

Further, because transverse alignment can be secondary among some ossicle systems, it might also be secondary among all others. *Platasterias* therefore does not readily fit into a somasteroid/asteroid phylogeny based on growth gradients. This does not challenge the hypothesis as applied only to known fossils.

Primitive and derived states could be rearranged so that abactinal alignment is considered primitive and actinals derived, or vice versa, but this only combines inherent difficulties in different ways.

It would be possible to argue the large actinal field was not lost in the connecting links between somasteroids, luidiids, and remaining asteroids, but this alternative removes *Platasterias* and *Luidia* from the main line of asteroid evolution, for there is no known platasteriid or luidiid, fossil or living, with the appropriate morphology (i.e. well-defined fascioles, and a large actinal field). *Tethyaster* is an astropectinid that comes quite close to this morphology, and indeed Jangoux (1975) argued that this genus is in many ways intermediate between *Luidia* and *Astropecten*. The marginal fascioles in *Tethyaster*, however, are relatively small, and the development of fascioles also was important in Fell's hypothesis, serving as feeding and respiration channels.

In any event beginning with the assumptions of Spencer (1951) and Fell (1962a *et seq.*), and assuming either that abactinal alignment and actinal occurrence is primitive or secondary, known fossil and modern taxa permit no application of the hypothesis of growth gradients to somasteroid/asteroid phylogeny that does not require ignoring important aspects or morphology. In essence, alignment is too extensive in *Platasterias*, more extensive than in the fossil somasteroids, and this calls for explanation other than phylogenetic inheritance from a crinoid ancestry. Such an origin is suggested below, under a functional explanation for alignment in *Luidia*.

As noted earlier here, individual ambulacral column and marginal ossicles of *Platasterias* are transversely more elongate than are those of the fossil somasteroids. Again, *Platasterias* is showing an inferred primitive trait more strongly than it is seen in the earliest known somasteroids, and therefore an explanation other than inheritance of a primitive condition is demanded.

5. Other morphologic characters

The nature of the mouth frame. In modern sea stars, all ambulacral pairs are united across the furrow by muscles and articular structures. In the somasteroids, Spencer argued that the proximal ambulacrals (three pair in *Chinianaster*) were not linked across the furrow, resulting in broad, V-shaped openings termed buccal slits. These slits, however, are likely to have resulted from post-mortem events. Spencer (1951, p. 100) argued that ambulacrals of certain small *Chinianaster* were pulled apart after death, and Fell (1963a, p. 403) suggested that the buccal slits of Spencer

resulted from such changes. The ossicles of the buccal slits in *Archegonaster* apparently show no significant, distinctive morphologic characters (Spencer, 1951, fig. 9) as might be expected of ossicles that form the margin of an opening rather than an articulated double column. Minor differences are illustrated in these ossicles, but near-oral ambulacral column ossicles also are somewhat distinctive in certain living sea stars (e.g. the Astropectinidae).

Arrangement of spinelets, along the fasciolar margins. In *Platasterias*, a series of small spinelets, termed cover plates by Fell, line the edges of the adoral surfaces of the marginals and adambulacrals. These spinelets were described as being held in a web and, when depressed, they cover the fasciolar grooves between subsequent metapinnules or transverse gradient series (1963a, p. 397). The arrangement was inferred derived from the crinoid ancestor, but differs in closing over the interpinnular groove rather than over the pinnule surface, as in crinoids. The cover plates in *Platasterias* were seen as protecting the fasciolar or feeding grooves.

A similar arrangement is found in *Luidia*, *Astropecten*, and other sea stars, although the ossicles in these taxa typically are more slender, i.e. spine-like, and much more numerous than in *Platasterias*. As in *Platasterias*, these ossicles can be depressed over the furrows. I was unable to recognize true webbing in preserved specimens of *Luidia* (although such a covering is present in *Goniopecten*, suborder Cribellina, order Paxillosida), but a mucus covering is present that in dried specimens available to me can extend to the tips as well as between adjacent spinelets. The dense, overlapping arrangement of many spinelets provides an effective cover for the fasciolar furrow. Various sea stars, e.g. *Dermasterias imbricata* (Pl. 21, fig. 9), are capable of pulling the sides of the furrow (i.e. the adambulacrals) together and arching the furrow spines over the furrow. Functionally, these are cover plates and such plates are widely distributed among the Asteroidea.

The arrangement found in *Platasterias* could be readily derived from that of *Luidia* by reduction of spine number and minor changes of spine shape. Arrangement of fasciolar spinelets therefore provides little justification for significant taxonomic separation of *Luidia* and *Platasterias*.

Superambulacrals. Fell (1963a) argued that the superambulacrals of *Platasterias* and *Luidia* are occluded second virgals. This explanation of origins is plausible, however, superambulacrals are unknown in fossil somasteroids but they are present throughout the Luidiidae and Astropectinidae. This distribution can only serve to isolate the fossil from the extant sea stars, not link them in a single phylogenetic sequence.

Soft parts. *Platasterias* has a blind gut with caeca extending into the arms, an arrangement Fell (1963a, p. 396) thought probably existed in fossil somasteroids. In addition, *Platasterias* has small, simple non-suctorial tube-feet considered similar to those in *Chinianaster* (Fell 1962c, p. 474) and small, double internal ampullae also inferred to be similar to those in Ordovician somasteroids. *Luidia*, like *Platasterias*, has simple, non-suctorial tube-feet, double ampullae, and a blind gut with caeca extending into the arms.

6. Feeding habits

Spencer (1951, p. 87) emphasized feeding behaviour in his tripartite division of stelleroids: 'The grouping of starfish adopted here is based upon the activities of the arms, especially during feeding.' The asteroids were seen as carnivores on larger organisms, primitive ophiuroids were believed adapted for feeding on small particles on or in the bottom, and the somasteroids inferred to have lived on planktic particles (in the suggested relatively primitive genus, *Villebrunaster*) or particles from the surface sediment layers (in the suggested advanced somasteroid *Archegonaster*).

Fell also stressed observed and inferred feeding behaviour in his phylogenetic sequence. He (1962a, p. 14) suggested two types of feeding are present in *Platasterias*, 'microphagous ciliary feeding', and 'selective detrital feeding'. In the former, particles of food were believed to be conveyed in water currents along the fascioles to the arm radius, then proximally toward the mouth. In specimens of *Platasterias* available to him, Fell observed amphipods in the mouth and in a food groove; he suggested that the amphipods were collected by the tube-feet and passed to the mouth.

He inferred that this would be the limit of carnivorous feeding, because of the relatively small mouth of *Platasterias*. A specimen of *Platasterias* in the U.S.N.M. collections has a foraminiferan, small snail, and arthropod fragments in the mouth area; the presence of this small prey does not appear fortuitous.

As observed by Fell (1963a), *Astropecten* and especially *Luidia* (Pl. 21, fig. 6) are living species with quite similar fasciolar furrows extending between the marginals and ambulacra, yet these are voracious predators of other echinoderms, molluscs, and arthropods. Although suspension feeding has been suggested for both (Fenichel 1965, for *Luidia sarsi*; Gemmill 1915 and Gislén 1924 for *Astropecten*), Feder and Christensen (1966) doubt this behaviour occurs in these genera. The furrows in both, as Fell (1963a, p. 391) observed for the Luidiidae, are probably respiratory in nature. In contrast, taxonomically diverse genera in which suspension feeding has been observed do not possess fasciolar furrows (e.g. *Henricia*, Spinulosida, Rasmussen 1965, ossicles are aligned in this genus, yielding unobstructed channels between ossicle rows; *Oreaster*, Valvatida, Halpern quoted in Anderson 1978; unidentified Brisingidae, Forcipulatida, Pawson 1978). Fell recognized the differences in function between the fascioles of the modern sea stars and that inferred for the somasteroids and assumed the function changed with the evolution of the asteroid grade.

Suspension feeding is difficult to document without direct observation. Gislén (1924) found surface ciliary currents to be widespread in sea stars and therefore the potential for ciliary feeding as well, although the currents flow away from the oral area in some species. Gislén (1924), however, considered the functions of the currents to be largely for respiration and cleaning, although he did observe some capture of particles.

The size of the mouth does not provide a useful guide to potential prey size limits, as suggested by Fell for *Platasterias* (1962b, p. 14), for both *Astropecten* and typical *Luidia* species, although

EXPLANATION OF PLATE 22

- Fig. 1. *Luidia alternata* (Say). USNM 7528. Inclined view of disc region of specimen not distorted by food; specimen in alcohol, $\times 1$.
- Figs. 2, 3. *Luidia alternata* (Say). USNM 7528. 2, inclined aboral, $\times \frac{1}{2}$; and 3, oral view, $\times 1$, of individual containing unbroken corona of *Lytechnius varegatus* (Lamarck). The peristome of the echinoid (arrow, pointing to gill slit) is centred on that of the sea star. The sea star major radius is 140 mm, relaxed minor radius 20 mm, and height 15 mm. The echinoid corona diameter about 50 mm, height 25 mm. All dimensions approximate. Spines and organic materials are missing from the echinoid but pieces of the Aristotle's Lantern are present. The echinoid thus apparently was dead or nearly so at time of ingestion and it had been consumed and presumably was soon to be expelled at time of collection. In alcohol.
- Figs. 4, 5. *Luidia clathrata* (Say). USNM E17599. 4, view into disc; and 5, lateral view of fragmentary individual, radius about 100 mm, containing a specimen of *Moiria atropos* (Lamarck), length about 40 mm. The echinoid is now incomplete (arrows point to remaining coronal plates) but the aboral surface of the sea star retains the form of the sea urchin, hence the echinoid was complete when ingested. Fine lines beyond the echinoid plates are its spines; the echinoid apparently was ingested alive, or very recently dead; specimen is dry, $\times 1$.
- Fig. 6. *Luidia clathrata* (Say). USNM 8442. Inclined aboral view of specimen, radius about 110 mm, containing *Moiria atropos*, length about 40 mm. Spines are retained on prey, $\times 1$.
- Figs. 7, 8. *Luidia clathrata* (Say). USNM E3268. 7, aboral view; and 8, oral view of sea star containing a broken but not distorted *Mellita quinquesperforatus* (Leske). The spines are missing from the echinoid. Sea star radius about 150 mm, that of the echinoid is about 50 mm. Aboral ossicles of the sea star are distorted from life position, beyond the edge of the sea star in a relaxed state (arrow); the aboral surface of the sea star was partially opened after collection. Compare colour marking with that of *L. (P.) latiradiata*, Pl. 20, fig. 1; specimen is dry, $\times \frac{1}{2}$.
- Fig. 9. *Luidia clathrata* (Say). Oral view of mouth area of specimen not distorted by food; specimen is dry, $\times 1$. *Luidia* can consume particles of dimensions many times greater than the 2 or 3 mm mouth diameter, and of volumes greater than that of the relaxed disc. Much caution is needed in interpreting possible food particle size in fossil organisms with flexible bodies.



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effective predators, also have relatively small oral frames. The lack of importance of mouth size is clearly seen in a series of *Luidia* specimens in the U.S.N.M. collections (Pl. 22). In each example illustrated, the size of the ingested echinoid exceeds that of the relaxed diameter of the disc. Peristome size, measured in related *Luidia* specimens of comparable sizes, is 2 to 3 mm; oral spines mounted around the mouth of the sea star overlap over the peristomial opening. Occurrence of large prey in a number of specimens clearly demonstrates the behaviour is not unusual. *Astropecten*, too, is capable of feeding on relatively large prey organisms (Clark 1962, pl. xiii).

Thus, *Luidia* has fasciolar grooves similar to those of both *Platasterias* and presumably of the ancient somasteroids, but there is no clear evidence that either *Platasterias* or *Luidia* make use of suspension feeding and therefore the presence of fascioles in Palaeozoic somasteroids provides no morphologic evidence of suspension feeding in these organisms. The presence of very large prey in *Luidia* means that mouth and body size provide no clear guide to food particle size in echinoderms with a loosely articulated skeleton, including the Palaeozoic somasteroids.

Summary

Platasterias is very close to typical species of *Luidia* in all characters except those related to the transverse elongation of ossicles, and similar to Palaeozoic somasteroids only in ways it is also similar to *Luidia*. Greater differences in ossicle morphology, except for this transverse elongation, are seen between species of the Ciliaris Group of *Luidia* (*sensu* Döderlein 1920) and Clathrata Group (*sensu* Döderlein 1920) than are seen between *Platasterias* and the Clathrata Group of Döderlein. I therefore consider (Blake 1972) *Platasterias* to be a subgenus of *Luidia* assignable to the Clathrata Group, and not a somasteroid as suggested by Fell. As noted above, Madsen (1966) carried this interpretation one step further, for he did not believe *Platasterias* warranted subgeneric recognition. Summary comparison among sea star taxa is provided in Table 2, with *Porania* included as an example of an asteroid well removed from the Luidiidae.

If *Luidia* were to be extensively subdivided, perhaps along the lines suggested by Döderlein (1920), then *Platasterias* could be recognized at the generic level, but on a morphologic basis, it still would have to be included in the same family as other *Luidia* species. *Luidia*, as noted by Fell (1963a), clearly is a member of the Asteroidea.

THE NATURE OF *LUIDIA*

The affinities of the Luidiidae

In his work, Fell assumed the sea stars with nonsuctorial tube-feet, and in particular the astropectinids and luidiids are primitive among extant sea stars. I agree with this interpretation but, although consensus might lean toward the families cited, no general agreement has ever been reached.

Mortensen (1922), noting that few authors had commented directly on the question of primitive position, queried the then-active sea star workers as to their opinions. W. K. Fisher, H. L. Clark, and R. Koehler all considered the astropectinids to be primitive, as did Mortensen himself, whereas Döderlein thought the asterinids were primitive. Earlier, Perrier (1884) argued the forcipulates were primitive on inferred directions of pedicellariae evolution.

Most active sea star taxonomists list the Paxillosida first in their faunal lists, seemingly thereby implying an inferred primitive position, but as A. M. Clark pointed out to me (*pers. comm.*), this is simply because they are following Fisher (1911).

In this diagnosis of the Platysterida (including the Palasteriscidae and Luidiidae), the only character listed by Fell (1963a, p. 392) was the development of transverse growth gradients. Spencer and Wright (1966) expanded upon the diagnosis, but most features listed by these authors also apply to members of the Paxillosida. They did include the presence of a single row of marginals in the Platysterida. Although relatively small in *Luidia* compared to those in, for example, *Astropecten*, supermarginals are present in *Luidia* (Pl. 20, figs. 9, 10), recognizable on the basis of position of origin at the terminal (see criteria listed by Blake 1978), and by size among primitive

(*sensu* Döderlein 1920) *Luidia* species. This leaves only the transverse gradients to unite the Luidiidae with the Palaeozoic Palasteriscidae, but this character, as discussed above, appears unreliable. Based on illustrations provided by Spencer (1919 in 1914–1940), however, *Luidia* and the Palasteriscidae are distinct in ossicle morphology, and fascioles apparently are lacking in the fossil family. In addition, they are separated by a Devonian to Miocene interval.

The Luidiidae, however is similar to the Astropectinidae in many soft and hard part characters, as summarized by Fisher (1911), Fell (1963a), and other workers; included here are the nature of the paxillae and other ossicles, and the presence of non-suctorial tube-feet. Following McKnight (1977), I therefore have herein returned the Luidiidae to the Paxillosida.

A partial revised classification of the stellate echinoderms based on Spencer and Wright (1966), McKnight (1975) and the arguments presented here is provided below. For comparative purposes, the equivalent classification of Spencer and Wright (1966) is also included.

Revised classification:	Spencer and Wright (1966):
Class Somasteroidea	Class Stelleroidea
Order Goniactinida	Subclass Somasteroidea
Family Chinianasteridae	Order Goniactinida
Family Villebrunasteridae	Family Chinianasteridae
Family Archegonasteridae	Family Villebrunasteridae
Family Archophiactinidae	Family Platasteriidae (includes <i>Platasteris</i>
Family Helianthasteridae	<i>latiradiata</i>)
Class Asteroidea	Family Archegonasteridae
Order Platyasterida	Family Archophiactinidae
Family Palasteriscidae	Subclass Asteroidea
Order Paxillosida	Order Platyasterida
Suborder Hemizonina	Family Palasteriscidae
Suborder Diplozonina	Family Luidiidae
Family Luidiidae (includes <i>Luidia</i>	Order Paxillosida
(<i>Platasterias</i> <i>latiradiata</i>)	Suborder Hemizonina
Family Astropectinidae	Suborder Diplozonina
Family Porcellanasteridae	Family Astropectinidae
Suborder Cribellina	Family Porcellanasteridae
Class Ophiuroidea	Suborder Cribellina
	Subclass Ophiuroidea

The gap in the fossil record of the Platyasterida sensu Fell 1963a

The fossil record does not support an inference that the lineage leading to *Luidia* has endured nearly unchanged from the Palaeozoic. The order Platyasterida *sensu* Fell (and Spencer and Wright 1966) includes three genera assigned to two families: *Platanaster* (M. Ord.) and *Palasteriscus* (L. Dev.), both belonging to the Palasteriscidae, and *Luidia* (Mio.-Rec.), belonging to the Luidiidae. There is thus a gap from Lower Devonian to Miocene in the inferred record of the order. At first inspection, this appears trivial because of the sketchy record of sea stars, but I believe it becomes more important when this record is carefully considered.

Among post-Palaeozoic sea stars, *Astropecten* and its close allies have a relatively good fossil record. This record seems to result from body structure, habitat, and habits. The sea stars have relatively stout marginal frames and at least *Astropecten* frequently lives in shallow waters on unconsolidated substrates, and burrows beneath the surface. The relative abundance of *Astropecten* as fossils does not necessarily result from a greater, enduring abundance (although they are very common today), but from where and how individuals live. *Luidia* lives in similar environments, and it too is a burrower; although the marginal frame is not as stout as in *Astropecten*, the inferomarginals of many species are comparable to those in *Astropecten*, and sturdier than those of the Asteriidae, a family known from the Jurassic and whose representatives are also sometimes found in similar habitats.

TABLE 2. Comparison of somasteroids and asteroids. Criteria available do not permit separation of *Platasterias* as a somasteroid. *Porania* (Poraniidae) is taxonomically distant from the somasteroids but still has many features in common with them. Data in part from Fell (1963a).

	ossicle alignment	ambulacral furrow	super-ambulacral	terminal	tube feet
somasteroids	primarily transverse in some, others longitudinal	not erect	absent	present or absent	?
<u>L. (Platasterias)</u>	both transverse and longitudinal	erect	present	present	non-suctorial
<u>Luidia clathrata</u>	both transverse and longitudinal	erect	present	present	non-suctorial
<u>Porania</u>	primarily longitudinal	erect	absent	present	suctorial
other asteroids	primarily longitudinal	erect	present or absent	present	non-suctorial and suctorial
	anus	body shape	feeding habits		
somasteroids	?	petaloid to large oral disc	inferred suspension or small particle bottom feeder		
<u>L. (Platasterias)</u>	absent	petaloid	carnivore		
<u>Luidia clathrata</u>	absent	small disc, strap-shape arms	carnivore		
<u>Porania</u>	present	large oral disc	suspension feeding, other		
other asteroids	present or absent	varied	varied		

Luidia is a common genus, with sixty or more species (many described since Döderlein 1920) widely distributed in temperate to tropical seas; further, individuals commonly are abundant. Individuals of most species of *Luidia* are relatively large and would not be readily overlooked in the fossil record. *Luidia superba* specimens have been reported from the Galapagos Islands with major radii up to 415 mm and an arm breadth at the disc edge of 60 mm (Downey and Wellington 1978). The absence of a fossil record for platyasterids (*sensu* Fell) from Devonian to Miocene certainly is not conclusive evidence that they were not present, but because structurally comparable sea stars known from similar environments do have long records, the absence of *Luidia* or its relatives requires explanation.

A functional explanation for the transverse alignment of ossicles in Luidia

Fell argued that the body plan of *Luidia* is the direct phylogenetic heritage of Cambrian crinoids; in effect, that functional explanations of the morphology of these contemporary, mobile carnivores, living with their oral surfaces toward the substrate, are to be sought in ancient, attached suspension-feeding organisms living with their oral surfaces directed into the water column. I believe an explanation for the *Luidia* body plan can be developed that is more closely linked to the life needs of sea stars.

The arms of *Luidia* are very flexible in part because they are narrow and low and in part because the alignment of ossicles yields essentially a segmented pattern in which each radial row of ossicles is relatively weakly connected to adjacent rows. This arrangement weakens toward the middle of the aboral surface of the arm, where the abactinals are too small to interfere with flexibility.

The value of flexibility to *Luidia* can be correlated with preferred food and habitat. *Luidia* is a predator on larger solitary organisms—molluscs, arthropods, and other echinoderms—in which long, flexible arms are useful for the manipulation of prey. *Luidia* is commonly an inhabitant of shallow, often agitated, bottoms and, further, it frequently burrows into the substrate. Arm flexibility is useful for burrowing (Heddle 1967) and also for righting (Blake 1981).

L. (P.) latiradiata shares the ossicle arrangement of traditional *Luidia* species, and it, too, is an active predator (see above), but in it the demands of environment (Madsen 1966) might have dominated the need for maximum arm flexibility.

A superficially similar transverse alignment is seen in *Asterias* and other asteriids in the rows of arm ossicles immediately lateral to the furrow columns (Pl. 21, fig. 7). The ancestry of the Asteriidae is unknown, and therefore it is not known when this alignment evolved, but asteriids, like *Luidia*, are active predators with a need for relatively flexible arms.

Another hypothesis for ossicle alignment in *Luidia* and *Astropecten* can be based on the burrowing habits of these sea stars combined with the respiratory current flow described by Gislén (1924). Although surface currents appear typical of sea stars, deep fascioles seemingly are restricted to burrowers. These channels, combined with their cover spinelets, should provide protection from sediment interference for the current flow. Alignment of ossicles and their intervening channels in turn would permit a more efficient water flow than that possible in a species with an irregular arrangement of ossicles. Surface-dwelling species presumably would suffer less from current disruption and, in them, furrows generally are lacking.

Archaster is an extant genus superficially very similar to *Astropecten* in both form and habit. It too has relatively deep fascioles (Pl. 21, fig. 8), but only between the infero-, and not the superomarginals. *Archaster*, however, is an atypical member of the Valvatida rather than the Axillosoida, as is *Astropecten*. It is possible that *Archaster* was derived directly from an *Astropecten*-like source but the skeletal morphology in this genus does not seem to support such an idea; convergence resulting from habitat similarities is a preferable hypothesis.

Thus, both the alignment of ossicles in the arm and the grooves between the aligned ossicles seem subject to convergent evolution; use in any phylogenetic scheme must be made with great care.

SUMMARY

Platasterias latiradiata Gray is removed from the Somasteroidea and assigned at subgeneric rank to the genus *Luidia* of the monogeneric asteroid family Luidiidae; *Luidia (Platasterias)* therefore should not be singled out as a model for the reconstruction of the biology of early stellate echinoderms. Reasons for the transfer of *L. (Platasterias)* are: (1) The single distinctive feature of the Palaeozoic somasteroids seems to be the absence of a permanent ambulacral furrow. In contrast the adambulacral/ambulacral arrangement in *L. (P.) latiradiata* is the same as that found in *L. clathrata* and essentially as in all other living asteroids; a true furrow is present in *L. (P.) latiradiata*. (2) Individual ossicle morphology and ossicle and muscle arrangement of *L. (Platasterias)* are easily within a reasonable range of variation for *Luidia*. Although many (but not all) ossicles of *L. (P.) latiradiata* are proportionately broad, they are morphologically closer to the Clathrata Group species of *Luidia* than these ossicles are in turn to the Ciliaris Group species of *Luidia*. (3) A reconstruction of phylogenetic history based on ossicle alignment (growth gradients) requires important reversals of direction of evolution in order to enable fossil somasteroids and extant *L. (Platasterias)* and other luidiids to fit the hypothesis. (4) Two important ossicle types, the odontophore and superambulacral, are present in *L. (Platasterias)* and other extant sea stars, but they apparently are absent from the fossil somasteroids. (5) Although *L. (Platasterias)* has a petaloid arm shape suggestive of that of certain crinoids, weakly developed petaloid arms are present in

other taxonomically widely separated sea star taxa; the character is subject to convergence. (6) Known food habits of *L. (Platasterias)* suggest similarities to those of typical *Luidia* species and not to those habits inferred by Spencer (1951) for the fossil somasteroids. (7) Available data suggests soft-part morphology of *L. (Platasterias)* is essentially that of a typical *Luidia*.

The Luidiidae is transferred from the otherwise Paleozoic order Platysterida to the common post-Paleozoic Paxillosida.

The origin of the transverse alignment of ossicles in *Luidia* (including *Platasterias*) is ascribed to habits and habitats of the sea star. This ossicle arrangement enhances arm flexibility, useful to an active, burrowing predator living in shallow, often turbulent, environments. The presence of deep furrows between aligned ossicle series also provides an open channel, unimpeded by sediment, for the flow of respiratory water currents.

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A LOWER CARBONIFEROUS AĪSTOPOD AMPHIBIAN FROM SCOTLAND

by CARL F. WELLSTEAD

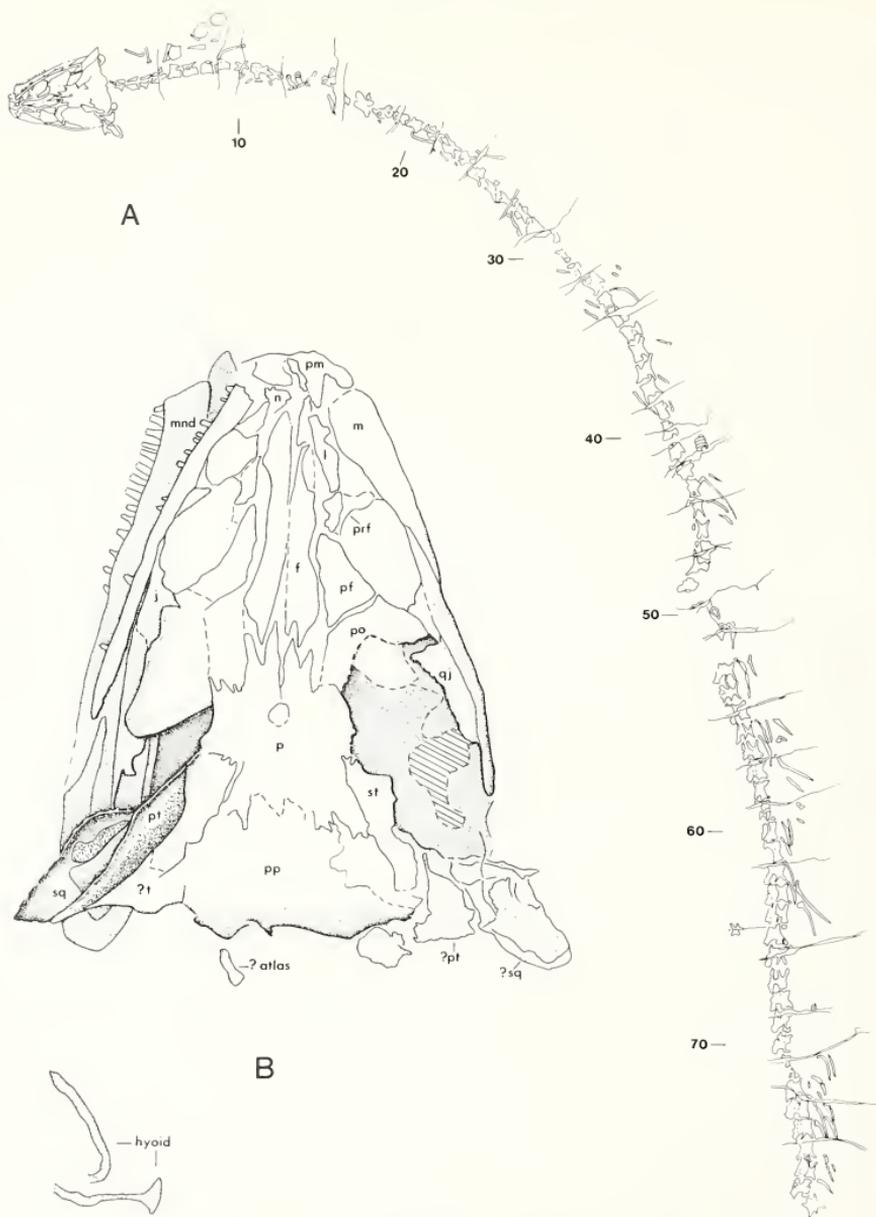
ABSTRACT. '*Ophiderpeton*', a mid-Viséan aĭstopod from the Wardie Shales near Edinburgh is described. Although '*Ophiderpeton*' possesses many of the attributes characteristic of aĭstopods and seems generally more closely comparable to ophiderpetontids than to phlegethontiids, details of cranial anatomy such as possession of a relatively short skull, short parietals, and the absence of a tabular-parietal contact, as well as the presence of spinal-nerve foramina in only a portion of the vertebral column and the absence of tetra-radiate ribs, postcranially, distinguishes '*Ophiderpeton*' from both of the currently recognized aĭstopod families. On the basis of these differences, '*Ophiderpeton*' is renamed, *Lethiscus stocki*, and a new family, Lethiscidae, is erected to hold the new species.

OF all Palaeozoic amphibians, the aĭstopods are the most specialized and phylogenetically isolated. The genera known from the Upper Carboniferous are totally without limbs and have up to 230 trunk vertebrae. The vertebrae are simple cylinders, without a trace of trunk intercentra or caudal haemal arches. The skull has lost much of the dermal cover common to labyrinthodonts and rhipidistians. These snake-like aĭstopod genera have been classified among the lepospondyls along with nectrideans and microsaurians, sharing with them such features as holospondylous vertebrae, lack of an otic notch, absence of labyrinthine infolding of teeth, and absence of palatine teeth. It is not certain that these features indicate common ancestry.

In addition to the familiar Upper Carboniferous genera, a single specimen from the Lower Carboniferous, originally identified by Thomas Stock (1882) as an aĭstopod, has lain undescribed for nearly a century. The latest discussion of this specimen was that of Baird (1964), who accepted Stock's identification, and cited a number of broad similarities it held with the Upper Carboniferous genera. Baird also mentioned the difficulty in studying the specimen which had contributed to its neglect. To gain more information about the early differentiation of Palaeozoic amphibians, a further attempt has been made to study the specimen.

The specimen (text-fig. 1) is 49 cm long and is preserved in a very elongate nodule, which was originally broken into dozens of pieces, each of which was split through the middle to give a series of sections through the skull and vertebrae. No attempt was made by Stock to prepare the specimen further. Preliminary efforts to remove the matrix from the bone, mechanically and chemically, have not been successful, although X-ray photography and tomography have revealed some detail of the skull and postcranial skeleton otherwise concealed in matrix.

Presently, enough detail can be seen in the sections to give a general description of the animal and to provide sufficient information about its anatomy to allow discussion of its relationships to other lepospondyls. The only further 'preparation' has been to clean glue and a century's accumulation of grime from the specimen. This cleaning revealed with startling clarity vertebrae, ribs, scales, and sections through the skull. The bone is preserved, but is outlined with a thin coating of pyrite. The neural and notochordal canals and large lacunae within the bones and skull are filled with calcite. Details of bone histology are evident, and the random breakage of the nodule has produced a series of sections in many planes. Information provided by these sections would be lost were the bone to be removed for production of latex casts following Baird's technique (Baird 1955); therefore, this otherwise very effective method of preparing specimens was not attempted. Normal external views of the bone are rarely evident, but those available reveal sufficient detail along the column to allow



TEXT-FIG. 1. *Lethiscus stocki*, MCZ 2185. A, whole specimen, $\times \frac{1}{2}$. B, skull, $\times 3$.

description of some regional differentiation. Revealed in the cleaned specimen were several characteristics which ally it with the Aistopoda, but also others which distinguish it from aistopod families Phlegethontiidae and Ophiderpetontidae.

MATERIALS AND METHODS

A standard medical X-ray machine and the Stratomatic tomography X-ray machine with tri-spiral movement and 0.6 focal spot were used to produce the X-ray photographs critical to the description of this specimen. The film used was Ilford X-ray film.

Text-fig. 3 is an X-ray of the half-nodule containing the skull less the posterior skull roof. X-rays of the half-nodule bearing the posterior skull roof revealed no more than can be seen with the naked eye. The matrix of the nodule is too dense for successful application of X-rays to the assembled skull-bearing nodule halves.

Abbreviations used in figures

bo—basioccipital; bs—basisphenoid; c—coronoid; cap—capitulum; ect—ectopterygoid; ep—epipterygoid; f—frontal; it—intertemporal; j—jugal; l—lacrimial; m—maxilla; mnd—mandible; n—nasal; ot—otic capsules; p—parietal; pf—postfrontal; pm—premaxilla; po—postorbital; poz—postzygapophysis; pp—postparietal; prf—prefrontal; prz—prezygapophysis; ps—parasphenoid; pt—pterygoid; q—quadrate; qj—quadratojugal; sq—squamosal; st—supratemporal; t—tabular; tub—tuberculum; v—vomer.

SYSTEMATIC PALAEOLOGY

Class AMPHIBIA
 Sub-class LEPOSPONDYLI
 Order AISTOPODA
 Family LETHISCIDAE fam. nov.

Diagnosis. Same as for the only known genus.

Lethiscus gen. nov.

Type species: *Lethiscus stocki* sp. nov.

Diagnosis. A small elongate amphibian with holospondylous vertebrae and short-snouted skull bearing lateral temporal fenestrae. Orbits placed in the anterior third of the skull and separated from the temporal fenestrae by the postorbital bones. The bones of the prefrontal-postfrontal-postorbital series increase in size posteriorly. Intertemporal absent. Parietals roughly equivalent in length to the frontals and surrounding a large parietal opening. Tabulars do not contact the parietal bones. Postparietals relatively large. Mandibles deep and long, approximating the length of the skull.

The trunk is very long. Differentiation along the vertebral column is expressed by the presence in the posterior portion of the column of spinal-nerve foramina, serrated neural spines and transverse processes rising, in part, from the centra. Anteriorly, transverse processes arise solely from the neural arches and spinal-nerve foramina are absent. Ribs are bicipital and robust.

Etymology. The generic name extends Cope's practice of naming serpentiform 'lepospondyls' for rivers in Hades. In this case, *Lethe* is a stream named for the Greek god of forgetfulness.

Lethiscus stocki sp. nov.

Diagnosis. The same as for genus. Specific name honours the discoverer of the specimen.

Holotype. MCZ 2185. Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A. Skull and postcranial skeleton. This is the only known specimen.

Locality and horizon. Stock (1882) discovered the specimen in the shales of the Wardie shore, north of Edinburgh, Scotland (Wood 1977, gives further locality data). These beds, the Wardie Shales, lie in the middle of

the Lower Oil Shale Group (Mitchell and Mykura 1962) and have a mid-Viséan age (text-fig. 2a). The base of the Arthur's Seat Volcanic Beds defines the base of the group in the Edinburgh vicinity, though they cannot be traced regionally. Fitch, Miller, and Williams (1970) report a potassium-argon date of 347 ± 5 my B.P. from these volcanics. George, Johnson, Mitchell, Prentice, Ramsbottom, Sevastopolos, and Wilson (1976) place volcanic rocks dated at 338 ± 4 my B.P. (Fitch *et al.* 1970) in the lower portion of the Upper Oil Shale Group. The Wardie Shales can, therefore, be estimated as approximately 340 million to 345 million years old. George *et al.* (1976) correlate the mid-Viséan with the Middle Mississippian (Meramec) of North America.

DESCRIPTION

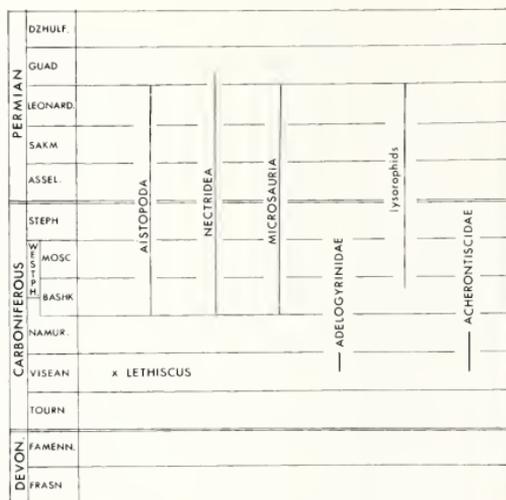
Skull

The skull (text-fig. 1) is exposed in an irregular para-frontal fracture which in one half-nodule yields an unobscured view of a portion of the left suspensorium and of the ventral surface of the skull table posterior to the fronto-parietal suture. In the other half-nodule only extremely irregular sections of the remainder of the skull can be seen. A second fracture yields an oblique section of the left lateral aspect of the skull. The circum-orbital bones have been interpreted through study of the specimen, an X-ray of the second half-nodule (text-fig. 3) and tomographs. The remainder of the skull, including the snout, lateral and ventral margins, portions of the palate and mandibles have been interpreted almost entirely from this X-ray and from the tomographs.

The skull is preserved in three dimensions with some distortion and fracturing of the snout, ventral skull margins, and tabular-suspensorium regions. As is the case with the post-cranial portion of the specimen, the

EAST W LOTHIAN	SMITH <i>et al.</i> 1967 (P ₂ -D ₂) GREEN & WELCH 1965 (S ₂ -K)	MIOspore ZONES NEVES <i>et al.</i> 1972 CLAYTON <i>et al.</i> 1974	STAGES
LOWER LIMESTONE GROUP	P ₂	NC (pars)	BRIGANTIAN
	D ₂	VF	
UPPER OIL SHALES GROUP	D ₁	NM	ASBIAN
LOWER OIL SHALES GROUP	S ₂	TC	HOLKERIAN
		PU	
LOWER OIL SHALES GROUP	C ₂ S ₁ (pars)	VISEAN	ARUNDIAN
			CHADIAN
			COURCEYAN
CEMENT- STONE GROUP	C ₁	TOURN.	COURCEYAN
	Z	VI	
	K		
	O. R. S. FACIES		

A



B

TEXT-FIG. 2. A, correlation chart of Lower Carboniferous stratigraphy in the Scottish Midland Valley (after George *et al.* 1976). B, range chart of the 'lepospondyls' (Carroll 1977; Olson 1972; Thomson and Bossy 1970).

bone is well preserved, but much softer than the enclosing matrix, rendering mechanical preparation hazardous. Bones are coated with pyrite, which accentuates sutures as well as cracks, but adheres closely to the bone. This coating obscures any ornamentation and evidence of lateral line canals which might exist. The skull is triangular in shape, widest at its posterior extreme and is approximately twice as wide as it is high. Openings are present in the skull roof for external nares, orbits, the parietal opening, and temporal fenestrae. The orbits are in the anterior third of the skull.



TEXT-FIG. 3. X-ray photograph of skull, *Lethiscus stocki*, MCZ 2185, less the skull roof posterior to fronto-parietal suture. $\times 3$.

The relationships of the bones in the skull table can be viewed directly and are, therefore, more confidently interpreted than are those seen in X-ray. The bones surrounding the parietal opening are assumed to be the parietals and further homologies within the skull table follow the discussion of the skull bones in *Ophiderpeton* by Thomson and Bossy (1970, p. 24).

The parietals bear dentate sutures with surrounding bones and are fused to one another posterior to the parietal opening. The postparietals are also fused and together with the parietals comprise two-thirds of the skull table area. The postparietals are broader posteriorly than at the parietal border and extend to the rear margin of the skull.

The postparietals are excluded from the temporal fenestrae by the supratemporal and tabular bones. Intertemporal bones are absent. The supratemporals are rectangular bones approximately three times as long as they are wide. Their medial sutures with the postparietals and parietals are smoothly sinuous while their anterior margins have dentate sutures with the parietal bones. The posterior margins are poorly defined. Ventrally, the supratemporals appear to bear sutures with the pterygoids, although the contact is obscured by sediment and breakage along the parafrantal fracture.

A suture-like lineation, seen in the specimen intersecting the posterior margin of the left postparietal, taken in conjunction with the posterolateral borders of the skull table and the posterior regions of the supratemporals, provides the evidence for the tabular bones. An element between the right supratemporal and the fused postparietals appearing to bear a contact with the parietals may be a medial process of the right tabular. However, the mate of this 'tabular' process is not found on the left side of the skull table, suggesting that the feature is more probably an irregular fracture within the postparietals and that the tabulars have no contact with the parietals. The ventral margins of the tabulars are obscured by sediment and breakage, but would seem to have had a short suture with the squamosal posterior to the squamosal-ptyergoid contact.

The relationships of the frontals, parietals, and the right orbital series can be observed directly. The frontals are paired, narrow, and equal in length to the parietal and postparietal. They share an interdigitating suture with the parietals, but have a sinuous suture with pre- and postfrontals and postorbitals.

The fragment anterolateral to the left frontal is taken questionably as the small left nasal.

The postfrontal and postorbital separate the orbit from the temporal fenestrae. The prefrontals are small elements of indistinct shape. The postfrontals are approximately twice as long as the prefrontals and are wedge-shaped. While the posterior portion of the right postorbital is missing, the left one seems to be complete and is large, approximately 2.5 times the size of the postfrontal. The exact nature of the relationship of postorbital to the lateral edge of the parietal is obscured by sediment.

The lacrimals are elongate bones which seem to form the anterior portions of the orbital margin and extend to the external nares.

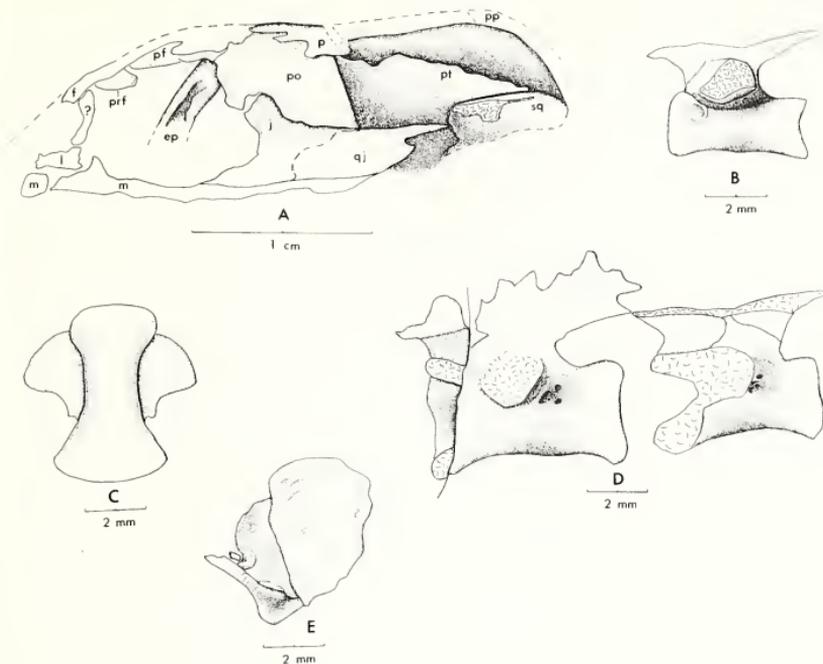
The left and right jugals can be seen directly in the specimen, although the left jugal is the better exposed along the oblique lateral fracture surface (text-fig. 4A). The indefinite suture indicated between jugal and quadratojugal represents a conspicuous separation between two bony elements in the specimen, but which cannot be interpreted confidently as either a suture or fracture. The dorsal surfaces of these two bony elements appear in text-fig. 3 as one distinct dark element. The orbital margin of the jugal is visible in X-ray as well. This portion of the orbital margin is completed dorsally by a large anterodorsal process of the jugal.

The quadratojugal is an elongate bone which bears a long suture with the maxilla and a comparatively brief one with the postorbital. The posterior portion of the left quadratojugal appears to have been lost through breakage. However, some indication of this portion of the right quadratojugal is supplied by the lateral margin of the subtemporal fossa (text-figs. 3 and 5B), which is interpreted as quadratojugal. The manner of attachment of the quadratojugal to the suspensorium is uncertain.

An element appearing in the X-ray at the anterior extremity of the specimen to the right of the midline is interpreted as the right premaxilla. The element has one process directed laterally toward the right maxilla and a second directed posteriorly toward the right frontal bone. No teeth can be distinguished, however.

Both left and right maxillae appear in X-ray. They are long slim bones which extend well posterior to the orbits and form a portion of the narial margin. The right maxilla is essentially in place and is cracked along its orbital margin. It is expanded anteriorly into a broad process. The identification of this process is uncertain, for depending upon the amount of distortion in this region of the skull, it may be either a nasal process or palatal process of the maxilla. There are 11 teeth in the left maxilla and 18 in the right.

A limited portion of the left squamosal (text-figs. 1 and 4A) is exposed. It is a rounded, rectangular bone and is somewhat displaced to exhibit a portion of its sutural contact with the quadrate ramus of the pterygoid.



TEXT-FIG. 4. *Lethiscus stocki*, MCZ 2185. A, lateral view of skull. Composite of information from left and right sides of skull, $\times 3$. B, left lateral view of vertebra seven. Composite, $\times 5$. C, ventral view of vertebra fifteen, $\times 5$. D, left lateral views of vertebrae 57 and 58, $\times 5$. E, notched sarcopterygian scale and associated elongate element, $\times 5$.

Temporal fenestrae

The temporal fenestrae (text-figs. 4A and 6A) are bounded dorsally by the parietal, supratemporal, and tabular bones, anteriorly by the postorbital, laterally by the quadratojugal, and medially by the squamosal and by the ascending flange of the quadrate ramus of the pterygoid. The fenestrae continue to the posterior margin of the skull.

Palate

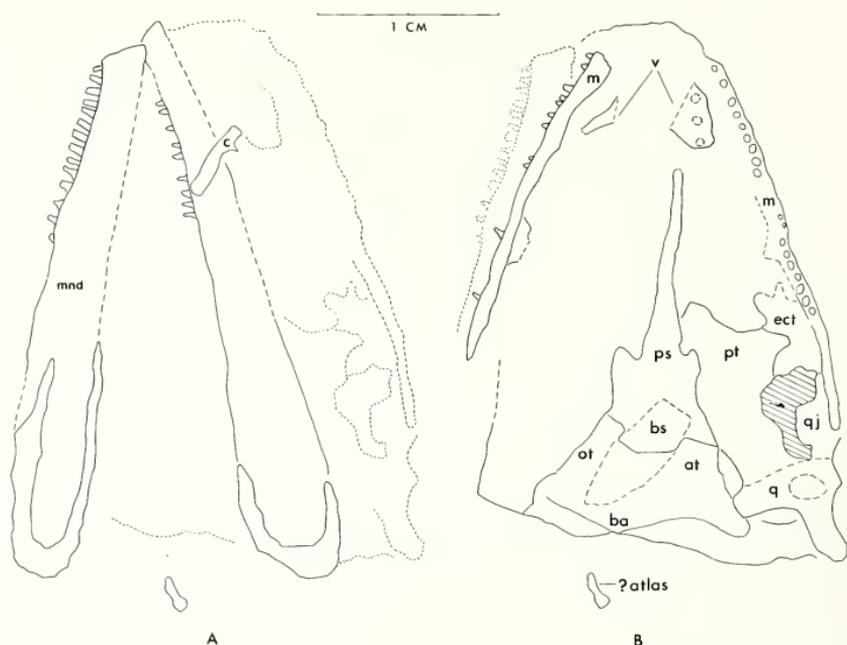
Elements of the palate (text-fig. 5B) are interpreted entirely from the X-rays.

Two elements, which appear in tomographs of ventral portions of the skull, may be vomers judging from their relatively anterior position. Their relationships to each other and to surrounding bones are not known. The right vomer appears to bear three teeth comparable in cross-sectional area to maxillary teeth. Nothing of the palatine bones can be distinguished in the X-rays.

Portions of the right pterygoid and ectopterygoid are seen in text-fig. 5. The pterygoid bears a high dorsal flange (text-fig. 4A) which extends from the quadrate ramus toward the supratemporal and posteriorly contacts the squamosal. The portion of the right pterygoid identified in text-fig. 1B is probably a fragment of this flange. The anterior portions of the pterygoids cannot be discerned in the X-ray and may be missing. Sutural contact between the pterygoid and supratemporal is obscured by matrix and bone loss along the fracture surface of the nodule.

The subtemporal fossa is defined by the pterygoid, ectopterygoid and quadratojugal. The fossa is small and is constricted by a blunt portion of the quadratojugal. Its small size and irregular lateral margin suggest that this region has been distorted.

The parasphenoid appears clearly in X-ray. It is displaced to the right, partially overlying the medial edge of the right pterygoid. The cultriform process is long and has a narrow base. The basicranial processes can be confidently interpreted on either side of the base of the cultriform process of the parasphenoid. The posterior portions of the parasphenoid cannot be distinguished from the basisphenoid.



TEXT-FIG. 5. *Lethiscus stocki*, MCZ 2185. A, mandibles interpreted from X-ray and viewed dorsally, $\times 3$. B, portions of palate and braincase interpreted from X-ray and viewed dorsally, $\times 3$.

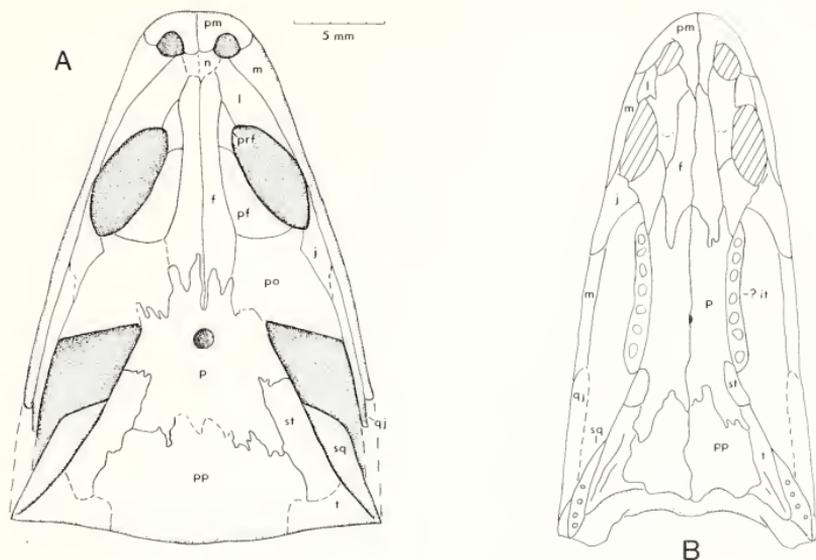
Braincase

There is no evidence of braincase contact with the dermal roofing bones, suggesting that the dorsal portions of the braincase were not ossified.

The oblong, X-ray opaque structure (text-fig. 3) centrally placed in the braincase is taken to be the matrix-filled brain cavity. It is distorted to the right as is the entire braincase-parasphenoid unit.

A suture distinguishes the basisphenoid region of the braincase from the basioccipital. The structures lateral to the brain cavity are assumed to be the otic capsules, although pro- and opisthotic bones cannot be individually distinguished nor are the otic regions clearly delimited from the occipital elements.

A tubular bone is exposed in the calcite filling of the inter-orbital space (text-fig. 4A). It tilts posteriorly as it rises toward the skull roof and is broken at its ventral extremity. From its structure the bone appears to be the left epipterygoid, although displaced anteriorly from its normal position dorsal to the basicranial articulation.



TEXT-FIG. 6. Comparison of skulls. A, reconstruction of *Lethiscus stocki*, MCZ 2185, $\times 3$. B, *Ophiderpeton* (Thomson and Bossy 1970), drawn to length of *Lethiscus* skull.

Mandibles

With the exception of tooth alveoli revealed in a fracture section of the left mandible, the lower jaws are visible only as outlines in X-ray. The left mandible lies with its medial surface turned dorsally. The right mandible has its lateral surface upward. In the posterior margin of each mandible, U-shaped structures corresponding to the positions of surangular, articular, and angular can be differentiated, but no sutures can be discerned between these elements.

An elongate, rectangular element lies across the right mandible approximately one-third of its length from the symphysis. It bears a pointed process and is tentatively identified as a coronoid, probably of the right mandible.

Fourteen teeth are apparent in the left mandible. Nine can be counted in the right. The teeth of the mandibles seem to be short and peg-like as are those of the maxillae, though the nature of their crowns is not certain.

Hyoid elements

Two elongate elements revealed in the X-ray (text-fig. 3; also 1B) are hyoid elements, perhaps epibranchials. Fragments lateral to vertebrae 4 and 5 (text-fig. 7A) may be additional hyoid elements or possibly ribs, but no positive identification can be made. There is no evidence of gill rakers, internal or external gills, nor of the sickle-shaped hyoid noted in other aïstopods (Baird 1964).

Vertebrae

Seventy-eight vertebrae are visible in sequence (text-figs. 7, 8, 9). An additional vertebra can be distinguished in X-rays dorsal to vertebra 65. Vertebrae 1 through 5, 9 through 12, 15 through 28, and 42 through 46 are viewed ventrally. Alternating with these series are vertebrae exposed in lateral view and vertebrae 49, 50, and 51 which are seen end-on.

The vertebrae are clearly holospondylous. Bony elements seen between centra of the sixth, seventh, and eighth vertebrae are found nowhere else in the column and may be mineralized intercentral cartilages similar to those described in salamanders (Wake 1970; Wake and Lawson 1973) or merely displaced fragments of the adjacent centra.

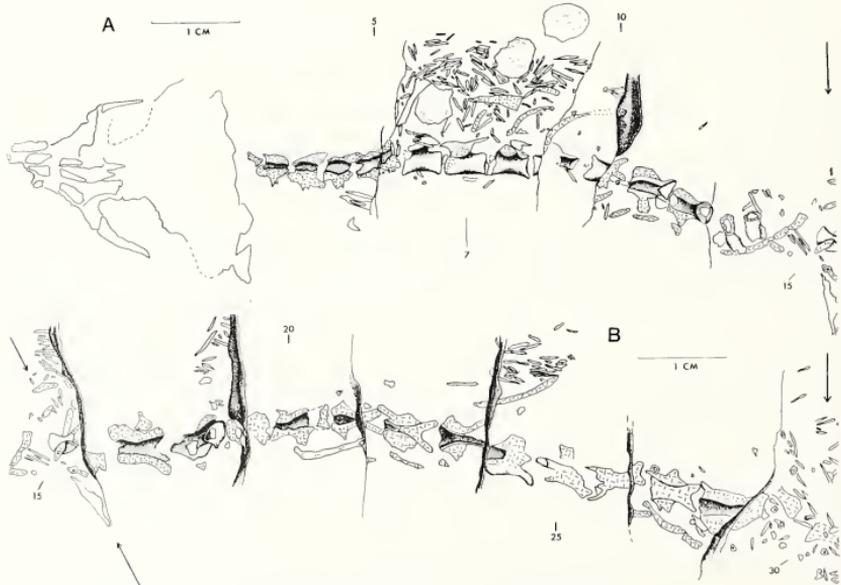
The centra are hour-glass-shaped and deeply amphicoelous. Sections along the column show the notochord to be severely constricted and possibly discontinuous at midcentrum. The lateral and ventral surfaces of the centra are smooth except for slightly concave, round facets near the anterior rim which are the articular surfaces for the rib capitulum (text-fig. 4B). The centra bear no pits, grooves, or accessory processes.

Vertebral length increases antero-posteriorly along most of the column. The average length for vertebrae 6, 7, and 8 is 4.5 mm. Vertebrae 34, 35, and 37 average 5.2 mm in length, while vertebrae 52 through 78 average approximately 6 mm in length. The untapered nature of these vertebrae, as well as the presence of ribs along the column, suggests that this portion of the skeleton represents the trunk of *Lethiscus*. The isolated vertebra is only 4 mm long and, by virtue of its small size, is the only indication of a tail in the specimen.

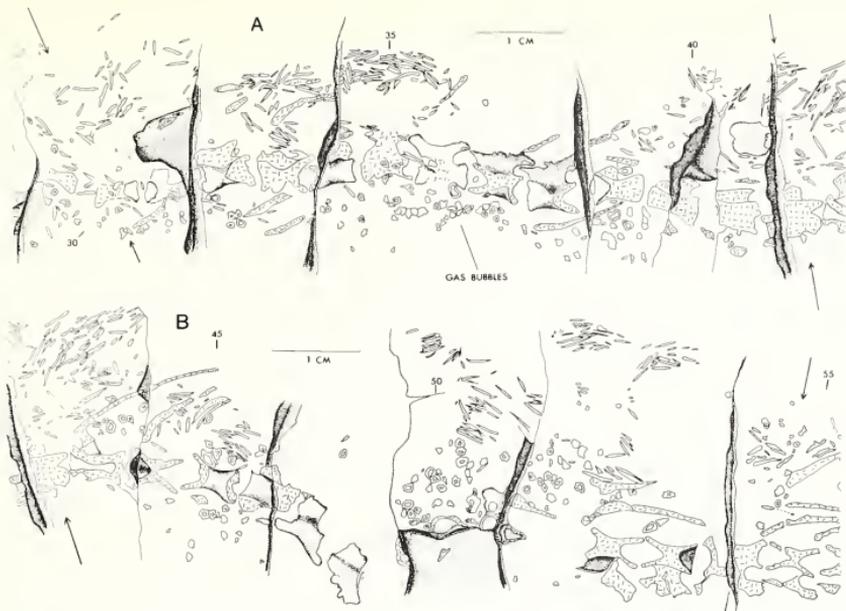
Neural arches of the vertebrae are swollen, unpaired, and are fused to their centra with no trace of suture. The pedicel length is approximately two-thirds that of the centrum. The neural spines anterior to vertebra 37 are not well exposed. However, a transverse section of vertebra 9 (text-fig. 10A) shows the spine to be relatively high. More posteriorly, the neural arches can be seen to extend the length of the neural arch and to be tall, rising antero-posteriorly (text-fig. 9A and B). The spines bear jagged edges and have faint grooves between the teeth of the serrations, suggesting a crinkled appearance. It is not clear whether the jagged appearance is natural or due to poor ossification or breakage. Transverse sections through the vertebral column show that the neural spines bifurcate at their posterior extremities and bear a deep medial groove (text-fig. 10 C and D).

Neural-arch processes bearing zygapophyses project at approximately 30° from the sagittal plane, but extend little laterally beyond the centrum (text-fig. 10C and D). Zygapophyses are oblique to the sagittal plane.

All post-atlantal vertebrae bear stout transverse processes which, in the more anterior vertebrae, are located on the neural arches (text-figs. 7A and 10A), rather than on the centra as in other aistopods. The processes project laterally, but breakage obscures the surface of rib articulation. In contrast to the transverse processes of the anterior vertebrae, the transverse processes of vertebrae 44, 57, and 68 through 78 can be seen to arise, in part, from the centra (text-figs. 9 and 10B).



TEXT-FIG. 7. *Lethiscus stocki*, MCZ 2185, postcranial skeleton, $\times 1.4$. A, vertebrae 1 through 15. B, vertebrae 15 through 30.



TEXT-FIG. 8. *Lethiscus stocki*, MCZ 2185, postcranial skeleton, $\times 1.4$. A, vertebrae 28 through 43. B, vertebrae 42 through 56.

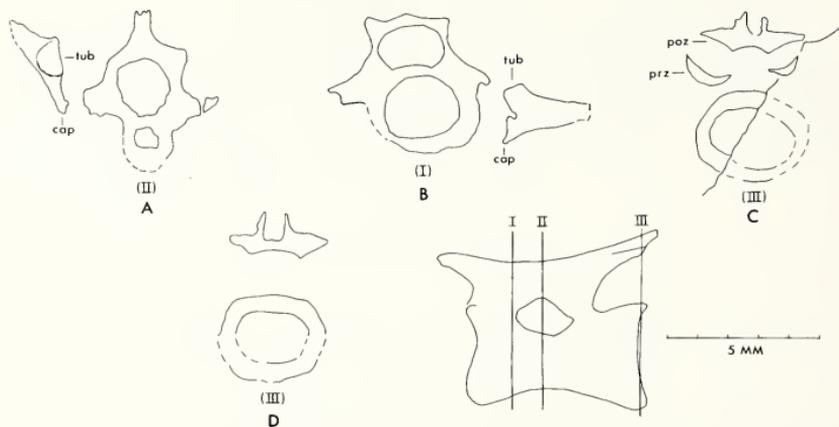


TEXT-FIG. 9. *Lethiscus stocki*, MCZ 2185, postcranial, $\times 1.4$. A, vertebrae 55 through 68 and isolated vertebra. B, vertebrae 68 through 78.

Where the lateral surfaces of the posterior vertebrae are exposed, as in vertebrae 57, 58, and 68, a fossa is seen immediately posterior to the transverse processes (text-fig. 9A). In the floor of this fossa are foramina, presumably for exit of spinal nerves. Such foramina cannot be identified in vertebra 7, the only anterior vertebra suitably exposed.

Ribs

Fragments of ribs are exposed along the length of the vertebral column, but are best revealed posterior to vertebra 36. Here, ribs are seen to have a dog-legged bend just posterior to the rib head. Distal to this bend the ribs are straight. An accessory rib process is suggested by the sharp angle of the bend, but no substantial evidence of the characteristic K-shaped aistopod rib is exhibited in the specimen. The ribs are bicipital anterior to vertebra 44 (text-fig. 10A and B), but the nature of their vertebral articulation is not exposed more posteriorly. The rib head is set at a sharp angle to its body as can be seen in the vicinity of vertebrae 19, 20, 43, and 60.



TEXT-FIG. 10. Selected sections of vertebrae, $\times 5$. Roman numerals indicate approximate position of section in reference vertebra. A, vertebra 9. B, vertebra 44. C, vertebra 15 and prezygapophyses of vertebra 16. D, vertebra 23.

Ventral armour

Numerous, spindle-shaped dermal elements comprise the ventral armour, which would seem to have been continuous posterior to the level of the sixth vertebra. The pattern of the ventral armour has been severely disrupted. The ventral armour elements in *Lethiscus* appear to be stouter and to have blunter ends than those in *Ophiderpeton*, but this appearance may be due to the irregular sections in which the elements are exposed.

Dorsal osteoderms

Baird (1964) noted dorsal osteoderms in this specimen, but the only elements which might be interpreted as osteoderms are actually mineralized gas bubbles (text-fig. 8A). Sections of these elements show them not to be bone, but calcite cores coated with pyrite. Gas bubbles preserved in this manner have been reported in specimens from the Wardie Shales previously (Wood 1977).

Enterospira

In the vicinity of the forty-first vertebra is what appears to be a coprolite. Its segmented appearance is likely due to a spiral valve in the intestine of *Lethiscus*. As the coprolite has not been excreted, the term *enterospira* may be more correct (Williams 1972).

Sarcopterygian scales and possible pectoral girdle

Dorsal to vertebrae 6, 7, and 8 are many bony elements. Most of these are the spindle-shaped armour seen elsewhere in the specimen. Four others are probably slim fragments of rib. Most interesting are the three largest elongate bones and three irregularly round elements near them.

The round elements bear faint concentric rings and compare favourably with scales of sarcopterygian fishes. It should be noted, however, that concentric growth structures similar to these rings occur in endochondral limb and girdle elements of tetrapods as well (Mesosaurus, de Ricqlès 1974). The middle 'scale' has a notch in its rim which is similar to a glenoid fossa (text-fig. 4E). In the notch is a tiny fragment of bone, but whether the fragment has actually come to rest in a notch-like glenoid or whether compressional forces merely created the notch by forcing the fragment into the rim is uncertain.

The three large elongate elements could be posteriorly displaced hyoid elements or possibly remnants of the dermal pectoral girdle.

Although these six bones occur where a pectoral girdle would be expected, their lamentably poor exposure allows no confident identification. There is no other evidence of girdles or limbs in the specimen.

COMPARISONS

Skull

The skulls of both *Lethiscus* and *Ophiderpeton* (text-fig. 6) are relatively high-sided and possess temporal fenestrae bordered by identical elements of the skull roof. The orbits are anterior in position. Maxillae are elongate, slim, and extend far posterior to the orbit. The frontal bones have a similar proportional length relationship with the orbits. In *Lethiscus*, *Ophiderpeton*, and neotridians (Thomson and Bossy 1970) the skull table is comprised primarily by the parietal and postparietal bones. *Lethiscus*, however, appears to represent a more primitive pattern in that its parietal-postparietal suture is anterior to the supratemporal-tabular suture (Panchen 1970). As a result, *Lethiscus* lacks the tabular-parietal contact, the presence of which has been suggested as linking aïstopods and neotridians (Thomson and Bossy 1970). The later establishment of the tabular parietal contact in *Ophiderpeton* may then have come as the result of the posterior movement of the parietal-postparietal suture as suggested in anthracosaurs (Panchen 1970). Concomitant with the movement of this suture may have been the proportional increase in length of the parietal bones seen in *Ophiderpeton*.

In contrast to *Ophiderpeton* the supratemporals of *Lethiscus* are large and the skull table is much shorter. There is no indication of the intertemporal in *Lethiscus*. This bone may have been incorporated into the large postorbital. However, elongate pustulated bones have been identified as intertemporals in *Ophiderpeton* (Thomson and Bossy 1970).

In contrast to *Ophiderpeton* the jugal and quadratojugal in *Lethiscus* contact one another. The quadratojugal in *Lethiscus* also bears contacts with the postorbital and maxilla, perhaps strengthening the connection of the lateral skull margin with the skull table in response to bone loss resulting from fenestration of the skull roof. In *Lethiscus* the maxilla contacts the narial margin, but is excluded from it by the lacrimal in *Ophiderpeton* as reconstructed by Thomson and Bossy.

Other possible differences, such as the presence of nasals and the extent of the lacrimals and prefrontals cannot be determined unequivocally. The mandibles in *Lethiscus* and the palate and braincase in both *Lethiscus* and *Ophiderpeton* are also too poorly known to allow useful comparison.

Vertebrae

The vertebrae of *Lethiscus* differ from those of other aïstopods in lacking basiphysal accessory articulations and median ventral ridges (as seen in *Ophiderpeton nanum*, Steen 1931) and in possessing high neural spines. Absence of incontestable limb girdles makes distinction of trunk and caudal regions difficult. *Lethiscus* does, however, exhibit antero-posterior differentiation of the vertebral column in the position of transverse processes and by the possession of spinal-nerve foramina only in the posterior portion of the column. Similar differentiation has not been found in *Ophiderpeton*, although McGinnis (1967) reported that the two anterior-most vertebrae in *Phlegethontia* do lack spinal-nerve foramina.

The anterior vertebrae of *Lethiscus* are remarkable in their similarity to those of some microsaur, as well as to those of early reptiles. These in each case have smooth, unpitted surfaces, and are hour-glass-shaped. The neural-arch pedicels also bear the transverse processes. In contrast, neuro-central sutures are present consistently within the microbrachiomorph microsaur and variably within the tuditanomorphs, but are absent in *Lethiscus*. *Lethiscus* also lacks trunk intercentra, which occur in several microsaure genera.

The vertebrae of adelogyrinids and 'lyisorophids' (including both the Molgophidae and Lysorophidae) differ from those of *Lethiscus* in the consistent presence of neuro-central sutures, but are similar in lacking accessory articulations and in bearing the transverse processes on neural arches. The lysorophids further differ in the paired nature of their neural arches. The paired status of neural arches in the adelogyrinids is equivocal (Carroll 1967; Brough and Brough 1967; Watson 1921-1923).

The trunk vertebrae of nectrideans are similar to those of *Lethiscus* in lacking intercentral elements and in ossifying as single units. However, the only described nectridean in which intravertebral spinal nerve foramina can actually be seen is the urocordylid *Crossotelos*; keraterpetontids do not possess such spinal nerve foramina (Milner, A. C., pers. comm.). Furthermore, nectridean neural spines are specialized in their possession of accessory articulations, and rugose ornamentation (as in *Diploceraspis* and *Diplocaulus*), or in being flat-topped, fan-shaped structures with crenulated edges (as in *Sauropleura* and *Keraterpeton*, Baird, 1965; Steen 1938). Some faint suggestion of neural-spine crenulation is present in *Lethiscus*, but, as noted, the neural spines are otherwise serrated and inclined antero-posteriorly to the frontal plane.

The high number of trunk vertebrae found in *Lethiscus* is seen elsewhere only in aïstopods and in the tiny-limbed *Lysorophus* (Olson 1971) among the 'lepospondyl' amphibians. Nectrideans, in contrast, characteristically have short trunks (and long tails).

Limbs and girdles

Baird (1964) wrote that there is nothing interpretable as pectoral or pelvic girdle in any aïstopod. Although there is no contradictory evidence in *Lethiscus*, a recent study (see Boyd, M. J. F., this volume) has discovered an interclavicle in *Ophiderpeton nanum*.

Ventral armour

Spindle-shaped ventral armour like that in *Lethiscus* is seen in other aïstopods and nectrideans (Fritsch 1879; Huxley 1867) and with sculptured surfaces in the adelogyrinid *Adelospondylus* (Carroll 1967). Ventral armour in the microsaur is variable (Carroll and Gaskill 1978), but never consists of spindle-shaped elements. Such dermal armour is unknown in the lysorophids.

DISCUSSION

Lethiscus possesses nearly all the aïstopod characteristics compiled by Baird (1964). Aïstopod character states which can not be confidently identified in *Lethiscus* (e.g. hypapophyseal flanges of caudal vertebrae, K-shaped ribs, and sickle-shaped hyoid) are those in portions of the specimen not preserved or which are poorly exposed.

While *Lethiscus* is more closely comparable to *Ophiderpeton* than to *Phlegethontia* in the relatively primitive nature of its skull, robust ribs, and heavy ventral armour, it is distinct in further details of its skull and post-cranial anatomy. Its short skull and the absence of a tabular-parietal contact indicate a less derived state than that of *Ophiderpeton*, while the absence of accessory vertebral processes and K-shaped ribs and the presence of tall neural spines indicate that *Lethiscus* possessed a differently specialized post-cranial skeleton and trunk musculature than either the Ophiderpetontidae or the Phlegethontiidae.

The presence of spinal-nerve foramina in a portion of the vertebral column of *Lethiscus* is especially interesting, for such foramina are known to occur only in urodela lissamphibians, the Aïstopoda, and the nectridean *Crossotelos*. The presence of these foramina is considered to be a derived state in salamanders (Edwards 1976; Hecht and Edwards 1977) and would appear to be so in

aïstopods and *Crossotelos*. Particularly significant is the observation that the spinal-nerve foramina of salamanders are expressed in patterns characteristic of the various families (Edwards 1976). Although the pattern of spinal-nerve foramina is not well known in the vertebral column of *Ophiderpeton*, the contrast in patterns between *Phlegethontia* and *Lethiscus* suggests that the spinal-nerve foramina pattern may allow distinction of aïstopod families also.

The occurrence of an aïstopod in mid-Viséan rocks provides some limited confirmation of the estimated several million or tens of millions of years required to accomplish limb loss in tetrapods (Lande 1977). Although *Lethiscus* cannot be described with absolute certainty as lacking limbs or girdles, the rudiments of a possible pectoral girdle demonstrate the degenerate nature of any limbs it may have possessed. Assuming tetrapod monophyly, this limb reduction was achieved within a period of at least 30 million to 40 million years elapsing between Late Devonian tetrapod origins, represented by *Metaxygnathus* (Campbell and Bell 1977) and *Ichthyostega*, and the occurrence of *Lethiscus* in the mid-Viséan.

Lethiscus is the earliest known member of a group of small Palaeozoic amphibians known as 'lepospondyls', but unfortunately it reveals little about the evolution of any of these animals or of tetrapods in general because of the specializations of the skull and post-cranial anatomy already attained in the Lower Carboniferous. *Lethiscus* seems to confuse the issue somewhat, for, although Thomson and Bossy (1970) linked nectriceans and aïstopods through the shared possession of the tabular-parietal contact, the absence of such a contact in *Lethiscus* suggests that it was either achieved independently in the two orders or was lost in *Lethiscus* subsequent to a nectricean-aïstopod dichotomy. Similarly, the extremely limited occurrence of intravertebral spinal-nerve foramina in nectriceans suggests that these foramina were probably developed separately in nectriceans and aïstopods, arguing against consideration of the presence of the foramina as a shared derived-character state.

Acknowledgements. I am pleased to acknowledge Dr. Robert L. Carroll for giving me the opportunity to study this specimen. This report benefitted critically from comments received from Dr. Carroll, Dr. Donald Baird, Dr. A. R. Milner, Dr. A. C. Milner, Mr. Timothy Smithson, and Mr. Robert Holmes, to all of whom I am grateful.

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MORPHOLOGY AND RELATIONSHIPS OF THE UPPER CARBONIFEROUS AĪSTOPOD AMPHIBIAN *OPHIDERPETON NANUM*

by M. J. BOYD

ABSTRACT. The holotype and only recorded specimen of the Carboniferous aĭstopod amphibian *Ophiderpeton nanum* Hancock and Atthey 1868 is described in detail and figured for the first time. The vertebrae, ribs, dermal squamation, and premaxilla are characteristic of *Ophiderpeton* and confirm that *O. nanum* is a member of that genus. The relationship of *O. nanum* to other described *Ophiderpeton* species is obscured by the absence of most of the skull in the holotype and by the apparently sub-adult nature of the specimen. The ventral osteoderms are, however, unusually filamentous for *Ophiderpeton* and it is suggested that *O. nanum* be retained as a distinct species, pending revision of the Ophiderpetontidae. A small isolated bone in the holotype may be an interclavicle, suggesting the retention of a vestigial pectoral girdle in ophiderpetontid aĭstopods.

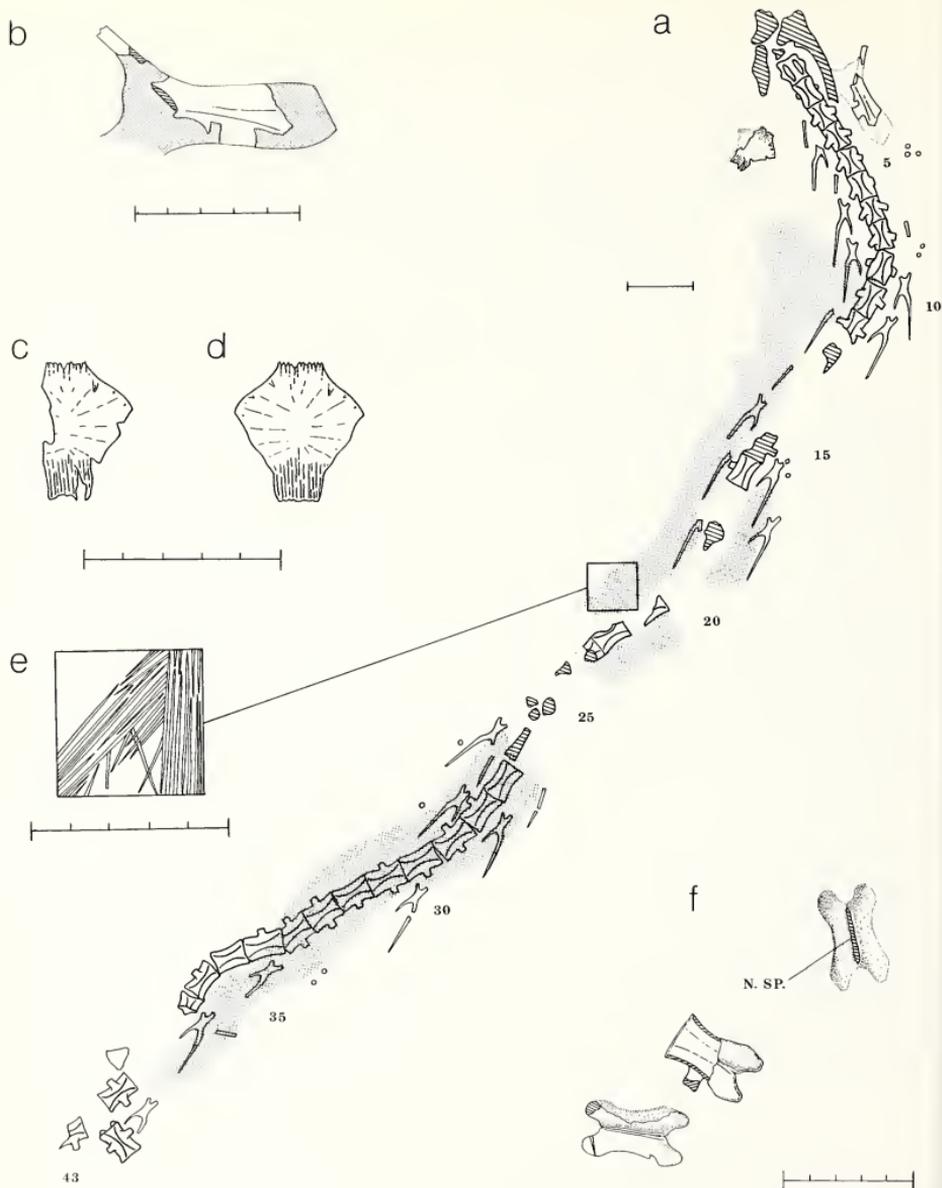
OPHIDERPETON NANUM Hancock and Atthey 1868, is a small 'lepospondyl' amphibian of the order Aĭstopoda from the Upper Carboniferous of Great Britain. The holotype and only described specimen of *Ophiderpeton nanum* was collected around the middle of the nineteenth century and is from the black shale immediately overlying the Low Main coal seam at Newsham, near Blyth, in Northumberland. This horizon lies within the Upper Modiolaris zone of the Middle Coal Measures (Land 1974) and is Westphalian B in age. *O. nanum* forms part of a large and well-known amphibian assemblage from Newsham, whose other members (listed by Land 1974, p. 61) include eogyrinid embolomeres, loxommatid temnospondyls, and keraterpetontid nectrideans. The above taxa appear to be characteristic of Upper Carboniferous coal-swamp lake environments (Milner 1978).

Although *O. nanum* was one of the first aĭstopods to be described, no detailed account of the structure or relationships of this species has hitherto been published and the holotype specimen has never been figured. Neither the original, necessarily superficial, description of *O. nanum* by Hancock and Atthey (1868) nor a subsequent brief account given by Steen (1938), are detailed enough to allow adequate comparison of this form with other described aĭstopods. The present paper is intended to remedy this deficiency.

The holotype of *O. nanum* consists of an incomplete skull and anterior postcranial skeleton preserved in counterpart on two small slabs of shale. The two halves of the specimen are registered in the collections of the Hancock Museum, Newcastle upon Tyne, as G25.34 and G25.35. Because of the small size and fragile nature of the holotype, the only preparation attempted has been the removal of small quantities of matrix from the immediate vicinity of the skull by means of mounted needles.

DESCRIPTION

The skull and most of the preserved postcranial skeleton are situated on slab G25.34 (text-fig. 1*a*). Slab G25.35, henceforth referred to as the counterpart, bears impressions of all but the most anterior seven vertebrae of G25.34, in addition to a small number of actual ribs and isolated patches of the ventral squamation. At some point in the past, small areas of the surface of slab G25.34, bearing sections of vertebral column and associated structures, have flaked away and been lost. However, as the resultant gaps in the vertebral series are all posterior to the seventh vertebra, the number of vertebrae originally preserved may be estimated by reference to the unbroken series of impressions on the counterpart. The skull and skeleton of G25.34 are preserved



TEXT-FIG. 1. *Ophiderpeton nanum* H & A. *a-c*, Hancock Museum specimen G25.34: *a*, semi-diagrammatic representation of specimen as preserved. Stippling indicates extent of ventral squamation; *b*, isolated (?) skull element. Stippling represents area preserved as impression only; *c*, interclavicle as preserved; *d*, interclavicle restored; *e*, detail of ventral squamation. *f*, Hancock Museum G25.35. Three isolated vertebrae as preserved. All scale lines represent 5 mm. N.SP., neural spine.

with their ventral surfaces uppermost. A large number of ribs is present. Although most of the vertebrae and ribs are overlain by a thin 'mat' of closely packed, filamentous gastralia, this is often so closely applied that the contours of the structures which it conceals may be clearly seen.

Skull

The skull apparently became disarticulated and scattered prior to preservation and is largely absent. Three distinct masses of poorly preserved bone lie immediately anterior to the first preserved vertebra. It is possible that they represent elements of the palate or neurocranium. A slight depression in the matrix anterior to these may mark the site of the isolated premaxilla noted by Steen (1938, p. 223). No trace of the bone itself remains; it has presumably become detached from the slab and lost.

A relatively large isolated bone, situated to the right of the most anterior four vertebrae in text-figure 1a, may, doubtfully, also belong to the dermal skull. Although much of the bone itself has been lost, the clear impression remaining in the matrix allows no question as to its original form. Its identity, however, is obscure. The element (text-fig. 1b) does not appear to correspond to any bone known in the skulls of either *Ophiderpeton* (A. C. Milner, pers. comm.) or phlegethontiid aistopods (e.g. Gregory 1948; McGinnis 1967). The triradiate form of the element makes it unlikely that it represents part of the dermal pectoral girdle. Possibly the bone in question does not, in fact, pertain to *O. nanum*.

A second isolated element, lying to the left of the vertebral column at the level of the third and fourth vertebrae (text-fig. 1a), is of some interest. Approximately one-quarter of the bone is missing but it is clear that the complete element was of roughly rhomboidal shape (text-fig. 1c-d). It is suggested that this element represents a displaced interclavicle. This hypothesis receives support from the presence of a slight (?parasternal) process at one angle of the bone and the fact that the margin of the element directly opposite the above process is noticeably fimbriated. Interclavicles with fimbriated anterior margins have been described in a number of both 'labyrinthodont' (e.g. Milner 1980, fig. 5) and 'lepospondyl' (e.g. Carroll and Gaskill 1978, fig. 120G) amphibians. No clearly defined ornament or areas for clavicular overlap are visible on the suggested interclavicle but it is possibly preserved with its dorsal surface uppermost.

Vertebrae

Although several vertebrae have been lost from the articulated series of G25.34 (text-fig. 1a), it is apparent from the impressions on the counterpart that the first forty-three vertebrae were originally present. The presence of a single median ventral ridge in all the vertebrae preserved indicates that all are precaudal; the centra of aistopod caudal vertebrae are characterized by a pair of hypapophyseal flanges demarcating the haemal canal (e.g. Zidek and Baird 1978). The vertebrae exhibit a gradual increase in size from anterior to posterior of the series, the most anterior centra measuring 2 mm in length and the most posterior approximately 3 mm. Well-developed parapophyses are borne by all but the most anterior two vertebrae, in which they are represented only by scarcely perceptible lateral projections from the centrum. In vertebrae 3-10 the parapophyses, as preserved, have a posterolateral orientation. In the remaining vertebrae (11-43) they project laterally. In the absence of any indication of the original position of the pectoral girdle it is impossible to determine how many of the vertebrae are cervicals. However, Baird (1964) has noted that the parapophyses of aistopod dorsal vertebrae change their orientation from posterolateral to lateral to anterolateral, from anterior to posterior of the column. It may therefore be concluded that, with the exception of an unknown number of cervicals, the vertebrae of G25.34 are all anterior- or mid-dorsal in position. The vertebral count in an entire specimen of *O. nanum* is unknown. However, a figure of 100+ has been given by Baird (1964, p. 6) for a juvenile of *O. granulosum* Fritsch.

The structure of a typical mid-dorsal vertebra of *O. nanum* will be apparent from text-fig. 2b-d. The centrum is holospondylous and probably deeply amphicoelous. The latter is the aistopod condition and is suggested in G25.34 by the high degree of compression undergone by most centra. Ventrally, the centrum bears a median ridge running the length of the element and broadening at its anterior and posterior ends. The ventral ridge, which appears to have been mistaken for a low neural spine by Hancock and Atthey (1868, p. 277), is flanked by a pair of elongate depressions. The parapophyses are dorsoventrally compressed structures, slightly expanded distally, and have their origins low on the lateral surface of the centrum at approximately the mid-point of its length. None of the vertebrae shows any evidence of the presence of basapophyseal processes.

The vertebrae of G25.34 are preserved with only their ventral surfaces exposed and yield no information on the structure of the neural arch. However, the counterpart slab bears, in addition to impressions of most of the vertebrae of G25.34, three isolated vertebrae from a more posterior region of the trunk (text-fig. 1f). Each of the three is incomplete but together they allow a restoration of most of the neural arch. Two are

almost entire vertebrae with their dorsal surfaces exposed, and the third is a very clear impression of the dorsal surface of the neural arch with the neural spine itself remaining in position. The neural arch is a long and low structure extending the full length of the centrum; whether the two are fused or merely sutured together cannot be determined. The neural spine is very weakly developed and forms a low and narrow ridge running the length of the, otherwise almost horizontal, dorsal surface of the neural arch. The zygapophyses are widely spaced and possess horizontally orientated articular surfaces. Unfortunately, the nature of the available material makes it impossible to determine whether the neural arch is pierced laterally by foramina for the spinal nerves, as is known to be the case in *Phlegethontia* (McGinnis 1967) and at least one *Ophiderpeton* species (Baird 1964).

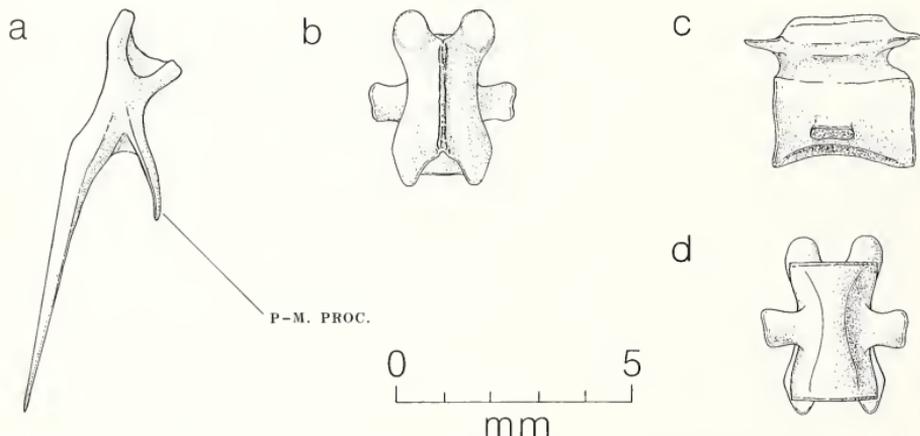
Ribs

Numerous ribs are preserved along the length of vertebral column of G25.34 (text-fig. 1a). Almost all are incomplete and most are at least partially obscured by overlying areas of the ventral squamation. However, a composite restoration of rib structure in *O. nanum* may be made with confidence. Free ribs appear to have been borne by all but the most anterior two of the forty-three vertebrae originally present. The first two vertebrae are also known to be without free ribs in *Phlegethontia* (McGinnis 1967). There is no apparent variation in rib form within the preserved series. The ribs do, however, show a slight increase in size from anterior to posterior.

The structure of a typical precaudal rib of *O. nanum* is depicted in text-fig. 2a. The rib is tetradactyl, in the manner characteristic of the Aistopoda (Baird 1964). The capitulum is short and stout, and appears to possess a slightly recessed head for articulation with the parapophysis of the vertebra. In all ribs in which it is preserved, the costal process is approximately twice the length of the capitulum and is connected to the latter for most of its length by a thin 'web' of bone. Whether the head of the costal process was recessed, as has been stated to be the case in *Ophiderpeton* by Baird (1964, p. 7), cannot be determined. The shaft, which contributes about two-thirds of the over-all length of the rib, is a robust, stiletto-like structure which tapers distally to a fine point. A well-developed posteromedial process is present. In most of the preserved ribs the posteromedial process exhibits a slight lateral curvature, towards the medial side of the shaft.

Scales

A well-developed ventral squamation is present and, as preserved, takes the form of a 'mat' of closely packed gastralia extending from the tenth vertebra to the forty-third (text-fig. 1a). The squamation has been displaced



TEXT-FIG. 2. Restoration of mid-dorsal vertebra and rib of *Ophiderpeton nanum* H & A. a, rib of left side in dorsal view; b-d, vertebra in b, dorsal view; c, left lateral view and d, ventral view. P-M. PROC., posteromedial process.

to one side of the vertebral column in the anterior part of the trunk, but more posteriorly it overlies the vertebrae and ribs. The individual gastralia are extremely elongate, almost filamentous, structures (text-fig. 1e). In their form they somewhat resemble the hair-like gastralia of the phlegethontiid *Aornerpeton mazouense* (Gregory) (Gregory 1948; Lund 1978), but their tightly packed arrangement and their extent beyond the anterior thoracic region are characteristic of *Ophiderpeton* (Baird 1964). As preserved, the orientation of the gastralia is very variable and Hancock and Atthey (1868, p. 277) suggested that the scales originally lay with their long axes at 90° to the vertebral column. It would seem more likely, however, they were originally arranged *en chevron*, as in many other Palaeozoic amphibians. Such an arrangement is still preserved in some areas of the ventral squamation. The absence of ventral osteoderms in the 'cervical' region and beneath the most anterior dorsal vertebrae is of some interest and may indicate, as Steen (1938, pp. 223, 224) suggested, that the specimen is a sub-adult individual.

Although not altogether absent, as had previously been thought (Steen 1938), the dorsal squamation is represented in G25.34 only by a small number of rounded, pebble-like osteoderms scattered at intervals along the length of the vertebral column (text-fig. 1a). The dorsal squamation of *Ophiderpeton* species usually consists of numerous such scales covering the dorsal and lateral surfaces of the trunk region and tail (Baird 1964). Its almost complete absence in the holotype of *O. nanum* may, like the restricted ventral squamation, indicate that the specimen is a juvenile animal. Such an assumption also offers an explanation of the ready dissociation of the skull elements subsequent to the death of the animal.

DISCUSSION

Despite the incompleteness of the only available specimen of *O. nanum*, it is apparent that this species is a member of the family Ophiderpetontidae, as defined by Baird (1964). Reference to the Ophiderpetontidae is suggested by the following characters of the holotype:

1. The structure of the ribs, in which the shaft is stout and stiletto-like and a well-developed posteromedial process present. In the phlegethontiids *Phlegethontia* and *Aornerpeton* the shaft is usually slender and flexible and the posteromedial process weakly developed or absent (Baird 1964; Lund 1978).
2. The presence of a well-developed ventral squamation composed of numerous, closely packed gastralia forming a continuous plastron. The phlegethontiid ventral squamation consists of a series of widely spaced, filamentous gastralia restricted to the anterior trunk region (e.g. Gregory 1948, pl. 1, fig. 4).
3. The apparent presence of an, at least partial, dorsal or lateral squamation of pebble-shaped osteoderms; no dorsal and lateral armour is known to occur in the Phlegethontiidae (Baird 1964).
4. The form of the premaxilla, now lost, described by Steen (1938, p. 223). This was stated exactly to resemble the premaxilla of *O. amphiuminum*, described by Steen in 1931 (fig. 17B-C). The premaxilla of *O. amphiuminum* and other *Ophiderpeton* species differs markedly from that of *Phlegethontia* in possessing an anterior ascending process (McGinnis 1967, p. 38).

As presently constituted, the Ophiderpetontidae contains only the type genus, *Ophiderpeton* Huxley 1867, and *Coloraderpeton* Vaughn 1969. The latter is a monotypic genus, established by Vaughn (1969) for a number of vertebrae, ventral osteoderms, and an attributed rib from the Upper Pennsylvanian of the Sangre de Cristo Formation in central Colorado. The vertebrae of *Coloraderpeton* are distinguished from those of both *Ophiderpeton* and *Phlegethontia* principally by the form of the neural spine. This, although relatively somewhat higher than in the last two genera, is restricted in its anterior-posterior extent to the middle one-third of the neural arch and possesses a crenulated dorsal edge. The dorsal vertebrae otherwise appear typically aistopod and possess foramina for exit of the spinal nerves. *Coloraderpeton* was placed in the Ophiderpetontidae by Vaughn on the basis of the form of the rib, which has a stout shaft and apparently also a posteromedial process, and of the closely packed, fusiform ventral osteoderms. It is clear from the structure of the vertebrae that the holotype specimen of *O. nanum* cannot be placed in the genus *Coloraderpeton*. On the other hand, the similarity of the ribs, vertebrae, and ventral squamation to those of other described *Ophiderpeton* species appears to confirm the correctness of Hancock and Atthey's (1868) reference of the Newsham aistopod to this genus.

O. nanum was distinguished by Hancock and Atthey (1868) from the only previously described *Ophiderpeton* species, *O. brownriggii* Huxley 1867, by its relatively small size and the almost filamentous nature of the ventral osteoderms. The former is clearly unreliable as a taxonomic criterion, especially in view of the probability, noted above, that the *O. nanum* holotype represents a sub-adult individual. The significance of the second character is uncertain. None the less, in view of the almost complete absence of a skull in the holotype specimen and the lack of adequately detailed descriptions of other *Ophiderpeton* species, it would seem advisable to retain *O. nanum* as a distinct species, at least pending thorough revision of the Ophiderpetontidae.

The possible presence of an interclavicle in *O. nanum* is a feature of some importance. Steen (1931, p. 876) identified two bones in a specimen of *O. amphiuminum* from the Westphalian D of Linton, Ohio, as clavicle and cleithrum, but these were subsequently reinterpreted by Baird (1964) as possibly representing hyoid elements. Most recent workers have concurred in regarding described aïstopod species as lacking both limbs and limb girdles. However, Goin and Goin (1971, p. 67) have pointed out that forelimbs are not known for most fossil members of the urodele family Sirenidae, despite their presence in the three extant species of this group. They suggested, therefore, that the Aïstopoda may possibly also have possessed vestigial forelimbs which, together with the pectoral girdle, were usually lost prior to fossilization. If the element tentatively identified as an interclavicle in the holotype of *O. nanum* is correctly so interpreted, its presence at least partially confirms the above hypothesis.

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A NEW SPECIES OF THE LYCOPSID *PLEUROMEIA* FROM THE EARLY TRIASSIC OF SHANXI, CHINA, AND ITS ECOLOGY

by WANG ZIQIANG and WANG LIXIN

ABSTRACT. A new species, *Pleuromeia jiaochengensis*, is recorded from the early Triassic of Jiaocheng district in Shanxi (Shansi) Province, China. Its small size, morphological features of the strobilus and sporophylls, abortive leaves, and the undeveloping rhizophore separate this from all other species. The succulent sporophylls may be a major area of photosynthesis. Based on lithology and distance from known marine strata, an inland desert environment is suggested for this new species. Its stratigraphic significance is discussed.

It is well known that Palaeozoic floras flourished during Upper Carboniferous and Permian time, but suffered from a worldwide arid climate at the end of the Permian. Only a few relics survived into the early Triassic where they faced severe climatic conditions. One such genus is *Pleuromeia* which is regarded as an important early Triassic index fossil, and thought to be a link between the Palaeozoic *Sigillaria* and modern *Isoetes*.

Pleuromeia was first recorded from the Bunter Sandstone in Germany nearly a century ago. Prior to 1960, apart from a few records from France, Spain, and the eastern U.S.S.R. all the records were from Germany. In particular, Mägdefrau (1930, 1931) provided much information about the genus from a large number of German specimens.

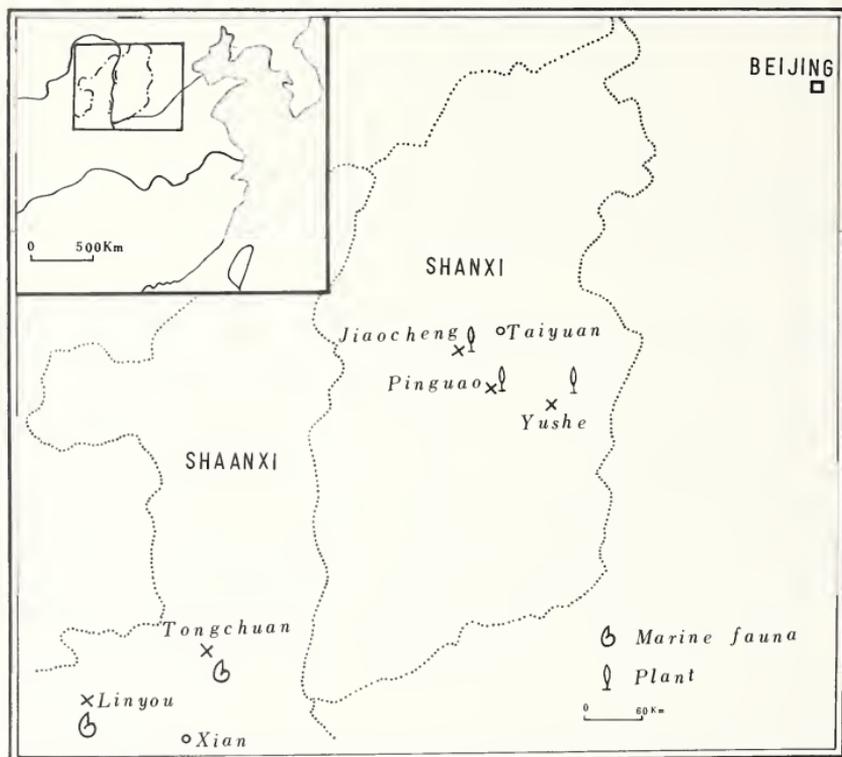
Since the 1960s new material has been recorded from the early Triassic in the Soviet Union, Japan, and China. *Pleuromeia rossica* was described by Neuberg (1960a) from the Russian Platform, whilst Krassilov and Zakharov (1975) added further information on the genus from material in the far eastern part of the Soviet Union. Kon'no (1973) described *P. hatai* from the Scythian in north-eastern Japan, and in China, Wang, Xie, and Wang (1978) described well-preserved specimens of *P. sternbergi* (Münster) Corda and *P. rossica* Neuberg from the early Triassic of the Qinshui Basin in Shanxi. The genus *Pleuromeia* therefore has a widespread distribution. It is worth noting that from the early Triassic of eastern Australia, *Cylostrobus* a lycopsid-like strobilus which shows some similarity to *Pleuromeia* of the Northern Hemisphere, has recently been regarded by Retallack (1975) as *Pleuromeia longicaulis* (Burgess).

After the discovery of *P. sternbergi* and *P. rossica* from the early Triassic Heshankou Formation in Qinshui Basin, Shanxi Province, the present writers found many well-preserved specimens belonging to a new species of *Pleuromeia* in the Luijiakou Formation beneath the Heshankou Formation in Jiaocheng district (text-fig. 1), not far from the famous Xuan-zhong Temple of Shanxi Province. This paper describes these specimens.

FOSSIL-BEARING STRATA

The Luijiakou Formation in Jiaocheng district is the western extension of the sandstone beds of the 'Shischienfeng Series' at West Hill in Taiyuan, and consists mainly of reddish-purple, fine-grained sandstones. According to data supplied by the Regional Geological Survey of Shanxi Province, its thickness in Jiaocheng district exceeds 460 m, the Formation being subdivided into three parts. The upper part, consists of 108 m of grey and reddish-purple fine-grained feldspathic sandstones intercalated with reddish-purple siltstones and sandy shales. The middle part is composed of 215 m of red, grey to greyish-purple fine-grained feldspathic sandstones interbedded with reddish-purple silty shales and shales. The shales contain abundant ripple marks,

sun-cracks, and cross-bedded structures sometimes intercalated with a few lenses of greyish-white sandstones containing fossil plants and greyish-green shales with fossil estherians. The lower part, consists of 138 m of reddish-grey and purplish-grey fine-grained, cross-bedded feldspathic sandstones containing abundant laminations of magnetite, intercalated with lenses of greyish-white feldspathic sandstones. The fossil plants, which include *Pleuromcia*, are within the middle part of the Formation approximately 130 m above its base at four localities (numbered Z01-Z04) near Jaertou village, in the north-western mountainous area of

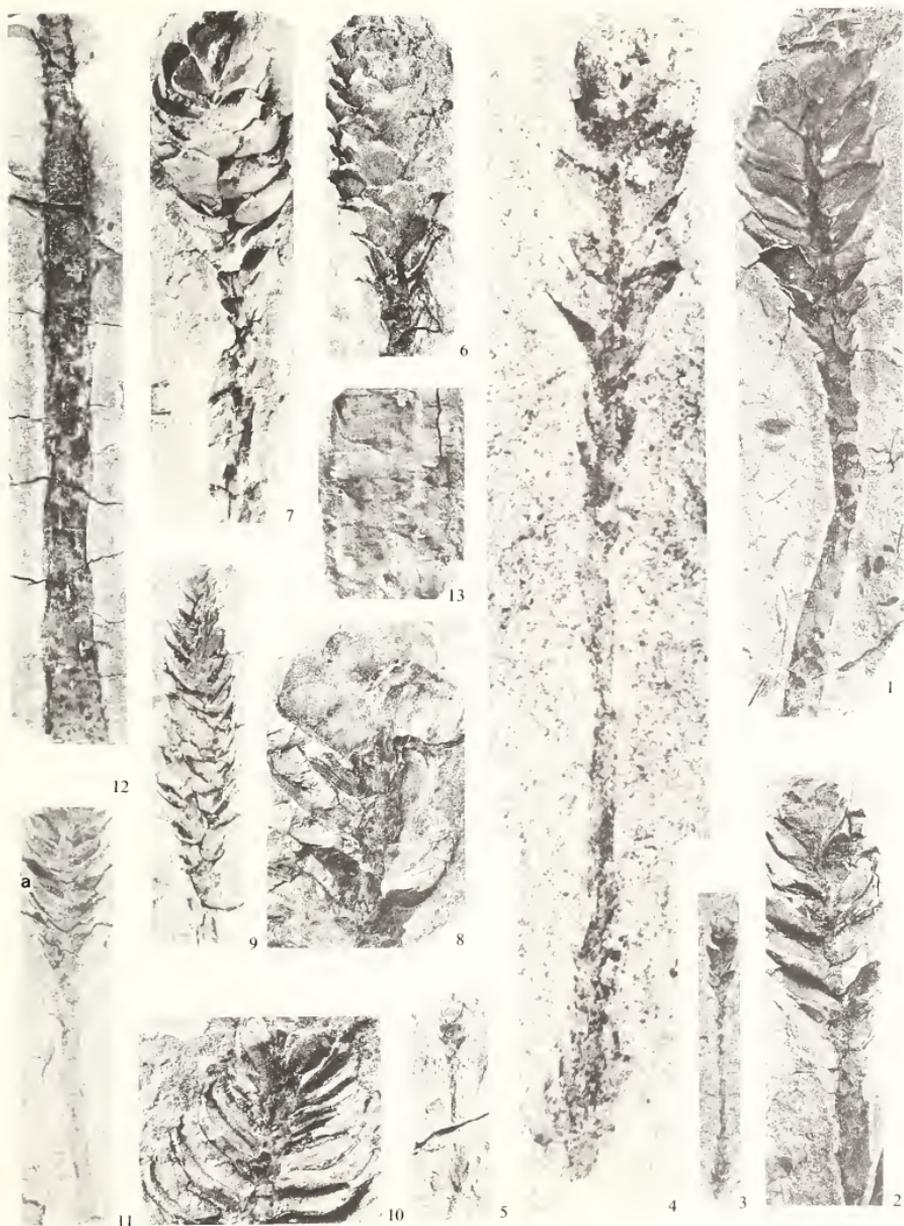


TEXT-FIG. 1. Map showing region of the fossiliferous localities. Inset shows eastern half of China.

EXPLANATION OF PLATE 23

All figures $\times 1$ unless otherwise stated. All specimens from the Lujiakou Formation, Shanxi Province.

Figs. 1-13. *Pleuromcia jiaochengensis* sp. nov. 1-2; 6-11. Various strobili; 1, Z01-021; 2, showing the awl-like leaves on the part of stem beneath the strobilus, Z01-01; 6, Z01-024; 7, Z01-027; 8, Z01-019; 9, Z01-022; 10, Z01-019; 11, syntype, a strobilus containing megaspores (at a), Z01-061. 3-5, complete young plants: 3, syntype, Z01-020; 4, the same $\times 4$, 5, Z01-061. 12. Shows a decorated stem, with short surface ridges, Z01-061. 13. Syntype, stem surface showing sparse, faint leaf-scars, Z01-206, $\times 2$.



WANG and WANG, *Pleuromeia*

Jiaocheng district. At locality Z01, there are many well-preserved specimens of strobili, stems, rhizophores, and even some complete plants in a lens of greyish-white sandstone, 0.2 m thick and 2 m across. At Z04, there are many sporophylls, stems, and rhizophores occurring in larger lenses. In addition, at localities Z02 and Z03, there are specimens tentatively included within the genera *Crematopteris* sp. *Phyllothecca* sp. *Taeniopteris* sp. *Neocalamites* sp. by the present authors. All specimens illustrated in this paper, are deposited in the Tianjin Institute of Geology and Mineral Resources, Ministry of Geology.

SYSTEMATIC PALAEOBOTANY

Family PLEUROMEIACEAE

Genus PLEUROMEIA Corda, 1852

Pleuromeia jiaochengensis sp. nov.

Plates 23, 24, text-figs. 2-3

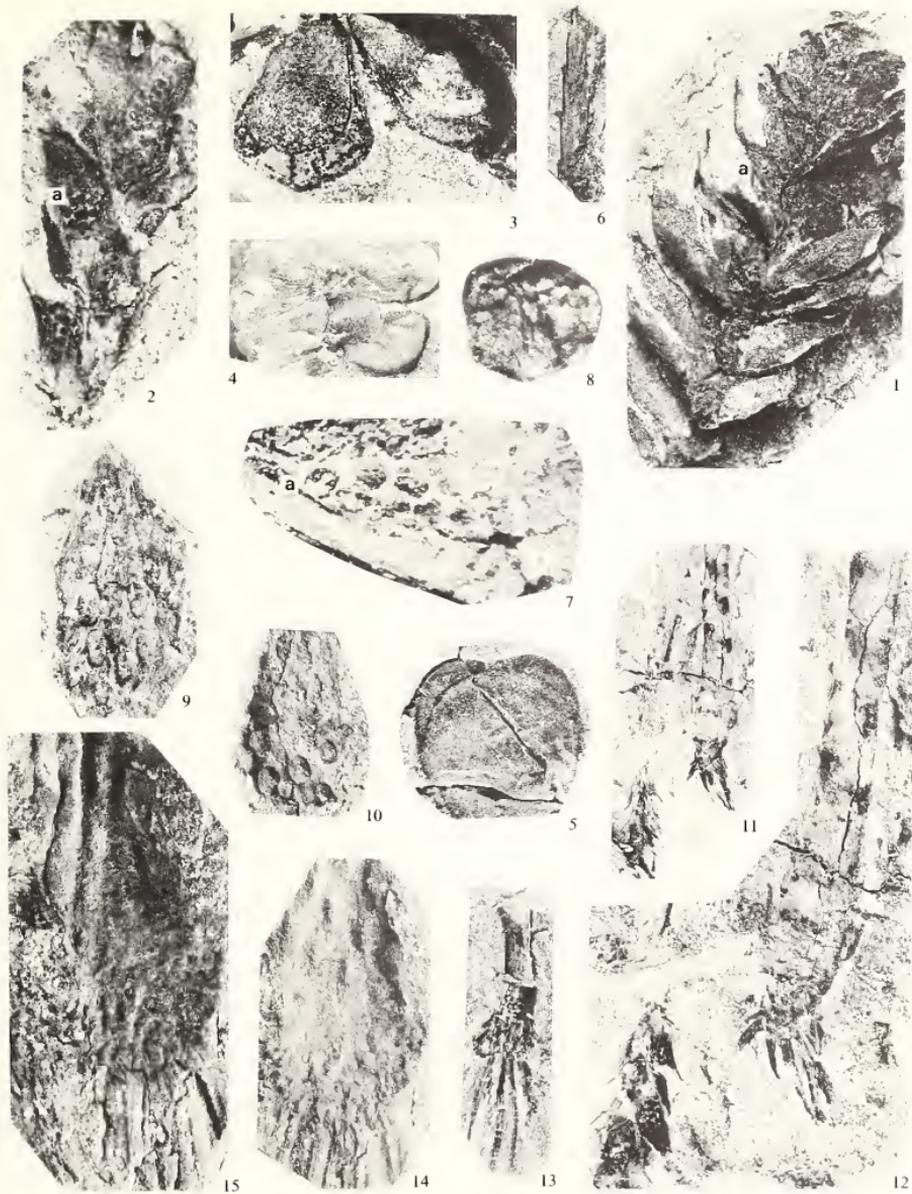
Syntypes. Z01-020 (small complete plant); Z01-061 (showing strobilus and megaspores; Z01-206 (showing stem surface); Z04-159 (showing rhizophore).

Diagnosis. A lycopsid of small shrub size, probably dioecious, generally 20-30 cm high but may reach almost 50 cm (see text-fig. 2, the reconstruction of a whole plant). Stem erect, unbranched, maximum diameter 1.5 cm, terminating in a large strobilus measuring one-quarter to one-third of the plant height (Pl. 23, figs. 3-4). Surface of stem covered with sparse, faint, at times barely visible leaf-scars, usually smooth, with small obscure pits where the leaves were originally attached. Decorticated stems with short ridges (Pl. 23, fig. 12). Leaf-scar lens-shaped, obscure in outline, with a central pit (Pl. 23, fig. 13). Leaves awl or spine-like, 2-3 mm in length, about 1 cm apart on the upper portion of the stem (Pl. 24, fig. 6), having dehisced from the lower part. Rhizophores tuberous when mature, covered with oblong to oval, well-separated appendage-scars; the younger rhizophores only slightly swollen at the base of the stem and covered with rather thick appendages, maximum length 3 cm, usually on the lower part. Strobilus probably unisexual, narrowly spike-shaped, maximum length 20 cm. Sporophylls spirally arranged, imbricate, 4-5 in each spiral (Pl. 23, fig. 6), the spiral from 60° to quite an acute angle to the rachilla, giving a total of more than 100 sporophylls in a mature strobilus. Sporophylls spatulate with a sagittate apex, longer than wide, ovate to oblong in outline, adaxially concave where the sporangium lies. The border of the sporophyll is wider anteriorly than laterally, and in mature strobili the apex of the anterior border of larger sporophylls is slightly reflexed upwards (Pl. 24, fig. 3; text-fig. 3*d* left), and is probably visible on the outside of the strobilus. Where the upward reflexed part of a sporophyll is truncated, it clearly shows a retuse, small anterior border (Pl. 24, fig. 5). Sporangium discoid, oval or orbicular in outline, attached to the rachilla only at its proximal end. Surface of sporangium with many more or less parallel lines (Pl. 24, fig. 4) which converge slightly at both ends. Thickness of

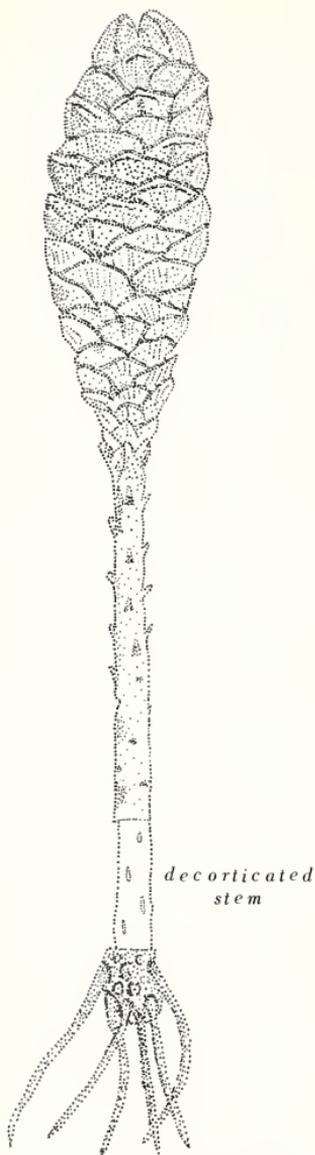
EXPLANATION OF PLATE 24

All figures $\times 1$ unless otherwise stated. All specimens from the Lujiaokou Formation, Shanxi Province.

Figs. 1-15. *Pleuromeia jiaochengensis* sp. nov. 1-2. Part of strobili containing megaspores (at *a*). 1, Z01-01, $\times 2$. 2, an enlargement of syntype, Pl. 21, fig. 11, showing megaspores associated with nearly all the sporophylls. 3-5. Sporophylls and sporangia. 3, two sporophylls, the right one with upward reflexed apex, Z01-08 $\times 2$; 4, sporangia near base of a strobilus, showing the parallel lines on their surface, Z01-042; 5, a larger sporophyll having lost its reflexed apex, Z01-061. 6. Part of a stem, showing spine-like leaves, Z01-00. 7. Enlargement of a sporangium containing megaspores (*a*), from the strobilus of Pl. 21, fig. 11, Z01-019, $\times 10$. 8. A megaspore, Z01-022, $\times 50$. 9-15. Various rhizophores; 9, 10, showing appendage scars, Z01-060, Z01-135; 11, on the right, a young rhizophore showing a few appendages on the lower part, Z01-054; 12, the same $\times 2$; 13-15, showing appendages on the lower part, and appendage scars on the upper part; 13, Z01-027; 14, Z04-151; 15, syntype, Z04-159.



WANG and WANG, *Pleuromeia*



TEXT-FIG. 2. *Pleuromeia jiaochengensis* sp. nov. Reconstruction of a whole plant, $\times 1$.

sporangium decreases gradually from proximal to distal end, resulting in an aggregation of spores at the proximal end near the rachilla. Megaspores tetrad, spherical or triangular, laevigate or granulate, 300–500 μm in diameter. Trilete mark distinct, shorter than spore radius. Microspores unknown.

Discussion and comparison. The single, erect, terminal strobilus terminating on unbranched woody stem, are characters associated with the genus *Pleuromeia* rather than *Selaginella* or *Isoetes*. Though the sporophylls of this new species have an elongate anterior border similar to those in *Selaginella*, they differ from it in lacking elongate acuminate distal tips (Retallack 1975). Also, the thick, spatulate shape is quite unlike the sporophyll of *Selaginella*. In addition, *Selaginella* is herbaceous with a dichotomous stem and dimorphic leaves often in four rows (Chaloner 1967; Smith 1955), quite unlike those of *P. jiaochengensis*.

Isoetes, which is usually considered a close relative of *Pleuromeia*, lacks a definite stem from the lobed rhizophore, and also lacks a distinct strobilus. Unlike *Pleuromeia*, the sporophylls of *Isoetes* are placed within the centre of a cluster of leaves.

In the past, when identifying species of *Pleuromeia*, authors have placed considerable emphasis on features of the leaf-scars on the stem surface. During the past two decades, more recent finds have greatly increased knowledge of the reproductive organs; for example, the strobilus, sporophylls, sporangia, megaspores, and microspores. These are now used much more in identification. Also, Dobruskina (1974) pointed out that the leaf-scars on specimens assigned to *Pleuromeia* and *Pleuromopsis* by Brick (1936) and Sixtel (1962) respectively, from the late Triassic of Central Asia, are not from these genera, and that the leaf-scars of *Pleuromeia* vary in shape depending on the degree of decortication prior to burial. Some specimens from the late Permian of the Petchora Basin in the Soviet Union included by Neuberg (1960b, pl. 5, fig. 2; pl. 14, right) in the genus *Viatscheslavia* have similar leaf-scars to those in *Pleuromeia*. Hence leaf-scar features are not now considered as important as in the past in identifying *Pleuromeia*.

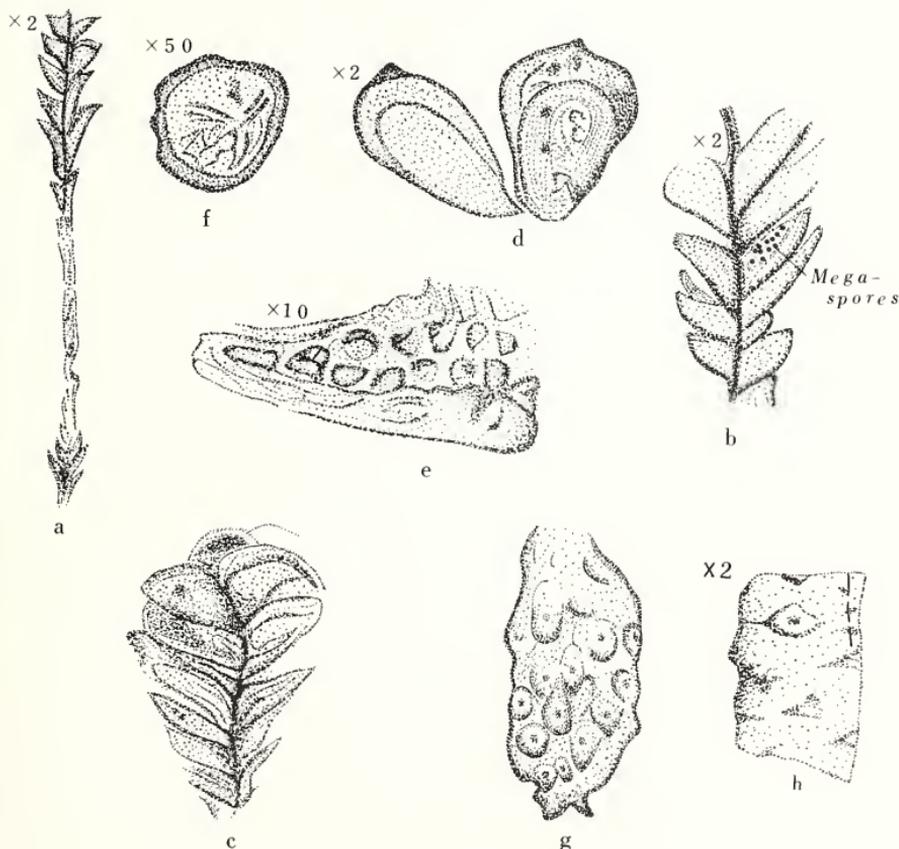
Of the six previously described species of *Pleuromeia* from the Northern Hemisphere, only three, namely *P. sternbergi*, *P. rossica*, and *P. hatai*, have been found in sufficient numbers and are well preserved enough to give knowledge of the complete plant. Of the rest, there is not enough real evidence for their assignation as distinct species. *P. oculina* (Blanckenhorn, 1886) lacks reproductive organs, *P. olenekensis* (Krassilov and Zakhlov, 1975) is too incomplete to compare with other species, and the designation of *P. obrutschewi* Elias is in dispute (Krassilov and Zakhlov 1975).

P. jiaochengensis differs from all previously described species, by its small size, relatively large strobilus with elongate

sporophylls, and its undeveloping rhizophore with appendage-scars which are less in number, and larger. *P. jiaochengensis* is usually 20-30 cm high, with a maximum height of under 50 cm. This compares with 2 m in *P. sternbergi* and 1 m in *P. rossica*. The smallest specimens of *P. hatai* may be of similar size.

The strobilus of *P. jiaochengensis* is larger in proportion to the whole plant than in other species, except *P. hatai*. The strobilus of *P. hatai*, however, differs from *P. jiaochengensis* in being cylindrical rather than spike-shaped. Also, in *P. hatai* there are more sporophylls in a strobilus, and they are smaller in size.

The sagittate shape of the sporophyll of *P. jiaochengensis* is slightly different from that in all



TEXT-FIG. 3. *Pleuromeia jiaochengensis* sp. nov. a, complete young plant, $\times 2$; b, a strobilus with megaspores, $\times 2$; c, a strobilus, $\times 1$; d, two sporophylls, the left one with an upward reflexed apex, $\times 2$; e, a sporangium containing megaspores, $\times 10$; f, a megaspore, $\times 50$; g, a rhizophore covered with appendage-scars, $\times 1$; h, a stem surface with a few leaf-scars, $\times 2$.

other species. Plate 24, fig. 5, right, shows a larger sporophyll of *P. jiaochengensis*; its upward reflexed tip having been truncated, exposing a retuse anterior margin which differs from *P. rossica*, in having a notched margin (Pl. 24, fig. 5). In *P. sternbergi* the mature sporophylls also have an elongate outline, but unlike *P. jiaochengensis* the lateral and anterior margins are of approximately equal width.

Although the nature of the sporangium of *P. jiaochengensis* is not as yet clear, the uniform megaspores are different from those in *P. rossica*, but similar to those in *P. sternbergi* and *P. hatai*. However, unlike these two species, the sporangium has a markedly thickened proximal end (Pl. 24, fig. 7; text-fig. 3e), which contains a mass of megaspores.

The awl or spine-like leaves of *P. jiaochengensis* is one of the most important characters in comparing this with other species. No clear leaf-scars are present after the leaves have dehisced. The leaves of *P. sternbergi* and *P. hatai* are linear in outline and, after dehiscence, leave obvious leaf-scars on the outer stem surface. The leaves of *P. rossica* are probably scale-like (Dobruskina 1974), and rather similar to those in *P. jiaochengensis*, but when dehisced they leave densely covered and distinctive leaf-scars.

An undeveloping rhizophore is also regarded by the present writers as an important character for distinguishing the new species. Its appendage scars are larger and less in number than other species. In addition, unlike the other species, the rhizophore has neither horns nor suture lines (klüfte) on the lower surface.

When describing *Pleuromeia* from the Qinshui basin of Shanxi, Wang *et al.* (1978) noted that the difference between the strobili of *P. sternbergi* and *P. rossica* was so great that, as pointed out by Kon'no (1974), they might represent different genera. With regard to this, *P. jiaochengensis* throws more light on *P. sternbergi* based on its unisexual strobilus without a pedicel, and on the character of the sporophylls.

Retallack (1975) transferred the lycopsid-like strobilus *Cylostrobus* (originally designated by Helby and Martin 1965) which had previously been considered more like the palaeozoic lycopsids, to *Pleuromeia longicaulis* (Burgess). The specimens are from the early Triassic of eastern Australia, and is the first record of this genus in the Southern Hemisphere. This type of strobilus shows some important features, for example, it is bisexual (monoecious), the sporophylls have a remarkable ribbed keel-like apex on their dorsal surface, and the microspores are monolet and covered with dense spines. All these features are strikingly different from Northern Hemisphere *Pleuromeia* species, including *P. jiaochengensis*. The basis for the designation of the Australian species given by Retallack, mainly results from an analysis of their environment and a few associated fossil stems. In fact, there are two types of stems associated with *Cylostrobus sydneyensis* from the upper Narrabeen Group; one bearing a stigmara-like stem-base, and the other with branchlets (Helby and Martin 1965, p. 399, pl. 1, fig. 6) more like a palaeozoic lycopsid than *Pleuromeia*. The present authors are not as yet convinced that this Australian species should be included within the genus *Pleuromeia*. Recently, Ash (1979) has described *Skilliostrobus*, a new type of lycopsid strobilus also from the early Triassic of Australia, and this is similar to *Cylostrobus* in having bisexual, monoecious features.

ECOLOGICAL PROBLEMS CONCERNING *P. JIAOCHENGENSIS*

Pleuromeia was originally regarded as a desert xerophyte similar to the present-day Cactaceae. More recently, linking the plant-bearing beds with associated sediments containing dolomite and halite, together with marine fossil animals, a marginal marine habitat was suggested. Mägdefrau (1931) was first to suggest an halophytic habitat for *Pleuromeia*. Hirmer (1933), Neuberger (1960b), and Kon'no (1973) have supported this view, and more recently Krassilov and Zakharov (1975) and Retallack (1975) have suggested a mangrove-type environment along the sea-shore, or marginally on deltas. This type of habitat is not envisaged for *P. jiaochengensis*. Unlike the records from western Europe, Siberia, and Japan, no marine animal fossils have been recorded from the strata containing *P. jiaochengensis* in Jiaocheng district. Also, there is no evidence for lagoonal sediments, with the absence of dolomite and halite, and only a few doubtful reports of gypsum.

According to the geological exploratory reports of the Shanxi Regional Geological Survey Team the Formation in this area contains a lot of unweathered minerals such as feldspar and magnetite. Cross-bedding, ripple marks, and sun-cracks are relatively common, and indicate an arid climate. The 'Shischienfeng Series' with marine intercalated beds are known only from Linyuao, and Tongchuan districts of north Shanxi (Shengsi), and are at least 300 km from the Jiaocheng district (see text-fig. 1 and Yin and Lin 1979). We therefore consider *P. jiaochengensis* to be a small plant growing near desert oases. As all specimens are found in greyish-green sandstones, the new species might grow very near or even partly in the water bodies. Its small size also suggests arid conditions; the undeveloped and abortive leaves probably resulted from extreme transpiration in an arid climate. The appendages are stout and strong, probably to withstand desert conditions. Further evidence for an arid environment comes from the Estheridae which are recorded from the shales intercalated with the plant-bearing sandstones. This type of small fauna is often found in temporary inland bodies of water.

Plate 23, figs. 3-4, show a small but complete plant which is only 3 cm high. The stem is almost smooth, the large strobilus is well developed at the apex, and has a few distinctive appendages at its base. The appendages are plano-concave and fleshy, and were probably succulent. They are more developed than the sterile leaves, and may well have carried out much of the photosynthesis.

TABLE 1. The stratigraphic sequence of the 'Shischienfeng Series' in Shanxi.

Early Triassic	Olenekian	'Shischienfeng Series'	Heshankou Formation	<i>Pleuromeia sternbergi</i> <i>P. rossica</i>
	Induan		Luijiakou Formation	<i>P. jiaochengensis</i>
Later Permian	Tartarian		Sunjiakou Formation	<i>Shiltienfenia permica</i>

STRATIGRAPHIC OCCURRENCE OF THE GENUS *PLEUROMEIA*,
AND THE AGE OF *P. JIAOCHENGENSIS*

In Germany the *Pleuromeia*-bearing beds have a rather short vertical range, extending from Middle to Upper Bunter (i.e. from Bausandstein to Chirotheriumsandstein). The age according to Lozovsky, Movschovich, and Mimich (1973) is considered to be equivalent to the *Tirolites-Columbites* ammonite zone of Middle and Upper Olenekian age, despite the lack of the ammonite evidence. At Russian Island near Vladivostok and north-east Japan, *Pleuromeia* occurs in rocks of early Triassic age dated on the ammonites. On the Russian Platform, *P. rossica* occurs in the Ribinsk Formation together with the amphibian *Benthosuchus*, and is dated as early Triassic. According to Lozovsky *et al.* (1973), this Formation is equivalent to the *Owenites* ammonite zone, and may be referred to the early Olenekian.

At Mangeschlack near the Caspian sea, *P. sternbergi* occurs with marine lamellibranchs which also occur in the Upper Bunter Sandstone in Germany (Dobruskina 1974) and so are dated as late Olenekian. The *Pleuromeia* localities in the Vosges, at Mangeschlack in Central Asia, and on Russian Island in the Far East, are suggested by some authors as being as late as Middle Triassic. However, in the present writers' opinion, the exact age is in doubt, through lack of detailed information.

The Lujiaokou Formation in central Shanxi is thought to be equivalent to the middle part of the so-called 'Shichienfeng Series'. For many years, no fossils were found, and the age was in doubt, but thought to be late Permian to early Triassic, depending on the exact age of the ?late Permian reptile *Shihtienfenia permica* Young, found in the underlying Sunjiakou Formation (see Table 1).

Recently Wang, Xie, and Wang (1978) described *P. sternbergi* and *P. rossica* from the overlying Heshankou Formation and suggested an early-middle Olenekian age for that Formation. The discovery of *P. jiaochengensis* in the Lujiaokou Formation lends further support to the above age determination. In addition, another of the fossil plants associated with *P. jiaochengensis*, is *Crematopteris* sp. This species is confined to the Bunter Sandstone in western Europe. If the age of the Heshankou Formation containing *P. rossica* is referred to the Olenekian stage, or is equivalent to the Ribinsk Formation on the Russian Platform, then the age of the Lujiaokou Formation can accurately be assigned to the Induan of early Triassic age.

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Cover: An acritarch of the genus *Multiplicisphaeridium* from the Tournaisian Bedford Shale of Ohio, U.S.A. Institute of Geological Sciences specimen number MPK 3569, S.E.M. $\times 1000$. Within the last twenty-five years the number of described acritarch taxa has increased dramatically, and these organisms are now used extensively to date rocks of late Precambrian to Devonian age.

ECOLOGY AND POPULATION STRUCTURE OF THE RECENT BRACHIOPOD *TEREBRATULINA* FROM SCOTLAND

by GORDON B. CURRY

ABSTRACT. The ecology and population structure of the Recent articulate brachiopod *Terebratulina retusa* (Linnaeus) are described. The population studied occurs around the margins of a depression of more than 220 m in the Firth of Lorne, Scotland, and is predominantly attached to the horse-mussel *Modiolus modiolus* (Linnaeus). Spawning occurs regularly in late spring and late autumn, and is initiated at temperatures of 10–11 °C. The highly synchronized reproductive cycle, from spawning to spatfall, occurs within 3 weeks in nature. Length-frequency histograms prepared from large representative samples collected at regular intervals during 1977–1979 are unimodal and right-skewed due to the predominance of juveniles. Regularly spaced subsidiary peaks in the histograms correspond to biannual settlement cohorts; in later life successive peaks merge to form a single annual peak. This pattern is identical to that predicted by computer-based simulations. Recently settled specimens grow rapidly to an average length of 2.75 mm within 3 months during both spring and autumn; thereafter the animals grow (initially by 4 mm per year) throughout life, although at a progressively reducing rate from the third year of life onwards. Growth slows or ceases in winter in all but recently settled specimens. The maximum life span is 7 years. The mortality rate remains constant, although the causes of death are not apparent. The growth-lines form biannually, at times of pronounced environmental and physiological disturbance.

It is not generally realized that the Recent brachiopod fauna of the British Isles (21 species of 17 genera, Brunton and Curry 1979) is significantly more diverse than that of New Zealand (12 species of 9 genera). Considering the relative diversity of the two faunas, it may appear strange that New Zealand has become the classic area for Recent brachiopod research. However, this apparent anomaly is readily explained since the New Zealand species are far more accessible, with 25% of the species abundant intertidally and a further 30% common in nearshore shallow subtidal habitats. By contrast, British brachiopods are very rarely found intertidally and the majority of species have only been collected in small numbers from widely dispersed and often inaccessible localities.

Intermittent research during the last 100 years has demonstrated that several of the British species are locally abundant, especially off the west coast of Scotland and in the Western Approaches (Atkins 1959*a, b*, 1960*a, b, c*, 1961; Davidson 1886–1888; Chumley 1918; see summary maps in Brunton and Curry 1979), although dredging is the only practicable method of sampling these predominantly deeper-water populations. The recent upsurge of interest in palaeoecology has emphasized the need for precise data on the life-habits and ecology of Recent representatives of fossil phyla, and more data are needed to augment the patchy and often contradictory information available to the brachiopod palaeoecologist. The present study was initiated in the light of such inadequacies, and when it became clear that the comprehensive dredging facilities available at Dunstaffnage Marine Research Laboratory, nr. Oban, Scotland, could ensure access to the abundant brachiopod populations off the west coast of Scotland.

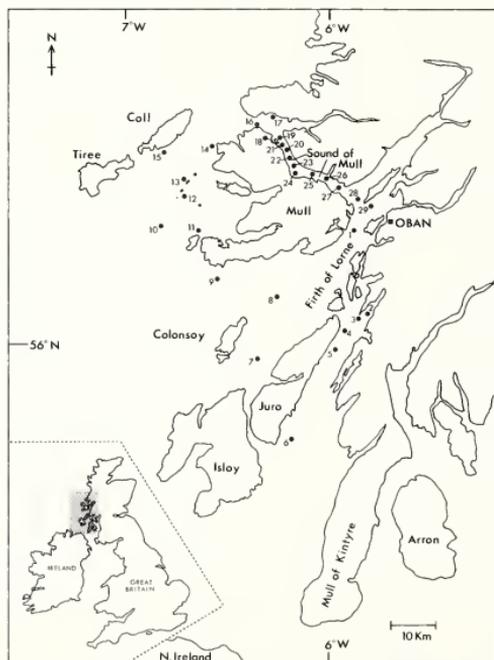
Although dealing entirely with living animals, this study was conducted from a palaeontological viewpoint. As such, the main interest was the interpretation of features on the shell, in particular the analysis of population structure and dynamics based on size-frequency histograms prepared from large samples of brachiopods collected at regular intervals throughout 1977–1979. The main advantage of working with living, as opposed to fossil, populations is that it is possible to seek

confirmatory evidence for conclusions reached by direct observations on the living population. This paper first describes aspects of the biology and ecology of the animal, and goes on to apply the results to the interpretation of size-frequency histograms.

MATERIAL

The species under investigation was *Terebratulina retusa* (Linnaeus), which is the most abundant of the Recent British brachiopods. Initially the intention was to collect regular bulk samples from the large populations of *T. retusa* which were known to occur in the Sound of Mull (text-fig. 1). However, during an exploratory cruise in March 1977 an extremely abundant population, ideally situated for regular sampling, was discovered near a depression in the nearby Firth of Lorne (text-fig. 1). This depression, which reaches a maximum depth in excess of 220 m, is mid-way between the Island of Kerrera and the south-west coast of the Island of Mull (Grid. ref. NM 745 265; Stn. 1 in text-fig. 1), and is thought to lie along the Firth of Lorne Fault (a subsidiary splay of the Great Glen Fault, Barber *et al.* 1979). At this locality the brachiopods are predominantly attached to the horse-mussel *Modiolus modiolus* (Linnaeus) which occurs in dense beds around the smoothly sloping margins of the depression.

The samples were collected, by the R/V *Calanus* or *Seol Mara*, using a conventional 'clam-dredge' (1.2 m wide \times 2 m long), the body of which consists of an outer framework of interlocking iron chain and an inner nylon meshwork with a maximum aperture of 15 mm. This dredge is designed to collect material resting on, or partially buried within, the substrate, and proved to be extremely efficient at sampling the Firth of Lorne mussel beds. For each sample the dredge was trawled slowly along the substrate for approximately 5–10 minutes, in a



TEXT-FIGURE 1. Map showing locations of R/V *Calanus* sample stations off the west coast of Scotland; station numbers refer to Table 1 (see opposite).

north-easterly or south-westerly direction. Once landed on deck, the sample was washed with sea-water to remove any adherent sediment, and then placed in plastic baths supplied with flowing fresh sea-water.

The disturbance caused by the dredging was minimal, and the majority of the sample had become 'acclimatized' to the plastic baths and commenced feeding within half an hour of arriving on deck. Mechanical damage during dredging was not significant, and only seven specimens out of the 818 brachiopods collected in March 1977 (i.e. 0.85%) proved unmeasurable because of shell damage. Due to the efficiency of the 'clam-dredge', and the density and abundance of both mussels and brachiopods, all attempts to sample the Firth of Lorne populations were successful. In addition, the Firth of Lorne depression is a prominent submarine feature, easily recognizable using the ship's depth-sounding equipment, and it was therefore possible to ensure that all samples were collected from the same population.

TABLE 1. Results of the dredging operations of the R/V *Calanus*, west coast of Scotland, 1977-1979 (*a* = abundant, *c* = common, *r* = rare, *x* = absent).

STATION NO.	LOCATION.	DEPTH.	SEDIMENT.	<i>T. retusa</i>		<i>C. anomala</i>		ASSOCIATED FAUNA.
				abund.	attachment.	abund.	attachment.	
1	Firth of Lorne	146-183m.	fine mud	a	Modiolus	a	Modiolus	see text.
2	Rabbit Island	13m.	--	c	rocks	r	rocks	Pecten
3	Garbh Reisa	20m.	--	X	--	X	--	Pecten
4	Sound of Jura (north-east)	73-128m.	--	X	--	X	--	Modiolus and hydroids
5	Sound of Jura	110m.	--	r	vesicular basalt	X	--	large no. of dis-articulated Modiolus
6	Sound of Jura (south)	37m.	--	X	--	X	--	Pecten, Balanus.
7	E. of Colonsay	37m.	sand	X	--	X	--	seaweed, crabs.
8	North-east of Colonsay	55m.	--	c	rocks and clinker	c	rocks and clinker	--
9	Torran Rocks	91-110m.	--	X	--	X	--	--
10	North-west of Iona	73-110m	--	r	rocks	X	--	--
11	North of Iona	73-128m.	sand	X	--	X	--	--
12	Freshnish Is.	29-55m.	--	X	--	X	--	Balanus, serpulids on rocks
13	Lunga	37m.	--	X	--	X	--	Balanus on rocks
14	North-west of Mull	37-46m.	--	X	--	X	--	Pecten, echinoids
15	East of Coll	146-183m.	--	X	--	c	rocks	--
16	Arimore Point, Mull	73-213m.	mud	X	--	X	--	--
17	Hingary Bay, Arinamurohan	37m.	mud	X	--	c	rocks	--
18	Tobermory Bay, Mull	73m.	mud	c	clinker	a	clinker and rocks	Modiolus
19	Sound of Mull (north)	110m.	mud	c	rocks	a	rocks	--
20	Sound of Mull (north)	91m.	mud	a	Modiolus	c	Modiolus	--
21	Sound of Mull (north)	91m.	mud	X	--	c	rocks	--
22	Sound of Mull (north)	91m.	mud	a	Modiolus	a	Modiolus	--
23	Sound of Mull (north)	91-146m.	mud	r	Modiolus	r	Modiolus	--
24	Sound of Mull (north)	13-37m.	--	c	shell fragments	X	--	--
25	Sound of Mull (south)	110-129m.	mud	a	Modiolus	a	Modiolus	--
26	Sound of Mull (south)	123-146m.	mud	c	clinker	r	clinker	--
27	Sound of Mull (south)	13-37m.	mud	c	clinker	r	clinker	--
28	Hismore Island	37m.	--	r	vesicular basalt	r	vesicular basalt	--
29	Hismore Island	15-26m.	--	r	rocks	X	--	--

The samples were transported back to the laboratory and placed in an outside aquarium through which fresh sea-water was continually being circulated. Because of the difficulty in seeing very small brachiopods (recently settled post-larvae are less than 0.5 mm in length and their shells are transparent), the surfaces of all mussels and other potential brachiopod substrates were examined using a binocular microscope. Once detected, each brachiopod was removed from its substrate by severing its pedicle with a sharp scalpel, measured to the nearest 0.1 mm using 'MITUTOYO' dial calipers, and then preserved in either 10% formalin or 70% alcohol. The samples have been deposited in the Department of Palaeontology, British Museum (Natural History), London, and the registration numbers quoted in the text (with the prefix ZB) refer to the Recent brachiopod collections in that museum.

ECOLOGY OF *TEREBRATULINA RETUSA*

Distribution. The precise geographic limits of the distribution of *T. retusa* are unknown, as there are two morphologically similar and often confused species of *Terebratulina* in the North Atlantic. Positively identified *T. retusa* have been collected from as far north as Norway (the type area) and as far south as Spain and the Mediterranean. The species would appear to be confined to the north-eastern North Atlantic, although it has been recorded from the east coast of Greenland (Wesenberg-Lund 1940). The possibility that the two named species are members of a *Terebratulina* cline has been considered by several authors (e.g. Wesenberg-Lund 1941), and certainly the presence of individuals with intermediate morphological characteristics in the mid North Atlantic could explain the confusion over the geographic distribution of the two species, which are quite distinct.

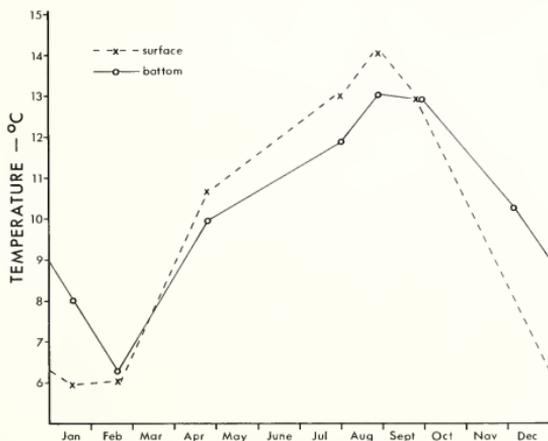
T. retusa is relatively common off the west coast of Scotland, and has been recorded from many of the sea-lochs (Davidson 1886-1888; Chumley 1918). On a more local scale the comprehensive dredging equipment available on the R/V *Calanus* provided an opportunity to investigate the pattern of distribution of *T. retusa* around the Islands of Mull and Jura (text-fig. 1). The results of these dredging operations provide strong evidence of an essentially patchy distribution, which is illustrated by the results of a comprehensive sampling programme in the Sound of Mull (Stns. 18-27 in text-fig. 1 and Table 1). In most of these samples the horse-mussel *M. modiolus* formed the bulk of the sample, whilst *T. retusa* varied from being the numerically dominant constituent (e.g. Stn. 22), to being a minor constituent (e.g. Stn. 23), or being totally absent (e.g. Stn. 21). Suitable substrate for brachiopod attachment was present at the latter station, and the fact that the habitat occupied by *T. retusa* is not occupied by other sessile epibenthos suggests that competition for space is not an important factor in these deeper water localities. It is likely, therefore, that the patchy distribution is an inherent feature of the *T. retusa* population, reflecting the short duration, and hence limited dispersal range, of the pelagic larval stage (see below). Many other Recent brachiopod populations appear to be patchily distributed (Rudwick 1970, p. 156).

It is appropriate to sound a cautionary note on the use of benthic dredging to determine the distribution pattern of sessile epibenthos such as *T. retusa*. Benthic dredges will only collect free-lying or loosely attached material which falls within a restricted size range, and it is clear that the substrates used by brachiopods are very variable both in grain-size and in the extent to which they are anchored to the sea bed. Therefore the absence of brachiopods in a particular sample may simply be due to the inability of the dredge to sample substrates such as large boulders or rock-faces. This feature was evident during the present study, as dredged samples from the Sound of Jura yielded no brachiopods (Stn. 4), and yet divers have reported quantities of *T. retusa* attached to large boulders in this region (R. Harvey, pers. comm. 1978). Benthic dredging is only a satisfactory method of sampling populations in which the predominant substrate is of a size and nature that can readily be collected, as is the case with the mussel beds in the Firth of Lorne.

Depth. Within the study area the most abundant populations of *T. retusa* occur at depths of 100-200 m, although a few specimens have been collected from an estimated depth of 3 m in the Sound of Raasay (M. K. Howarth, pers. comm. 1978), and a reasonably abundant population is known to occur at a depth of 13-20 m off the coast of Rabbit Island (Stn. 2 in text-fig. 1 and Table 1). Despite these occurrences, *T. retusa* is not a common constituent of the shallow subtidal ecosystem along the Scottish west coast, and there is no record of any dead shells being washed up on beaches in this

region. The known depth range of *T. retusa* is from 3–1478 m, although it is most commonly found between 100 and 500 m. Environmental conditions vary considerably with depth, and it is the tolerance of an organism to such variations which determines its depth range; depth in itself is not considered to be a controlling factor (Moore 1958). Presumably, therefore, *T. retusa* is prevented from colonizing intertidal or shallow tidal habitats by the combined effects of biological and physico-chemical factors characteristic of such habitats, such as competition with other organisms, rapid daily temperature fluctuations, the possibility of increased predation intensity, periodic desiccation, salinity fluctuations, wave turbulence, and intensity of incident light. Competition for space is certainly an inhibiting factor, as was illustrated during the present study when brachiopods collected from the Sound of Mull were reintroduced into the shallow marine environment of Dunstaffnage Bay in recoverable cages. These brachiopods were killed by a dense settlement of fast-growing barnacles which engulfed and smothered them within 3 months. Prolific swarms of barnacles are common in shallow-water habitats along the Scottish coast, but in the deep-water localities where *T. retusa* is abundant they are rare and solitary (in fact a different species). Clearly the relatively slow-growing *T. retusa* is at a considerable disadvantage in areas where suitable substrates are in short supply.

Temperature. Temperature is one of the most important environmental parameters for cold-blooded marine invertebrates (Moore 1958), limiting their geographic range, and affecting all aspects of life by virtue of its controlling effect on the rates of metabolic processes (i.e. Van't Hoff's Law—see Prosser 1973). The general pattern of temperature fluctuation experienced by *T. retusa* in the Firth of Lorne depression was determined (sea-water samples were collected from the vicinity of the brachiopod population using insulated sampling bottles), and has been compared with surface water temperatures in text-fig. 2. The temperature of bottom waters in the Firth of Lorne range from a February minimum of 6.5°C to a maximum of 13°C in August, an annual range of 6.5°C which is smaller than would be expected at this latitude because of the warming effect of the North Atlantic Drift Current. The over-all pattern and range is similar in surface waters, (minimum in January of 6°C and a maximum of 14°C in August—annual range of 8°C), although it is apparent from text-fig. 2 that the bottom and surface waters are virtually never isothermal and can differ by as much as 2.5°C. This vertical stratification of the water column, the thermocline, is a common feature of Scottish sea-lochs and, although complex, can be considered as reflecting the greater susceptibility of



TEXT-FIGURE 2. Annual temperature curves for the surface and bottom (approx. 150 m) waters in the Firth of Lorne, Scotland.

surface waters to prevailing air temperatures (e.g. being warmer in summer and cooler in winter). Other factors which enhance this vertical stratification are density and salinity gradients produced by the high levels of surface run-off of fresh water from the surrounding land. The thermocline breaks down during two short periods in spring and autumn when the water column becomes thoroughly mixed, isothermal, and uniformly saturated with oxygen (i.e. the points at which the curves in text-fig. 2 cross).

Substrate. The predominant utilization of *M. modiolus* as substrate by the brachiopods in the Firth of Lorne depression is well illustrated by the analysis of the substrate of attachment of the 786 specimens of *T. retusa* collected on 5 May 1977 (Table 2). The sample contained 204 living mussels, 166 of which

Substrate	No. of Occurrences	No. of Brachiopods	% of Total
Living mussel	166	591	75
Dead mussel	27	53	7
Mussel frags.	33	63	9
Hydrozoan	10	13	2
Dead gastropod	5	14	2
Dead brachiopod	4	10	1
Living & dead bivalve	4	8	1
Sponge/oscidian	4	16	2
Unattached	4	8	1
Rock	2	9	1
Tube-worm	1	1	0.1

TABLE 2. Substrate of attachment of the 786 specimens of *T. retusa* collected on 5 May 1977 from the Firth of Lorne.

(i.e. 81%) had been utilized as substrate by *T. retusa*. A total of 707 brachiopods (91% of the sample) were attached to living or dead mussels or to fragments of mussel shell. Mussels are ideal substrate for brachiopods, being sessile and of much longer life span (at least 20 years (Comley 1978) as compared with a maximum of 7 years for *T. retusa*). The relatively large surface area of the mussels is readily bored by the anchoring pedicle rootlets of *T. retusa*, and is free of obstructions which would hinder the rotation of brachiopods around their pedicles, a procedure which enables them to move away from localized disturbances and to take up preferred feeding orientations. In addition, the majority of brachiopods are attached anteriorly, close to the inhalant and exhalant feeding currents of the mussels, and are likely to benefit from the enhanced flow of nutrient-rich sea-water in such regions. The selective sampling bias of the benthic dredge makes it impossible to determine to what extent the data in Table 2 can be considered representative. However, the thin covering of fine-grained glauconitic mud in this area is likely to preclude dense settlements directly on to rock surfaces, because of the high risk of being smothered or choked by suspensions of sediment stirred up by bottom currents. Under such circumstances the elevated position resulting from attachment to mussels would be all the more advantageous for brachiopods, especially as the mussels' ability for limited reorientation will ensure that their anterior region remains above the substrate in the event of sediment accumulations. Nevertheless, direct attachment to substrates such as boulders or rock-faces is to be expected in the Firth of Lorne depression when suitable surfaces are free of sediment due to inclination or current scour.

Current. Little can be said about the currents in the vicinity of the Firth of Lorne population, as direct measurements of velocity was beyond the scope of this study. However, indirect evidence of strong bottom currents comes from the fact that the great majority of dead shells are moved away from the living population and have presumably accumulated in the deepest regions of the depression. This phenomenon is being investigated with the aim of assessing the fossilization potential of the Firth of Lorne brachiopod population. A strong and constantly flowing current is a necessity for sessile benthic invertebrates such as *T. retusa*, which feeds on material carried in suspension in the surrounding sea-water.

Associated fauna. Apart from *T. retusa* the surfaces of the Firth of Lorne mussels are used as substrate by a wide variety of sessile organisms and plants, the most numerous of which being the cemented inarticulate brachiopod *Crania anomala* (Müller), hydroids, sponges, chitons, spirorbid worms, foraminifera, the bivalve *Anomia*, and gastropods (e.g. *Cappula*). The dredged samples also contained abundant ophiuroids (*Ophiothrix* and *Ophiura*), and asteroids (*Crossaster*, *Solaster*, and *Asterias*) are often present but in much smaller numbers. Occasionally echinoids (*Echinus*) and decapods (*Munida* and *Galathea*) have been recovered. As compared with shallow-water localities in the Firth of Lorne, this fauna is impoverished, especially in sessile epibenthic organisms which would be in direct competition with *T. retusa* for space and nutrients. Burrowing animals, such as bivalves and polychaetes, are rare, presumably because of the thin sediment cover. The external shell surfaces of *T. retusa* are themselves used as substrate by a wide variety of animals and plants, in particular sponges, hydroids, bryozoans, and spirorbid worms. Shallow borings, almost entirely confined to the primary shell layer of *T. retusa*, are thought to be the work of phoronids and fungi (B. Akpan, pers. comm. 1980). These borings are not predatory, and none of the major predators in this fauna appears to feed on *T. retusa*, although it is impossible to assess the effect of all potential predators (e.g. fish). Some small worms have been found in the brachial cavity of a few specimens of *T. retusa*, but it is not clear if these are parasitic or have merely been drawn in by the feeding currents.

REPRODUCTION

It was of great importance to accurately determine the timing and frequency of spawning in *T. retusa*, as such information is necessary to establish the population structure and dynamics. In *T. retusa* the sexes are separate and can be distinguished on the basis of colour (males are whitish, whilst the tissues of females are orange-red), and by the examination of the gonads. Males and females are approximately equally represented (342 adult specimens could be sexed in the sample collected on 26 October 1977, 181 of which were male, and 161 female). One pair of gonads is present in each valve, developing within the mantle canals between the inner and outer mantle epithelium and extending posteriorly into the body cavity. Individual gametes develop along narrow interconnecting genital canals, which are anchored to the outer epithelium by linear membranes (Hancock 1859). Columns of tissue, situated in the interstices between the genital canals, prevent the gonads from being damaged or crushed between the two layers of tissue. It seems likely that the gonadal pits which have been recognized on the internal surfaces of some fossil brachiopods represent the points of attachment of the supportive columns rather than, as Rudwick (1970) suggests, the points at which the gonad itself was attached. Rigid calcareous spicules are present in many regions of the body tissues of *T. retusa*, but are particularly densely developed above the gonads thereby providing further protection.

The periodicity of larval recruitment was determined by monitoring the state of development of gonadal tissues throughout the year (by comparing at least twenty adult specimens from each sample), and by microscopically examining the surfaces of all potential brachiopod substrate for recently settled post-larvae. It became clear that the gonads of *T. retusa* pass through two full development cycles per year, culminating in the release of gametes in late spring and late autumn. Recently settled post-larvae have only been observed at these times, and the spawning event must be highly synchronized, of short duration, and affecting the vast majority of sexually mature individuals. For example, the entire reproductive cycle, from spawning through to spatfall, was completed within the 3-week period between samples collected in early and late May 1977. The precise timing of the natural spawning event must be related to temperature, as *T. retusa* spawns at a temperature of 10–11 °C in both autumn and spring. A similar temperature control on the timing of spawning activity has been recognized in both articulate (Rickwood 1968) and inarticulate brachiopods (Paine 1963; Yatsu 1902).

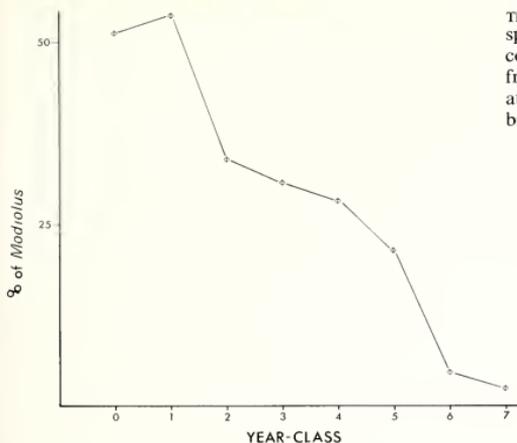
To investigate the spawning behaviour in greater detail, ripe individuals collected immediately prior to one of the autumn spawning periods were induced to spawn in the laboratory by rapid controlled fluctuations of temperature and the addition of mobile mature sperm teased from males.

Temperature variation is a common method of inducing spawning in marine invertebrates (P. Redfern, pers. comm. 1978) because the resulting stress stimulates the release of gametes. This method had previously been used by the author and Dr. J. Richardson in a successful attempt to induce spawning in the Recent New Zealand brachiopod *Terebratella inconspicua* (Sowerby). It seems that synchronization of spawning in neighbouring specimens depends upon the presence of male sperm, or perhaps hormones secreted along with it, in the surrounding sea-water; it was noticeable, both with *T. inconspicua* and *Terebratulina retusa*, that spawning commenced shortly after suspensions of sperm had been drawn into the brachial cavity by feeding current. Once spawning is initiated the ova and sperm are moved from the gonads to the brachial cavity via the metanephridia, and then extruded from the valves by a series of snapping movements similar to those used during the ejection of faecal or pseudofaecal pellets (Rudwick 1970).

Fertilization occurs both in the brachial cavity of females and on the surrounding substrate, and a high degree of synchronization is obviously vital as the sperm remain in suspension and is rapidly carried away from the breeding population by bottom currents. The ova, by contrast, settle in dense clusters around the margin of the parent. Only a small proportion of ova ejected during the laboratory experiment were fertilized, although in nature the proportion may be greater. Both fertilized and non-fertilized ova appeared to be particularly susceptible to bacteriological attack, although once again this may have been due to atypical laboratory conditions, in particular unavoidable increases in sea-water temperature due to the heat from the microscope lamps. The free-swimming larvae which developed from ova fertilized in the laboratory appeared to be very similar in size, shape, and activity to those of *T. septentrionalis* (Couthony) from the coast of Maine (Morse 1873) although no attempt was made to study them in detail. The laboratory-reared larvae of *T. retusa* had reached an advanced stage of development (with a third peduncular segment indicating settlement was imminent) within 5 days of spawning, which is in keeping with the observed maximum duration of 3 weeks in nature.

During one of the natural spawning periods, attempts were made to collect pelagic larvae from the Firth of Lorne using a plankton net trawled at the surface and at an estimated depth of 100 m. No brachiopod larvae were recovered, indicating perhaps that the larvae remain close to the sea-floor during their pelagic stage. However, the evidence for this is not conclusive, especially as the pelagic stage appears to be of at most a few days' or perhaps hours' (see below) duration, and it was impossible to conduct a comprehensive plankton study for the expected duration of the spawning period. Some pelagic larvae are known to actively swim towards light sources during their early development stages (e.g. Paine 1963), and certainly the larvae of the abyssal inarticulate *Pelagodiscus atlanticus* (King) has been recovered at the surface (Ashworth 1915). An alternative explanation for the lack of brachiopod larvae in the plankton samples is that the larvae are brooded to an advanced stage of development within the brachial cavity of adult females, thereby further curtailing the duration of the free-swimming stage. Such a phenomenon has been observed in *T. septentrionalis* from the Bay of Fundy, Canada (Webb *et al.* 1976), and is of particular significance as no special brood pouches are developed. Instead the brooded larvae are simply held between the filaments of the lophophore and the body wall. In the Firth of Lorne the disturbance caused by the dredging process would almost certainly cause the release of any brooded larvae within *T. retusa* and hence it will be difficult to determine if such a phenomenon is widespread. However, the space available for brooded larvae within the brachial cavity of *T. retusa*, assuming a mechanism similar to that of *T. septentrionalis*, would be insufficient to hold all ova shed by one individual during a spawning period, and therefore a proportion must still be extruded from the brachial cavity.

The density of larval settlement on the Firth of Lorne mussel beds following each spawning event is remarkable. The number and size of brachiopods attached to each mussel collected on 24 May 1977 was recorded, and the percentage of mussels with attached brachiopods from each year-class was plotted (text-fig. 3). Representatives of the '0' year-class (which in this sample had settled within the 3 weeks prior to collection) and the 1st year-class (the two 1976 cohorts) were both present on more than 50% of the mussels in the sample, which represents a considerably greater proportion of the available substrate, as the mussels live in dense clusters with the lowermost specimens being less



TEXT-FIGURE 3. Percentage of the total number of specimens of *Modiolus modiolus* (Linnaeus) collected on 24 May 1977 which had brachiopods from each of the seven year classes of brachiopods attached. The sample yielded 127 mussels and 554 brachiopods; a total of 21 mussels (= 16.5%) had no attached brachiopods.

accessible for brachiopod larvae. The fact that fewer mussels had '0' year-class brachiopods attached is probably due to the difficulty in picking out the former, and the trend of the graph would suggest that more than 50% of the mussels are covered at a spawning event. As many as thirty brachiopods of different ages have been found on a single mussel, and on average each mussel in a sample has 3-4 brachiopods attached. The density of settlement provides further indirect evidence of a short pelagic larval stage, as the degree of dispersion increases with the length of the free-swimming stage. Both autumn and spring spawnings appeared to be equally successful, although there was no practicable method of comparing the numbers of larvae produced.

POPULATION STRUCTURE AND DYNAMICS

Problems such as biased sampling, selective preservation, and *post-mortem* transportation have bedevilled attempts to interpret fossil population structure and dynamics by means of size-frequency distributions. Size-frequency distribution does, however, have considerable potential as an analytical tool in palaeontology, provided the fundamental problem of obtaining a representative sample can be overcome. The simplest and most effective method of checking for 'representativeness' is to collect a series of large samples from the population in question and to compare the resulting size-frequency distributions. Providing adequate care has been taken to eradicate recurring sampling inadequacies, similar results from a series of samples can be considered as good evidence that such results are an accurate reflection of the situation in the parent population. The ability to rationalize the recurring pattern of size-frequency distribution within the limits of theoretical population biology can be regarded as a further useful check on the validity of such results. In this study both approaches provided strong evidence that the regular samples from the Firth of Lorne population were representative, and certainly the favourable situation of the *T. retusa* population makes sampling bias unlikely, and obviously the distortion resulting from preservational bias is not pertinent to studies of living animals. The number of specimens in a sample is certainly a critical factor, however, and the necessity of having a large sample has been stressed by several authors (see Hallam, in discussion at end of Craig and Oertel 1966). The density and abundance of brachiopods at the Firth of Lorne locality, combined with their favourable situation for sampling, facilitated the collection of acceptably large samples.

Further problems have arisen because of confusion over the descriptive terminology applied to size-frequency diagrams, which warrants mention for the sake of clarity. In conventional statistical

usage the term 'skewed' refers to the gradually sloping 'tail' of an asymmetrical distribution (Simpson *et al.* 1960), and therefore a unimodal skewed distribution which slopes away gradually on the right-hand side (e.g. text-figs. 4, 6) would be described as right-skewed, or positively skewed. A left-skewed, or negatively skewed, distribution slopes gradually from the left-hand side to a prominent mode on the right-hand side of the diagram. This convention has been reversed by some authors, who relate 'skewed' to the mode rather than the 'tail' (e.g. Raup and Stanley 1978; Thayer 1978). Throughout this study the more conventional usage has been adopted.

The over-all shape of a size-frequency distribution reflects the relative proportion of animals of different age-groups, and is an important diagnostic feature. All samples analysed during this study yielded a unimodal right-skewed length-frequency histogram (e.g. text-fig. 4) with sexually immature juveniles forming considerably more than 50% of the sample at all seasons. For example, 71% of the 811 specimens collected in March 1977 were less than 9.6 mm in length (i.e. not more than 2 years old—see below). This predominance of juveniles is not unexpected, as the long-term success of any brachiopod population depends upon the regular influx of large numbers of larvae. The population structure of *T. septentrionalis* from the Bay of Fundy, Canada, is also unimodal and right-skewed at all seasons (Noble *et al.* 1976), although, just as in *T. retusa*, the position of the main mode varied slightly depending on the average size of the most recently settled cohort.

Significantly there is no over-all bimodality discernible in any of the length-frequency histograms of *T. retusa*. A bimodal size-frequency distribution is characteristic of some living brachiopod populations (e.g. Rudwick 1962; Doherty 1976, 1979), and it is now generally accepted that the secondary (right-hand) mode forms as a result of the merging of older age-groups because of the gerontic slowing or cessation of growth. Such a growth strategy (known as determinate growth (Doherty 1976) because adults continue to survive without growing after attaining their maximum, or determinate, size) is very different to that of *T. retusa*, which continues to grow throughout life.

When examined in greater detail, it is apparent that the length-frequency histograms of *T. retusa* are characterized by regularly spaced subsidiary peaks (e.g. text-fig. 4). Once the biannual spawning season and its timing had been determined by direct observation, it was then possible to interpret these peaks in terms of settlement cohorts. The underlying principle on which this analysis is based is that each of the peaks represents a cohort of brachiopods which settled on the mussel beds after one

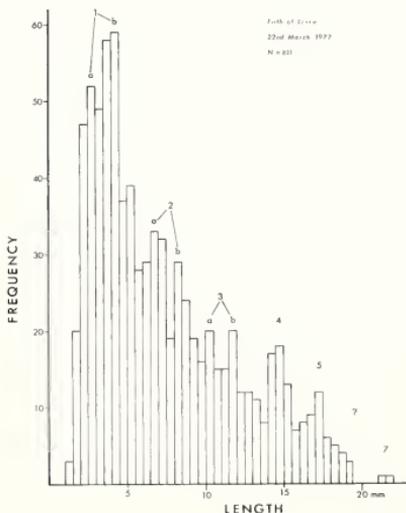
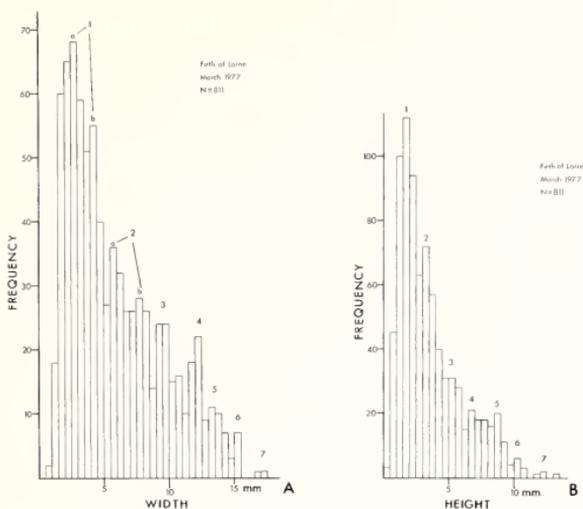


TABLE 3. Analysis of the March 1977 length-frequency histogram (Fig. 4). All measurements are in mm.

Annual Increment	Peak	Biannual Increment	Date of Settlement	Year-Class
	2.75	1.5	Autumn 1976	1 a
4	4.25	1.5	Spring 1976	1 b
4	6.75	1.5	Autumn 1975	2 a
3.5	8.25	1.5	Spring 1975	2 b
3.5	10.25	1.5	Autumn 1974	3 a
3	11.75	1.5	Spring 1974	3 b
	14.75		1973	4
2.5	17.25		1972	5
2.5	19.75		1971	6
1.75	21.50		1970	7

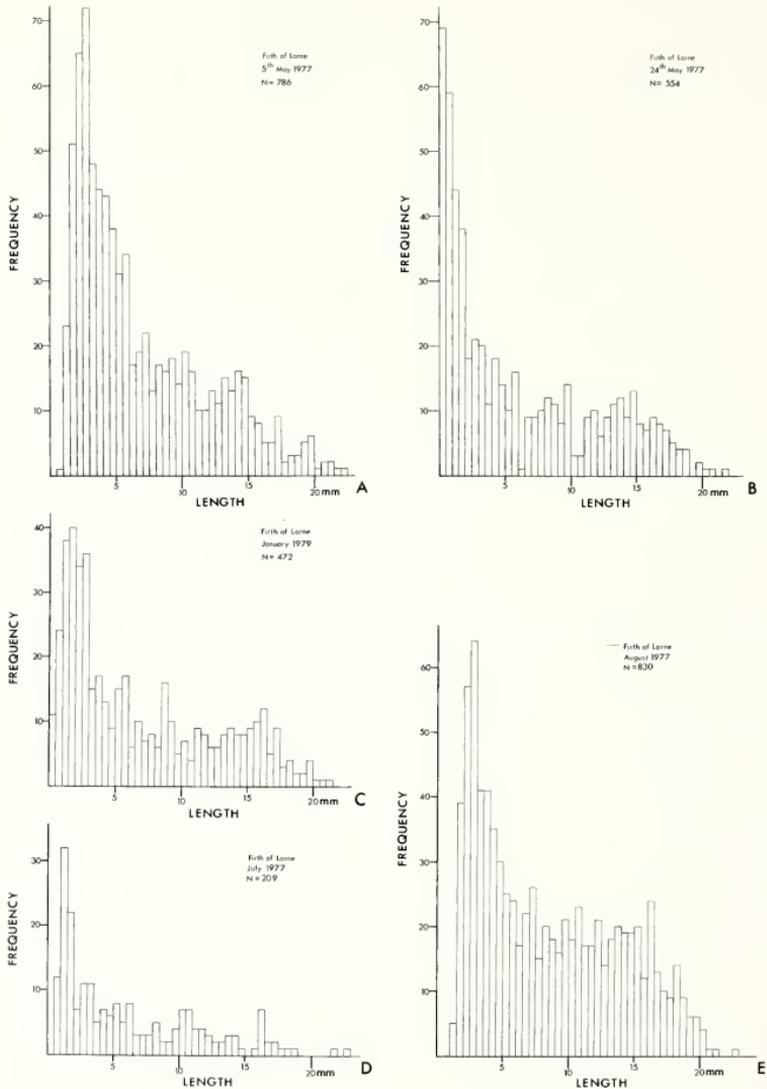
TEXT-FIGURE 4. Length-frequency histogram of *T. retusa*, March 1977 sample (ZB3727–ZB3736). 1a, b, etc., refer to settlement cohorts (see text).



TEXT-FIGURE 5. Width-frequency (A) and height-frequency (B) histogram of *T. retusa*, March 1977 sample (ZB3727-ZB3736). 1a, b, etc., refer to settlement cohorts (see text).

of the biannual reproductive events. Such a technique has been widely used, and is a logical assumption provided that the animals have a sharply defined breeding season, and that the average growth-rate of individual cohorts is such that successive peaks do not merge (at least in the early stages of life). The majority of these subsidiary peaks can be recognized in all histograms, but the March 1977 length-frequency histogram (text-fig. 4) has been selected as a standard and will be analysed in detail. It can be demonstrated that the width-frequency histogram (text-fig. 5A), and to a lesser extent the height-frequency histogram (text-fig. 5B), yield essentially the same results as the length-frequency histogram, but in *T. retusa* the maximum incremental increase in shell dimensions occurs anteriorly (i.e. in length) throughout ontogeny, and hence the measured shell width and height dimensions are of smaller absolute value with the result that the resolution between peaks in the frequency distribution is reduced. An alternative method of analysing length-frequency data, in which the data is plotted on probability paper, is described in the Appendix.

The March 1977 sample was collected approximately 2 months prior to the spring 1977 spawning period, and therefore the first two peaks on the left-hand side of text-fig. 4 (at 2.75 mm and 4.25 mm) correspond to the autumn and spring cohorts in 1976, and are therefore labelled 1(a) and 1(b) respectively in text-fig. 4 and Table 3. Similarly the paired peaks at 6.75 mm (2a) and 8.25 mm (2b) represent the two cohorts which settled in autumn and spring 1975 respectively; the autumn and spring cohorts in 1974 are likewise clearly represented by twin peaks at 10.25 mm (3a) and 11.75 mm (3b). Each of these pairs of peaks have identical spacing (i.e. 1.5 mm—'Biannual' Increment in Table 3), and the interval between cohorts which settled 1 year apart remains remarkably constant (i.e. approx. 4 mm—Annual Increment in Table 3). Clearly the rate of growth of *T. retusa* remains constant throughout the first 3 years of life, at least within the limits of resolution of this method of mensuration. Another striking feature of this analysis is that each of the biannual spawning periods in the previous 3 years has been highly successful, indicating that this relatively deep-water population is not subject to environmental disturbances known to cause aperiodic disruption to the



TEXT-FIGURE 6. Length-frequency histograms of *T. retusa* A, 5 May 1977 sample (ZB3737-ZB3746). B, 24 May 1977 sample (ZB3747-ZB3756). C, January 1979 sample (ZB3717-ZB3726). D, July 1977 sample (ZB3757-ZB3766). E, August 1977 sample (ZB3767-ZB3776).

reproductive cycle of shallow-water marine invertebrates. As mentioned above, the spawning events observed subsequently during 1977–1979 appeared to be equally successful.

The position and spacing of the remaining peaks in text-fig. 4, indicates that the growth-rate progressively decreases from the third year of life onwards, resulting in the merging of the paired peaks to form a single broad peak representing the biannual cohorts in 1973 (14.73 mm—labelled 4 in text-fig. 4 and Table 3) and in 1972 (17.25 mm—labelled 5). There is no peak corresponding to the 1971 cohorts in text-fig. 4, but such a peak is present at 19.75 mm in the 5 May 1977 sample (text-fig. 6A) and such a value is included in Table 3 for the sake of completeness (as described below there is very little movement of peaks between March and May). Ambiguity over the position of the peaks corresponding to the older age-groups is not surprising considering the rarity of specimens—the grouping tentatively identified as representing the 1970 cohorts in text-fig. 4 (i.e. 21.75 mm—labelled 7) includes a mere two specimens out of a total sample of 811. However, similar groupings of slightly more specimens do occur in other samples, and its interpretation as a 7th year-class can also be justified on the basis of the spacing between previous peaks in text-fig. 4 (see Table 3).

TABLE 4. *T. retusa* age-groups in the March 1977 sample; size range refers to maximum shell length measured in mm.

Age Group	Year of Settlement	Size Range	No. of Specimens	% of Total	% Rate of Mortality
1	1976	up to 5.5	365	45	
2	1975	5.6 – 9.5	213	26	42
3	1974	9.6 – 13.5	121	15	43
4	1973	13.6 – 16.0	63	8	45
5	1972	16.1 – 18.5	40	5	40
6	1971	18.6 – 20.0	7	0.9	83
7	1970	over 20.0	2	0.2	71

Following on from this analysis it was possible to divide the March 1977 sample into age-groups (= year-classes) on the basis of a range of lengths (Table 4). The boundaries of the age-groups are somewhat arbitrary, and the higher and lower values in each grouping include specimens which rightly belong in the age-groups on either side. Nevertheless, the exercise is useful as it quantifies the relative proportions of age-groups and provides an estimation of mortality-rates.

Comparison with theoretical model. One of the most significant contributions to the study of population structure and dynamics in recent years has been the comprehensive theoretical simulations of Craig and Oertel (1966). Having identified five main factors which influence the overall shape of a size-frequency distribution, Craig and Oertel programmed a computer to produce an exhaustive series of histograms using various combinations of these five factors. Having established the characteristic population structure of *T. retusa* in nature, it was obviously of interest to identify which of Craig and Oertel's experiments was conducted using a combination of factors similar to those prevailing in the Firth of Lorne population, and to compare the theoretical simulation with the actual population structure.

Craig and Oertel's five factors are (1) recruitment strategy, (2) growth-rate, (3) coefficient of variation of growth-rate, (4) mortality-rate, (5) cessation of growth. *T. retusa* clearly falls within the 'boreal' recruitment strategy of Craig and Oertel, which was defined as two short spawning periods in autumn and spring. The growth-curve of *T. retusa* is intermediary between the 'linear' and the 'high-to-low' curves used by Craig and Oertel, but is closer to the former than the latter. The third factor, the coefficient of variation of growth-rate, was an attempt to allow for the effects of the varying growth-rates of individuals in a single cohort. There is no indication of the extent of such variability in *T. retusa*, but Craig and Oertel mostly used a coefficient of 2, which they believed to be an acceptable average value. The mortality-rate of *T. retusa* remains constant, at least during the first 5 years of life (see below). The final factor related to the timing and duration of any cessation of growth during the year, and there is good evidence that *T. retusa* falls within Craig and Oertel's category (a), namely a winter stoppage of 3 months' duration (see below).

This permutation of factors was combined in Craig and Oertel's experiment number 34, and the resulting size-frequency histogram (Craig and Oertel, 1966, fig. 17, p. 346) is strikingly similar to the length-frequency histograms of *T. retusa*. The over-all shape of all these distributions is identical,

being unimodal and right-skewed. The computer simulation had evenly spaced peaks corresponding to the biannual cohorts, which merge into a single annual peak in later life, exactly as in the natural population. Craig and Oertel described this experiment as follows:

Boreal recruitment, three winter months cessation of growth with doubling of mortality, coefficient of variation 2 . . . growth-rate linear . . . mortality constant.

Boreal recruitment consists of two equal waves in late spring and early autumn, separated by a short summer interval and a long winter interval. This forms twin peaks in the living population . . . the groups of twin peaks are equidistant, and the twins have identical intervals. This peak spacing is diagnostic for linear growth.

Obviously there are differences in detail between the theoretical and the actual, especially as the critical factors in nature tend to vary slightly with increasing age rather than remain constant. Nevertheless, the results of this comparison are very encouraging, and demonstrate the potential of a combined theoretical and empirical approach to the study of population structure and dynamics.

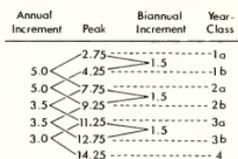


TABLE 5. Analysis of the peak spacing in the width-frequency histogram of *Rostricellula rostrata*, Ulrich and Cooper (data, in mm, are from Walker and Parker 1976).

Relevance for fossil populations. The analysis of the population structure and dynamics of fossil brachiopods is best conducted using both size-frequency histograms and growth-line counts, as the inherent deficiencies of one method are compensated for by the strengths of the other. However, under ideal conditions of preservation, a frequency histogram prepared from a sample of fossil brachiopods can, on its own, yield precise data on the autecology of that species. In preparing a width-frequency histogram from a sample of the Middle Ordovician species *Rostricellula rostrata*, Ulrich and Cooper from Tennessee, Walker and Parker (1976) used the same grouping adopted for the *T. retusa* histograms (i.e. 0.5 mm), and hence the prominent peaks in the *R. rostrata* histogram can be analysed in the usual tabular form (i.e. Table 5) allowing direct comparison with the living population (i.e. Table 3).

This method of analysis emphasizes the remarkable similarity in the population structure between the living and fossil population, especially in the pattern of peak spacing. Both histograms have prominent regularly spaced twin peaks, with the separation between each peak in a twin (i.e. the 'biannual increment'—see Tables 5 and 3) being identical in both populations (i.e. 1.5 mm). Just as in the *T. retusa* histogram, these twin peaks are not discernible on the right-hand side of the diagram, because the slowing of the growth-rate in older specimens has resulted in the merging of the twins to form a single peak representing the total annual recruitment (e.g. at 14.25 mm in Table 5). There are differences in the absolute values of comparable increments (e.g. annual increments—compare column 1 in Tables 5 and 3) and the fossil species had a shorter life span and a more rapidly decreasing growth-rate, but such differences are of minor significance compared to the similarity in the over-all pattern of peak spacing. Both theoretical and empirical data indicate that this pattern of regularly spaced twin peaks is characteristic of animals inhabiting temperate latitudes, and the fossil population can reasonably be assumed to have experienced broadly similar seasonal cycles of temperature, food supply, etc., to those prevalent today in the Firth of Lorne or other temperate habitats. Apart from comparison with equivalent living populations, the reconstruction of population structure and dynamics in fossil brachiopods would, under ideal circumstances, be based on the analysis of several large samples rather than just one, and would also take into consideration pertinent localized environmental and biological factors; as mentioned above, the interpretation of growth-lines can further refine the resulting data. Nevertheless, the success of this preliminary comparison between the population structure of living and fossil brachiopods augers well for this technique.

Seasonal growth pattern. To obtain a more precise picture of the pattern of seasonal growth in *T. retusa*, the position of peaks corresponding to individual cohorts was recorded in samples collected throughout the year. The results (Table 6) suggest that the growth-rate of adults decreases significantly in winter months, as the peaks appear to remain stationary between January and May.

TABLE 6. Movements of peaks corresponding to the 4th and 5th year-classes of *T. retusa* (measurements, in mm, refer to maximum shell length).

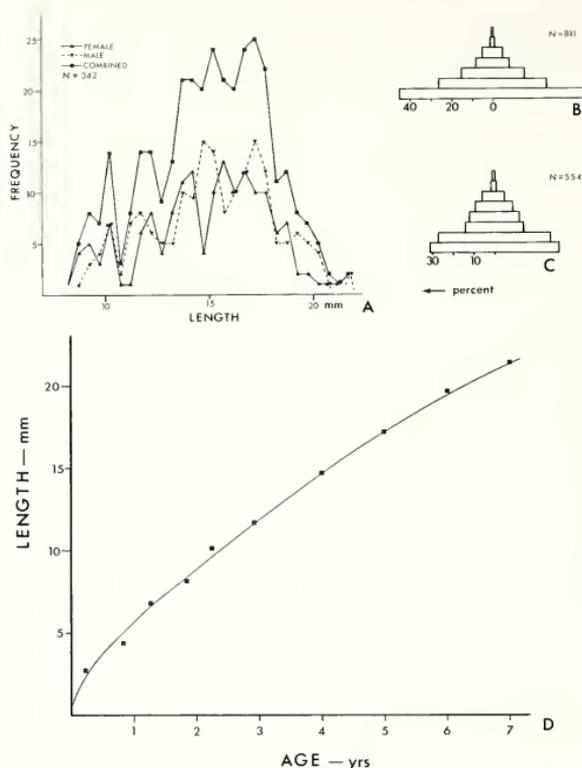
Age Group	Mar	May	Aug	Oct†	Jan	Expected in Mar
4	14.75	14.75	16.25	17.25	17.25	17.25
5	17.25	17.25	18.25	18.75	19.75	19.75

The evidence for this is based on the assumption that the mid-point of a particular peak is an acceptable measure of the average length of specimens in a cohort; although the growth-history of individuals within a cohort will vary depending on localized environmental conditions. The slowing of growth in winter is an expected and readily explained phenomenon, bearing in mind the direct relationship between decreasing temperature and a reduction of the rate of metabolic activity in cold-blooded invertebrates. It seems likely that the rate of growth of *T. retusa* slows progressively during the autumn and winter, and reaches a minimum, or perhaps ceases altogether, in mid-winter when temperatures are lowest and food supplies minimal. There is some evidence that sexually-mature females have a slightly slower rate of growth than mature males (text-fig. 7A), perhaps indicating that the production of ova is more demanding in terms of available nutrients. However, the pattern of modes in text-fig. 7A is rather confused and far from unequivocal, and this facet of sexual dimorphism does not appear to be noticeable in the combined length-frequency distributions. The increments involved, like those produced by variable growth-rates in a single cohort, are so small as to be outside the limits of resolution of the length-frequency histogram.

In contrast, the growth of recently settled post-larvae appears to proceed rapidly during the first 3 months of settled life, and to be independent of prevailing environmental conditions. For example, the cohort which settled in late autumn 1976 had attained an average length of 2.75 mm by the following March (i.e. 1(a) in text-fig. 4), a rate of growth greater than at any other stage of life. Similarly, the cohort which settled in May 1977 had grown to an average length of 2.75 mm by the following August (compare text-figs. 6B, 6E). The growth-history of *T. retusa*, therefore, has three distinct phases: (1) approximately 3 months of rapid growth immediately following settlement in both autumn and spring; (2) the remainder of the first 3 years of life, when the annual growth-rate remains constant, but varies seasonally depending upon ambient sea-water temperatures; (3) the remainder of life, during which annual growth-rates decrease progressively.

The initial period of rapid post-settlement growth is a prudent feature, as the early development of a rigid protective exo-skeleton will reduce mortality rates during this most vulnerable stage of settled life. The ability of the autumn cohorts to grow in winter months indicates perhaps that their modest nutrient requirements are adequately satisfied by even the reduced winter food supplies. It may also be of significance that the volume of the feeding 'chambers' in juveniles is considerably greater than that enclosed by the valves of the shell, as the filaments of the lophophore extend a considerable distance beyond the shell margin when feeding. In adults the filaments are almost entirely contained within the brachial cavity when feeding; in juveniles the increased risk of predation resulting from the exposed filaments and widely gaping shell (as much as 45° as compared to ≈ 15° in adults) may be offset by the advantages gained by the relatively rapid shell growth due to the proportionately high levels of nutrient intake. The reduction in the rate of annual growth-rate at the end of 3 years coincides with the onset of sexual maturity, and probably reflects a fundamental change, with the nutritional requirements of the developing gonads receiving precedence over other metabolic processes.

Growth-line analysis. The analysis of the pattern of growth-line formation in brachiopods is best conducted on a cumulative basis using a large number of individuals from a single population. The main difficulty of attempting a growth-line analysis of an individual is that the pattern is often incomplete, and hence difficult to interpret. Nevertheless, a sample analysis of a single adult specimen



TEXT-FIGURE 7. A, sexual dimorphism in shell growth as determined from 342 sexually mature specimens of *T. retusa* collected 26 October 1977 from the Firth of Lorne population. B, C, age pyramids for *T. retusa* population in the Firth of Lorne before (B, from March 1977 sample) and after (C, from 24 May 1977 sample) spatfall. D, Growth curve for *T. retusa* as determined from the analysis of the March 1977 sample (i.e. Table 3).

of *T. retusa* with a complete record of growth-line formation is included at this stage as it contributes further to our knowledge of the growth history of the population. The specimen (ZB 3717) was collected during January 1979 at an approximate depth of 165 m from the Firth of Lorne, and was 15.5 mm in length. Having measured the distance to each growth-line from the posterior margin of the shell along the medial axis of the pedicle valve (Table 7), and determined the spacing between individual growth-lines (column 2 in Table 7), it was then apparent that growth-lines form biannually. The age-group analysis in Table 4 indicates that a specimen of length 15.5 mm should be 4 years old; a conclusion which is confirmed by growth-line analysis which indicates that the 1st growth-line on this specimen was formed in autumn 1975 (Table 7) and therefore it must have settled in spring 1975.

The spacing between growth-lines (column 2 in Table 7) on this specimen indicates that approximately two-thirds of the annual growth occurs during the 'summer' period, whilst the

remaining one-third occurs during 'winter'. The exact timing of growth-line formation has not been determined, but is assumed to occur in autumn and spring, and at times of pronounced environmental and physiological stress. If so, the 'summer' and 'winter' periods would therefore be of approximately 6 months' duration, and would probably be more accurately designated as 'summer/autumn' and 'winter/spring' respectively.

TABLE 7. Analysis of growth lines on single specimen of *T. retusa* (ZB3717) collected from the Firth of Lorne on 21 January 1979 (data in mm).

Increment	Growth-line	Date of Formation
W/inter ----- 1.4	2.0	Autumn 1975
Summer ----- 2.9	3.4	Spring 1976
Winter ----- 1.6	6.3	Autumn 1976
Summer ----- 2.9	7.9	Spring 1977
Winter ----- 2.0	10.8	Autumn 1977
Summer ----- 1.4	12.8	Spring 1978
Winter ----- 1.3	14.2	Autumn 1978
	15.5	Spring 1979

Mortality. The data in Table 4 indicates that roughly 40% of the brachiopods in each age-group die per year. This estimation applies only to specimens more than 1 year old, as there is no viable method of determining the mortality rate during the periods prior to and immediately following settlement. Significantly higher mortality-rates are likely to occur during these early stages of life, as has been determined in other living brachiopod populations (e.g. Doherty 1976, 1979). As the number of specimens in the older age-groups is so small, the significant increase in mortality-rates amongst the 6th and 7th age-group (Table 4) may not necessarily be representative, although older specimens may indeed be more susceptible to disease, stress, etc.

The causes of mortality in the *T. retusa* population are not apparent, although it was not possible to examine large numbers of dead shells for signs of predation. There is, however, very little evidence of repaired shell damage in living specimens, which suggests that the level of predation is low. Probably a large proportion of deaths occur in winter because of the stress caused by less favourable environmental conditions. It may be significant that Craig and Oertel (1966) incorporated a doubling of the mortality rate in winter in the experiment which yielded a size-frequency distribution similar to that of *T. retusa*. The fact that a few adult specimens did not develop gonads during spawning periods may be symptomatic of diseases or infections which may account for a small proportion of the annual mortality. However, as gonad development is discernible during winter months, it would appear that starvation is not a major cause of death.

The small tissue content of brachiopods probably partially explains the apparent lack of predators on *T. retusa*, although predatory gastropod borings have been found in other species (e.g. Logan 1979). Because of their low nutritional value, it may indeed be more reasonable to look for potential predators at the 'micro' rather than the 'macro' level, and certainly carnivorous micro-organisms could readily gain access to the brachial, and perhaps body, cavity via the feeding currents. Some nematoid worms do appear to feed on brachiopod lophophoral filaments (McCammon 1971) although there has been no detailed study of the extent and effect of such predation/parasitism.

CONCLUSIONS

The large population of *T. retusa* in the Firth of Lorne is well established, and the species is relatively abundant in deeper waters off the west coast of Scotland. The main reasons for this success are the recurring efficiency of the reproductive activity and the absence of competing organisms or readily apparent predators. Representatives of the genus *Terebratulina* have a long history, and have been present in the North Atlantic since its inception. It survives as one of the most cosmopolitan and abundant of living brachiopod genera, occurring in all oceans. The longevity and success of this genus are probably due to an adaptability of pedicle morphology which greatly increases its range of substrates, combined with an ability to colonize habitats (such as the Firth of Lorne depression) inimical to other more 'successful' epibenthonic organisms. Critical factors in this latter capability may

be a generally low level of nutrient requirements, and the ability to survive prolonged periods of adverse conditions by a virtual cessation of metabolic processes, as demonstrated by the specimens which survive in the outside aquarium at Dunstaffnage despite being subjected to rapid daily temperature fluctuations. Clearly another important factor in the longevity and success of the genus is its remarkable morphological conservatism, with Cretaceous and Recent species being almost indistinguishable. *T. retusa* is unlikely, however, to reassume the role of its ancestors as a common constituent of shallow marine ecosystems because of its inability to compete for available space in such environments.

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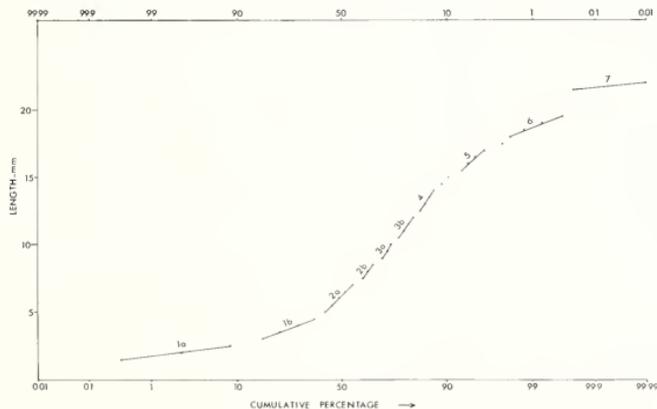
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APPENDIX. The use of probability graph paper for the analysis of polymodal length-frequency histograms

By way of an additional check on the interpretation of the population structure of *T. retusa*, the length-frequency data used to construct text-fig. 4 was also plotted on probability graph paper (text-fig. 8). By this means it is



TEXT-FIG. 8. Length-frequency data collected 22 March 1977 ($n = 811$) plotted on probability graph paper.

possible to check that text-fig. 4 is indeed composed of a series of more or less overlapping normal distributions corresponding to individual settlement cohorts. Harding (1949) was the first to realize that the ability of probability paper to pick out individual normal distributions in a polymodal distribution would be of great use to population biologists, but few workers have made use of this method (Cerrato 1980). The methodology of this method of analysis is straightforward. The data is plotted as a cumulative percentage (i.e. % of total sample less than x mm) on a non-linear horizontal scale, which is so arranged that a plot of points corresponding to a normal distribution yields a straight line. As Harding (1949) demonstrated, a polymodal distribution plots out as a series of straight lines corresponding to each of the constituent normal distributions. Although there is no information as to the size distribution of animals in each settlement cohort in the Firth of Lorne, it is a reasonable and widely accepted assumption that each cohort would plot out as an essentially normal distribution. By this method of analysis, therefore, it is possible to check that each peak in text-fig. 4 does represent a settlement cohort (or amalgamation of two cohorts in the adult specimens) as suggested in the main text.

When the March 1977 data is plotted in this manner the results (text-fig. 8) confirm the interpretation of population structure outlined in the text. Short discrete lines are clearly distinguishable amongst juvenile specimens, and correspond to biannual cohorts. The degree of differentiation is less amongst 3- and 4-year-old specimens, which is consistent with growth-rates decreasing following the onset of sexual maturity. The suggestion that biannual cohorts coalesce in later life to form annual peaks is confirmed by text-fig. 8, and the pattern of growth amongst adults is more discernible than in the original length-frequency histogram. For example, a 6th year-class is clearly marked in text-fig. 8, but could only be inferred from text-fig. 4 (i.e. Table 3). However, the clearly differentiated 7th year-class in text-fig. 8 must be considered as artificial, as the gap in the histogram before the last two specimens automatically results in a strong differentiation from the preceding groups of specimens.

A NEW ZOSTEROPHYLL FROM THE LOWER DEVONIAN OF POLAND

by DANUTA ZDEBSKA

ABSTRACT. A new genus and species *Konioria andrychoviensis* assigned to the Zosterophyllophytina is described from the Lower Devonian (Emsian) of two boreholes in the Bielsko-Andrychów area of the Polish Western Carpathians. *K. andrychoviensis* possesses dichotomous axes covered on their lower part with long subulate spines and on their upper part with short triangular spines. Apices of axes form hooks. In addition to spines, the axes show 1-4 longitudinal wings. The reniform to rounded sporangia are borne singly at dichotomies. The structure of pyritized axes shows a central exarch strand with scalariform tracheids and a hypodermis. In connection with the unusual position of the sporangia the problem of the evolution of the lycopod sporophyll is discussed. *Konioria* appears to suggest that the lycopod sporophyll originated from ends of fertile axes, in accordance with the Telome Theory of Zimmermann (1930). The Telome Theory, however, is based on the *Rhynia*-type of organization, while other evidence suggests that the lycopods originated from the Zosterophyllophytina.

THIS paper describes a single species obtained from two bore-holes, Andrychów 2 and Andrychów 4 in the Bielsko-Andrychów area of the Polish Western Carpathians (see Turnau 1974). The depth in Andrychów 2 is between 2300.8 and 2306.6 m and in Andrychów 4 between 2245.5 and 2250.8 m. The age of these rocks was determined as Lower Devonian (Emsian) on the basis of their lithology by Konior (1965, 1966, 1968, 1969) and this was confirmed by the miospores (Konior and Turnau 1973; Turnau 1974).

Fragments of *Drepanophycus spinaeformis* Goepf. and *Dawsonites* sp. have been recovered from the same cores, but have still to be described. Preliminary investigations of the plant material were carried out by Maria Reymanówna who gave a short description of *Konioria* under the name of *Psilophyton* sp. referred to in Konior (1965). Well-preserved fragments of the plant allow conclusions to be drawn on its systematic position and on the probable course of evolution of the lycopod sporophyll.

MATERIAL AND METHODS

The plant axes are preserved as coaly compressions in a dark-grey siltstone. These remain intact when removed from the matrix with hydrofluoric acid. When macerated in Schulze's solution, most disintegrated and showed no cells. Several axes yielded tracheid fragments with circular bordered pits. A few cuticle fragments of axes are in a state of natural maceration. These are translucent enough to show both a central dark vascular strand and stomata. Certain other axes were pyritized and were not very compressed. From these, thin sections were prepared for reflected light microscopy, using a modified method described by Edwards (1968). To prevent the crumbling of the pyritized axes during sectioning, they were embedded in dental plaster of paris, and were sectioned using a small dental saw. These sections were fixed to glass slides with Canada balsam and ground by hand in the usual way.

The photographs on Pl. 25, figs. 5, 6; Pl. 26, figs. 5, 7, 8; Pl. 27, figs. 3, 5, 6, 7, 9, and Pl. 28, figs. 2, 3, 8, 9 were taken with the Zeiss Photomicroscope III Stand, and the micrographs on Pl. 25, fig. 3; Pl. 27, figs. 1, 2, 4; and Pl. 25, fig. 4 with the Cambridge S 600 SEM in the Department of Botany, Birkbeck College, University of London.

The remaining photographs were taken with an Exacta camera and a Zeiss-Jena lightmicroscope in the Botanical Institute of the Jagiellonian University, Kraków.

SYSTEMATIC PALAEOLOGY

Order ZOSTEROPHYLLALES
 Family ZOSTEROPHYLLACEAE
 Genus KONIORIA gen. nov.

Konioria andrychoviensis sp. nov.

Plant fragments extracted from the rock samples include axes with both long and short spines, axes with only short or long spines, sterile and fertile apices, and pyritised axes (Table 1).

TABLE 1. Characters found on separate parts of the plant which indicate that they belong to the same plant (cross indicates presence of character)

PLANT PARTS CHARACTERS	Axis with long and short spines	Axis with long spines only	Axis with short spines only	Sterile apex	Fertile apex	Pyritised axis	Circoinately coiled axis
Long spines with minute teeth	+	+	-	-	-	+	+
Short spines	+	-	+	+	+	+	+
Wing	+	+	+	+	+	+	-
Stomata	-	-	+	+	+	-	-

Axes with spines. The *Konioria* axes are preserved on the bedding planes in a dark-grey siltstone. The core is 9 cm wide which limits the length of the specimens; originally they were longer. There are also many pieces which were broken into short lengths before deposition.

The axes dichotomize into unequal or almost equal parts diverging at about 30° (Pl. 25, figs. 1, 4). The distance between successive dichotomies is about 4 cm towards the top of the plant. Below dichotomies the axes widen and gradually change into two branches. One axis was 2 mm wide at 1 cm below its first dichotomy and 1.5 mm at 1 cm below its second dichotomy. The length of this axis is over 6 cm. Other specimens suggest a possible length of about 15 cm for the largest axes which are 4 mm wide. The length of the plant is unknown but some estimate is possible by relating the extent of tapering along a single axis to the extremes of axis diameter (0.3-4.0 mm).

The longest unbranched axis available is 7 cm but most branch at closer intervals than this and near the apex branching is very close together. Successive dichotomies are not all in the same place but the precise angle between them in the lower part cannot be given. Near the apex it is about 90°. A characteristic and remarkable feature of the axes is that they have one to four longitudinal wings. These may lie in the plane of compression (Pl. 25, fig. 4) where they appear as borders to the axis, or they may be present on the surface of the axis (Pl. 25, figs. 5,

EXPLANATION OF PLATE 25

Fig. 1. Paratype, axes with two branches, S/98/14; $\times 1.2$.

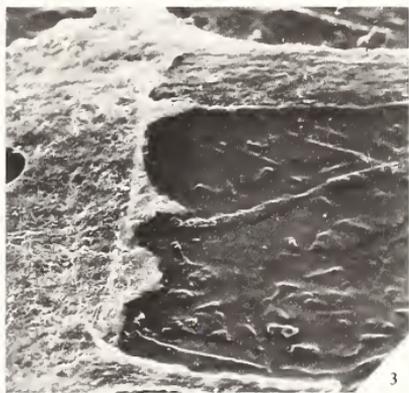
Fig. 2. Axes with long spines, S/98/12b; $\times 3$.

Fig. 3. SEM. Stem with long and short spines; $\times 120$.

Fig. 4. Axes with 'compression margin' (wings), S/98/9a; $\times 3$.

Fig. 5. Surface of axis showing three wings (arrowed) (specimen destroyed); $\times 126$.

Fig. 6. Compressed axis showing wing and a long spine at an acute angle (specimen destroyed); $\times 6$.



6; Pl. 26, figs. 7, 8; Pl. 27, fig. 6; Pl. 28, figs. 2, 9). These wings are present on tall axes. Occasionally, the wings take a spiral course (Pl. 28, fig. 9) which is not the result of twisting of the axis. Twisted axes are seen on Pl. 25, fig. 6. On wings as well as on the axes, the spines may be dense (Pl. 26, fig. 6). The author considered the possibility that the wings were mere compression borders, but decided they were not, on the evidence given below:

1. In transverse sections of pyritized axes the wing is continuous with the thick, carbonized layer (Pl. 26, fig. 6).
2. Cells of the hypodermal layer below the carbonized layer do not enter the wing (Pl. 26, fig. 6).
3. In a transverse section of a flattened pyritized axis the wing is not a continuation of the longer axis of the section. If the wing were formed as a result of flattening of the plant, it would occur in the same plane (Pl. 26, fig. 6).
4. Often the wing forms a spiral on the axis (Pl. 28, fig. 9).

Axes bear spines of varying size and frequency. The spines range from being short and triangular to long and subulate (Pl. 25, fig. 3). On the rock the spines are visible at the sides of the axes, while on their surface only their bases are seen as large and small dots. The spines are distributed irregularly; rarely are they very frequent on one surface of the axis and not on the other (Pl. 26, figs. 1, 2). The length of the spines is very unequal on different parts of the axis and range from 0.1 to 4 mm. The longest spines, up to 4 mm long and 0.3 mm wide at the base are on the thickest axes, but occasionally there may be fairly long spines on the narrower axes (Pl. 26, fig. 3), and occasionally just one long spine is present (Pl. 28, fig. 3). Usually the narrower axes bear shorter spines (Pl. 26, fig. 5; text-fig. 1) or occasionally none at all. On some axes (Pl. 26, fig. 2) both long and short spines occur. Most spines are at about 90° to the axis. The longer spines show longitudinal ridges (Pl. 27, fig. 2) with occasional minute teeth 12–16 μm long (Pl. 27, figs. 2, 4). Teeth are not obvious on the shorter spines (Pl. 25, fig. 3). The long spines with teeth are most numerous on some circinately coiled axes (Pl. 28, fig. 8) which the author thinks possibly represent early stages in the development of a shoot (these are not included in the reconstruction). Some spines show a dark core of unknown cellular structure (Pl. 28, fig. 3) suggesting a vascular strand. Such structures are spines and not sporangial stalks, because they are quite long and situated at the side of the axis and not below the dichotomies.

Cuticle preparations of axis showed no clearly marked epidermal cells (Pl. 25, fig. 3) apart from dark stomata. The stomata are visible as irregularly distributed elliptical dark dots, because they are usually covered with a dark substance (Pl. 28, figs. 1, 7). They are oval and orientated longitudinally, and sometimes show the guard cells. The spines have no stomata.

Apex of axis. All apices whether sterile or fertile are much branched and curved to form hooks (text-fig. 1; Pl. 26, fig. 5; Pl. 27, fig. 6; Pl. 28, figs. 1, 2). These illustrations show all the variation observed in both sterile and fertile apices. The spines on the ends of axes are never long, and are sometimes infrequent or absent (text-fig. 1). The vascular strand may be visible by scanning electron microscopy but not after maceration. The dark strand in Pl. 28, figs. 1, 7, shows an untreated specimen photographed by transmitted light.

Fertile axes. The sporangia cannot be distinguished on axes still in the rock, probably because the diameter of a sporangium is not much larger than the width of the axis below the dichotomy. They are visible only on axes removed with hydrofluoric acid. Most of the distal branches are sterile, but in some instances a single sporangium occurs at the final or penultimate dichotomy, and perhaps also further down. The sporangia are mostly situated slightly below the angle of the dichotomy and any stalk they possess must be very short and is concealed (Pl. 26, figs. 7, 8; Pl. 28, fig. 2; text-figs. 2, 3). It appears that the small mound visible on the surface of most sporangia is

EXPLANATION OF PLATE 26

Figs. 1, 2. Two sides of a pyritized axis, S/98/23; × 17.5. 1, surface with numerous short spines. 2, surface with bases of two long spines and a few short spines.

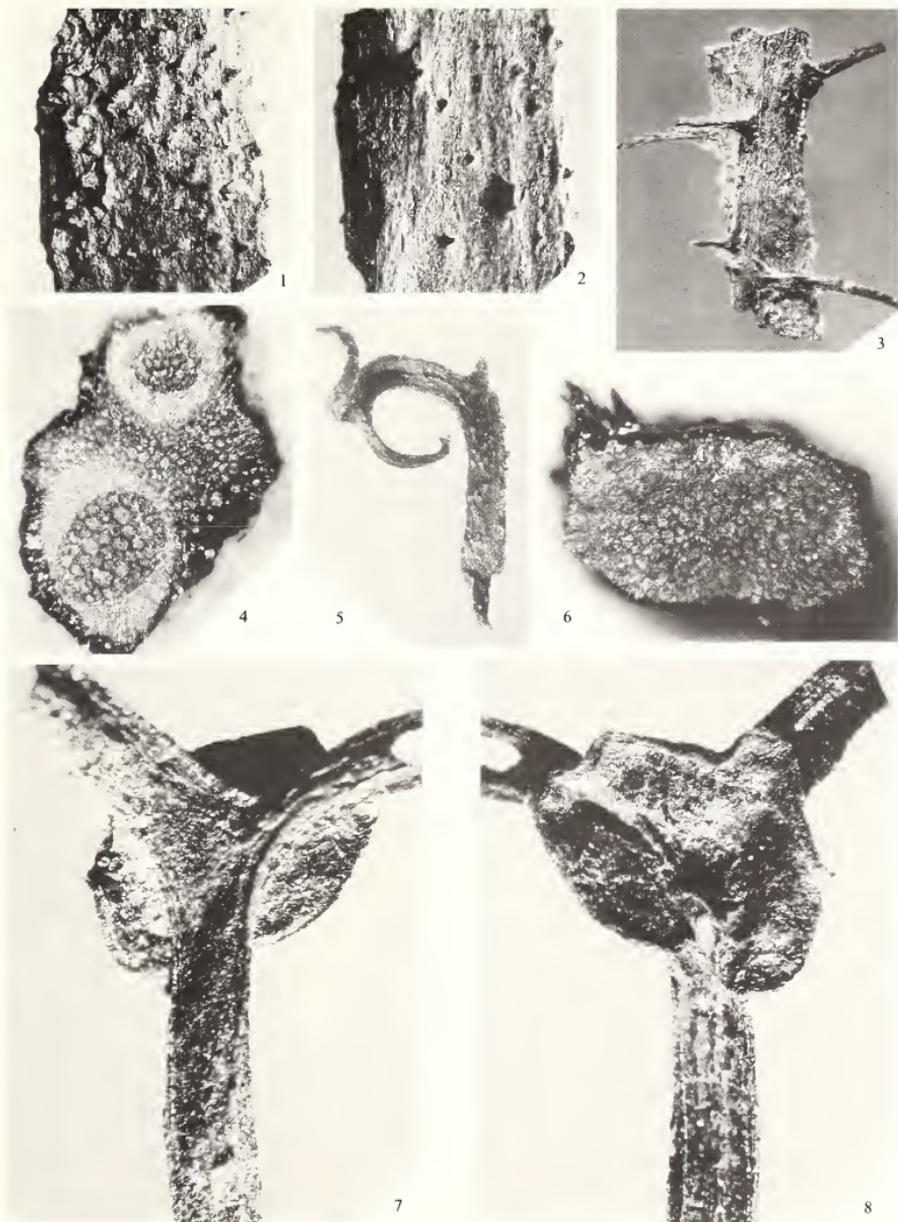
Fig. 3. Fragment of axis with long spines and wing, S/98/26; × 20.

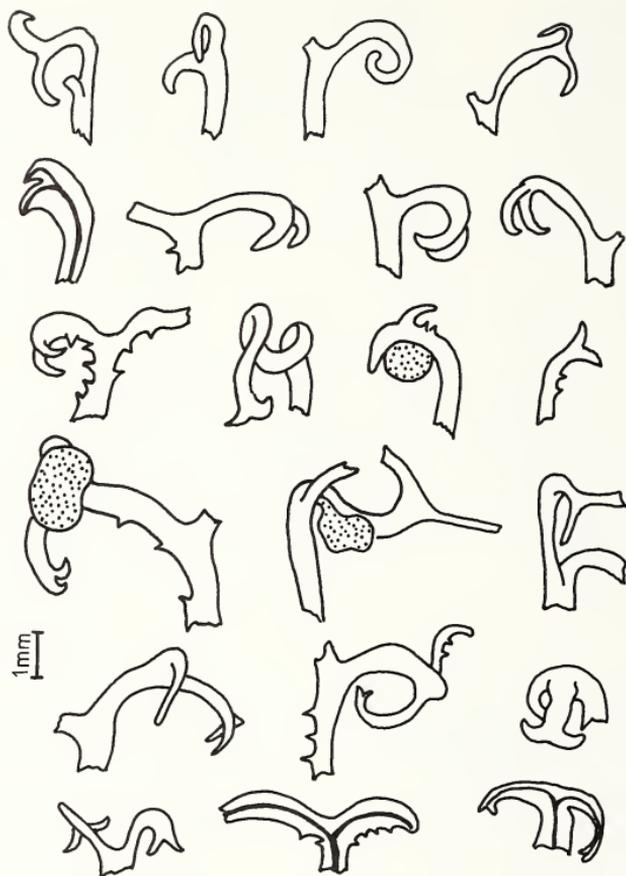
Fig. 4. Pyritized axis just below dichotomy (specimen destroyed); × 30.

Fig. 5. Apex showing short spines, S/98/26; × 20.

Fig. 6. Transverse section of pyritized axes. On the left-hand side is a wing with spines, S/98/79; × 25.

Figs. 7, 8. Holotype, fragment of axis with sporangium situated at the level of a dichotomy (both sides), S/98/31; × 30.

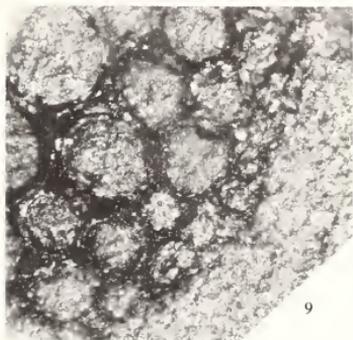
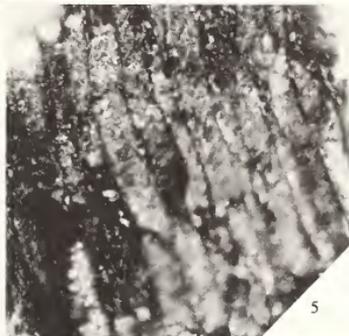




TEXT-FIG. 1. The variation in sterile and fertile hook apices, S/98/37-40.

EXPLANATION OF PLATE 27

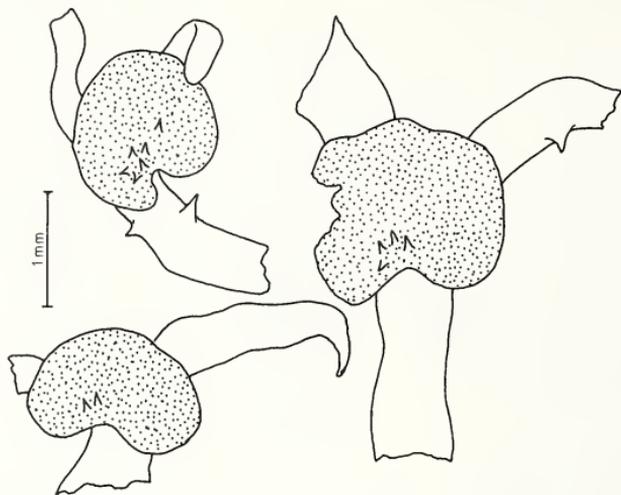
- Fig. 1. SEM. Axis with two flattened branches and a stalked sporangium (arrows); $\times 30$.
 Fig. 2. SEM. Surface of spine showing longitudinal ridges with minute teeth; $\times 300$.
 Fig. 3. Paratype, transverse section of uncompressed axis showing elliptical xylem strand, S/98/15; $\times 50$.
 Fig. 4. SEM. Long spine with round base and minute teeth; $\times 25$.
 Fig. 5. Cells of hypodermis in longitudinal section, S/98/18; $\times 125$.
 Fig. 6. Forked apex showing wing on under side (specimen destroyed); $\times 20$.
 Fig. 7. Protoxylem and metaxylem in longitudinal section showing scalariform tracheids, S/98/17; $\times 110$.
 Fig. 8. Pyritized axis split longitudinally and showing vascular strand with circular bordered pits, S/98/49; $\times 375$.
 Fig. 9. Metaxylem and protoxylem from fig. 3; $\times 167$.



caused by the stalk (Pl. 26, fig. 8). Some, however, have a longer stalk which is clearly inserted in the angle of the dichotomy (Pl. 27, fig. 1).

The sporangia are flattened and composed of two equal valves which separate along their entire margin. The largest are oval or slightly reniform (Pl. 26, figs. 7, 8; text-fig. 2) but some are round (Pl. 28, fig. 2; text-fig. 2). They are typically about 2.5 mm wide, but the round ones are smaller and one was only 0.5 mm wide. The surface of the outer valve may show diverging cells under scanning electron microscopy. Often the surface of a sporangium bears minute spines (text-fig. 2). Nothing is known of the deeper layers of the sporangial wall. Along the line of dehiscence the wall is flat and appears thin (Pl. 28, fig. 4). Although the two valves are always pressed together the sporangia seem to have dehisced and shed all their spores. Maceration yielded no spores nor did it yield a central mass which might represent compacted spores.

Pyritized axes. Ten pyritized axes were studied. They are rather narrow, 0.5–2 mm wide. Some show long spines (Pl. 26, fig. 3), some short spines and long broken spines (Pl. 26, fig. 2), and some all short spines (Pl. 26, fig. 1). These specimens were not sectioned, the sections being prepared from unfigured specimens which did show short spines or bases of long spines.



TEXT-FIG. 2. Sporangia attached below the dichotomy. Small spines present on the surfaces of sporangia.

EXPLANATION OF PLATE 28

- Fig. 1. Paratype, naturally cleared apex showing dark core and stomata as dark spots, S/98/29; $\times 25$.
 Fig. 2. Apex with sporangium (specimen destroyed); $\times 30$.
 Fig. 3. Fragment of axis with spines; large spine apparently with ?vascular strand coming from the axis, S/98/27; $\times 20$.
 Fig. 4. SEM. Fragment of sporangium valve; margin appears to be thin and smooth, but the wall shows ?papillae; $\times 300$.
 Fig. 5, 6. Tracheids isolated by Schulze maceration from carbonized axis. Tracheids show circular bordered pits. 5, S/98/75; $\times 600$; 6, S/98/76; $\times 546$.
 Fig. 7. Naturally cleared apices showing stomata as dark spots on the epidermis, S/98/30; $\times 24$.
 Fig. 8. Young coiled axis densely covered with long spines, S/98/25; $\times 20$.
 Fig. 9. One branch of the dichotomy (the other broken off) showing spiral wing (specimen destroyed); $\times 19.5$.



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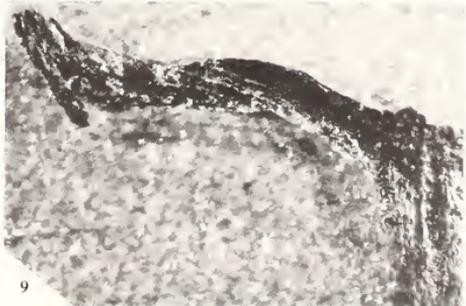
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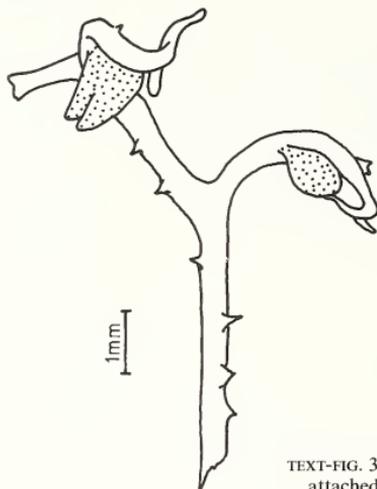


8



9

The transverse section on Pl. 27, fig. 3, shows a black, coalified outer layer which can be regarded as the epidermis, inside this are about four layers of thick-walled cells which represent the hypodermis. Occasionally the outer coalified layer is thicker, suggesting that the hypodermal cells are also coalified. In longitudinal section the hypodermal cells are elongated and show no obvious pits (Pl. 27, fig. 5). Length of cells from 150 to 450 μm , width from 30 to 85 μm .



TEXT-FIG. 3. Paratype, axis with two sporangia attached below the dichotomies, S/98/35.

Inside the hypodermis, there is a region in which the cells are scarcely visible, and these surround a circular (Pl. 26, fig. 4) or elliptical (Pl. 27, fig. 3) xylem strand, with small tracheids (regarded as protoxylem) to the outside and larger tracheids (regarded as metaxylem) to the inside (Pl. 27, fig. 9). The metaxylem shows well-developed scalariform tracheids (Pl. 27, fig. 7). Three different stems showed exactly similar scalariform tracheids with no round pits. However, a further specimen with the surface fractured longitudinally showed round pits in what appears to be a metaxylem tracheid (Pl. 27, fig. 8), but when this stem was polished, no pits were seen. The author believes that the round pits do not represent pyrite crystals, which usually have an angular outline. Yet another specimen (showing small spines), which was not pyritized, was unusual when macerated in Schulze's solution, in that it yielded excellent tracheids in longitudinal view, which showed round bordered pits in two rows in some of the tracheids (Pl. 28, figs. 5, 6). The variety of xylem pitting is large, but such evidence does suggest that all the specimens belong to one species.

Reconstruction of Konioria

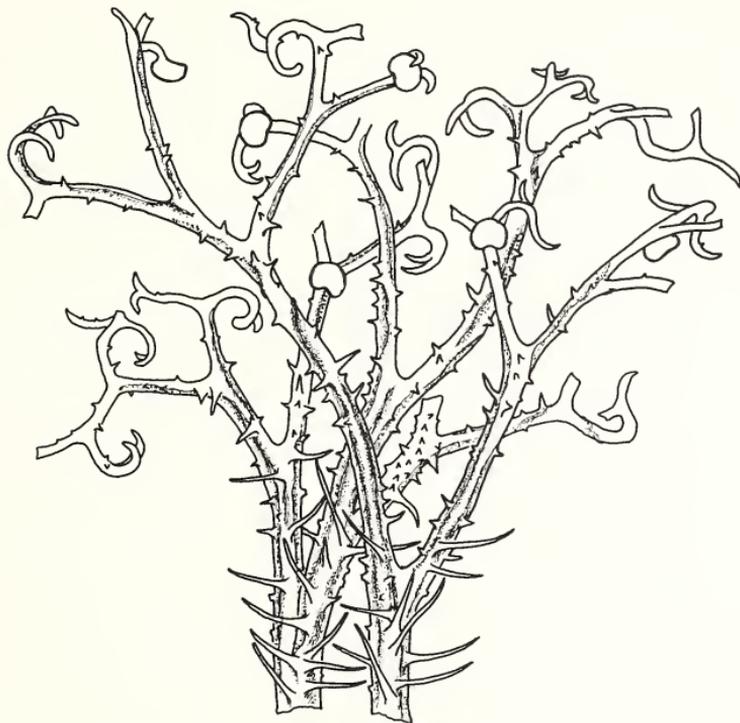
There are no large specimens of this plant available, but the separate fragments are linked by common characters (Table 1). The reconstruction (text-fig. 4) is made from the drawings of all those separate parts.

Konioria gen. nov.

Type species. Konioria andrychoviensis sp. nov.

Diagnosis. Erect axes slender, branching by more or less equal dichotomy in different planes. Lower dichotomies further apart than upper ones. Apices narrow to points, and are curved to form hooks. Axis usually with 1–4 narrow longitudinal wings. Surface of axes with spines, which range from long and subulate to short and triangular. Epidermis of axis with longitudinally orientated stomata. Inside the epidermis is a hypodermis of up to four layers of thick-walled cells. The hypodermal cells are rounded in transverse section but elongated longitudinally. The area of the cortex and phloem, is not

preserved. A central xylem strand has the smallest tracheids to the outside. Metaxylem tracheids have scalariform thickening. Sporangia are borne singly below dichotomies, usually on short stalks. The sporangia are round or reniform in outline, and composed of two equal valves, with the dehiscence line along the whole margin.



TEXT-FIG. 4. Reconstruction of *Konioria andrychoviensis*, $\times 3$ (approx.).

Konioria andrychoviensis sp. nov.

Plates 25–28

1965 *Psilophyton* sp. Reymanówna in Konior, p. 217, figs. 1, 3.

Diagnosis. Axes 0.3–4 mm wide, branching frequently, with short to long spines. Lower part of axis bearing subulate spines up to 4 mm long usually with minute lateral teeth, the upper part of the axis has shorter and triangular spines. Sporangia up to 2.5 mm wide but often smaller, frequently bearing minute spines near their bases.

Horizon. Lower Devonian, Emsian.

Locality. Two bore-holes Andrychów 2 and Andrychów 4 in the Bielsko–Andrychów area of the Western Carpathians, Poland.

Type specimens. All specimens are deposited in the Palaeobotanical Museum of Institute of Botany, Jagiellonian University, Kraków, S/98. Holotype: S/98/31, Pl. 26, figs. 7, 8. Paratypes: S/98/4, Pl. 25, fig. 1; S/98/35, text-fig. 4; S/98/15, Pl. 27, fig. 3; S/98/29, Pl. 28, fig. 1.

Derivation of name. The generic name *Konioria* is after Professor Konrad Konior who found the material and was kind enough to give it to the author for investigation. The specific name is derived from the name of the locality Andrychów.

DISCUSSION

Comparison with Psilophyton goldschmidtii and P. arcticum

Konioria might be confused with *P. goldschmidtii* (Halle 1916) and *P. arcticum* (Høeg 1942), because of similar external morphology of the axes as seen when on the rock surface. A character common to both *Konioria* and *P. goldschmidtii* is the 'compression margin' (wing), which is distinctly visible on specimens seen on the rock surface. Halle (1916) gives no explanation of its nature. In *Konioria* the 'margins' are in fact wings running along both sides of the axis. A second similar character are the subulate spines of variable length up to 4 mm. The spines of *P. goldschmidtii*, however, are less numerous. The two plants differ in their branching. In *Konioria* the axes dichotomize, whilst in *P. goldschmidtii* the branching is sympodial and dichotomous. The axes of *Konioria* are straight while in *P. goldschmidtii* they are zigzag shaped (Nathorst 1913; Halle 1916; Høeg 1967). In *P. goldschmidtii* the anatomical structure of the axes and the sporangia are unknown. Although these two plants show several common characters, the differences between them and the different mode of preservation suggest that the new plant should not be included in *P. goldschmidtii*. When comparing these two plants, the author was able to study the figured specimen described by Halle (1916). The similarities and differences between the two plants mentioned above were confirmed by this material.

In 1959 Ananiev described *P. goldschmidtii* from the Devonian of south-eastern Siberia. Ananiev gives no description of the plant, but his photographs (Pl. 7, figs. 1, 2, 4; Pl. 8, fig. 4; Pl. 12, fig. 1; Pl. 14, figs. 1, 2; Pl. 24, fig. 2a) clearly show the differences between the branching of *Konioria* and *P. goldschmidtii*.

In 1932 Lang described *P. princeps* and *P. goldschmidtii* from the Strathmore Beds in Scotland under the name *Psilophyton*. The *Psilophyton* figured by Lang on Pl. 2, figs. 24, 25, 27, is similar to *Konioria* in that it shows axes with a 'compression margin' (wing). His Pl. 2, figs. 24, 33, shows the presence of short spines and bases of broken long spines similar to *Konioria*. The differences in branching between the two plants are clearly seen when comparing Lang's Pl. 2, figs. 24, 25, 27, with *Konioria*. Lang describes the branching as pseudomonopodial, which is clearly different from the dichotomous branching in *Konioria*. An investigation of Lang's material in the British Museum of Natural History in London, confirms the similarities and differences between the two taxa.

Konioria shows some external similarity to *P. arcticum* Høeg 1942, which also possesses a distinct margin (see his Pl. 9, fig. 3; Pl. 12, fig. 1). Høeg does not explain the nature of this margin. Unlike *Konioria*, however, *P. arcticum* has pseudomonopodial branching and hair-like spines from 4 to 6 mm long.

Comparison with genera of the subdivision Zosterophyllophytina

Attributing *Konioria* to the Zosterophyllophytina, the author uses the classification of the 'psilophytes' given by Banks (1968, 1975). *Konioria* shows the characters of the subdivision Zosterophyllophytina, i.e. the lateral arrangement of sporangia and the exarch xylem strand.

Comparison with Crenaticaulis and Gosslingia. *Konioria* possesses a greater number of characters in common with *Crenaticaulis* (Banks and Davis 1969) and *Gosslingia* (Edwards and Banks 1965; Edwards 1970) than with other genera. All three plants show dichotomous branching, although *Crenaticaulis* and *Gosslingia* also have pseudomonopodial branching. *Crenaticaulis* and *Gosslingia* also show scars below dichotomies. In *Crenaticaulis* axillary branches are present which were compared by Banks and Davis (1969) with the rhizophores of *Selaginella*. Also, in *Konioria*, the sporangia are borne in the same position. Another character in common in these three genera is that the sporangia do not form spikes.

Konioria differs from *Gosslingia* in possessing spines. *Crenaticaulis* shows characteristic short tooth-like spines arranged in one or two rows, while *Konioria* has irregularly arranged spines ranging from long and subulate to short and triangular. The sporangia of *Gosslingia* and *Konioria* split into two equal valves whilst in *Crenaticaulis* there is a large abaxial and a small adaxial valve.

Comparison with Sawdonia and Euthursophyton. *Konioria* shows a certain similarity with *Sawdonia ornata* (Dawson) Hueber, see for example, Dawson 1871; Hueber 1964, 1971; Hueber and Banks 1967; Ananiev and Stepanov 1968. The two plants have the same dichotomous mode of branching and the lateral arrangement of sporangia which split into two equal valves. *Sawdonia* differs from *Konioria* in having glandular spines and sporangia distributed along the axis.

Konioria and *Euthursophyton hamperbachense* Mustafa (Mustafa 1978) are similar in their dichotomously branching axes covered with long spines, in occasionally showing circinate coiled axes and in possessing an exarch strand. In *Euthursophyton*, however, the sporangia are unknown. *Konioria*, unlike *Euthursophyton*, possesses differentiated spines, from long and subulate with minute teeth to short and triangular. In addition, wings on the surface of the axes are present in *Konioria* but absent in *Euthursophyton*. In the *Euthursophyton* axes no hypodermis has been described.

Comparison with Zosterophyllum and Rebuchia. *Konioria* differs from both *Zosterophyllum* (Croft and Lang 1942; Edwards 1969*a, b*; Lele and Walton 1961) and *Rebuchia* (Dorf 1933; Hueber 1970, 1972*a, b*) in not having the sporangia arranged in spikes. In addition, these two genera have smooth axes, which in *Zosterophyllum* show in their lower parts H-shaped branching. Common to *Zosterophyllum*, *Rebuchia*, and *Konioria* are lateral, reniform sporangia splitting into two equal valves. Edwards (1969) demonstrated exarch xylem in *Zosterophyllum llanoveranum*. In *Rebuchia* the xylem strand is not well known, and is mentioned only by Lepekhina, Petrosian, and Radchenko (1962). It is possible that this is also a common character of all three genera.

The systematic position of Konioria

The author accepts the classification of the early land plants into Rhyniophytina, Trimerophytina, and Zosterophyllophytina (see Banks 1968, 1975). The lateral position of sporangia and the exarch xylem strand of *Konioria* suggest its affinity with genera of the subdivision Zosterophyllophytina. Comparisons show that *Konioria* differs from other Zosterophyllophytina in having sporangia attached below a dichotomy, in showing wings on the axis, and in possessing spines ranging from long and subulate to short and triangular. These are the characters of the new genus and species *Konioria andrychoviensis*.

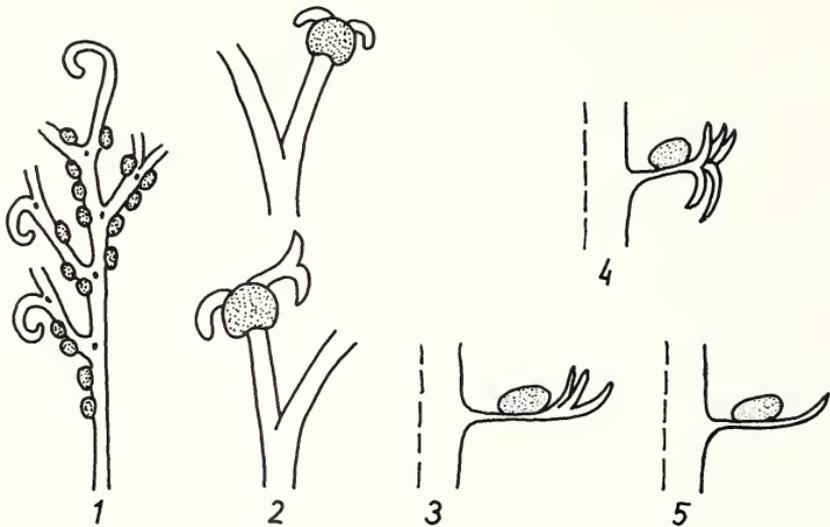
In his classification, Banks (1968) divided the order Zosterophyllales into two families, Zosterophyllaceae and Gosslingiaceae, which differ in the grouping of sporangia. In a later paper Banks (1975) distinguishes only one family, the Zosterophyllaceae. If this later publication were followed, *Konioria* would become a member of the Zosterophyllaceae, fitting well the diagnosis of this family. However, it would appear that a return to the former division of the Zosterophyllophytina into two families would be better, with the Zosterophyllaceae having sporangia in spikes, and the Gosslingiaceae having sporangia scattered along the axis. These two families were also recognized by Kasper, Andrews, and Forbes (1974). Perhaps *Konioria* would even merit the establishing of a third family, characterized by having sporangia attached below the dichotomies.

The morphology and the anatomical structure of *Konioria* provide additional data to support Banks's (1968) classification of the early land plants, in that the morphological characters discussed above are further evidence that the Zosterophyllophytina forms a natural group. This group, according to the hypothesis of Banks (1968; Chaloner and Sheerin 1979), gave rise to the Lycopytina.

Konioria and the evolution of the lycopod sporophyll

The unusual position of the sporangium of *Konioria* appears to be related to that in certain early lycopods. According to Zimmermann (1930) the sporophylls of the lycopods developed from

ultimate branchlets with sporangia of the *Rhynia*-type. However, according to Banks (1968), the Rhyniophytina gave rise to all groups of plants, except the lycopods which developed from the Zosterophyllophytina. This opinion is confirmed by the anatomical structure and the type and arrangement of sporangia in the Zosterophyllophytina. Accordingly, the intermediate forms leading to the sporophyll of lycopods have been looked for among the Zosterophyllophytina. In accordance with Zimmermann's Telome Theory, the processes of *Konioria* suggest an evolutionary sequence of the lycopod sporophyll from the Zosterophyllophytina. Text-fig. 5 is an attempt to arrange such a



TEXT-FIG. 5. Proposed evolutionary sequence of the lycopod sporophyll. 1, *Gosslingia*; 2, *Konioria*; 3, *Colpodexylon*; 4, *Leclercqia*; 5, *Cyclostigma*.

sequence of existing fossil plants, which could lead to the sporophylls of lycopods. The starting-point is *Gosslingia* (Edwards 1970), which bears lateral sporangia scattered along the axis. The next stage is *Konioria* with lateral sporangia borne below dichotomies. Therefore, *Konioria* would appear to be the link between the Zosterophyllophytina and such lycopods as *Colpodexylon* (Banks 1944) and *Leclercqia* (Banks, Bonamo, and Grierson 1972) which have a sporophyll divided into three or more segments. The unequal dichotomizing axes of *Konioria* can be regarded as the initial form from which the sporophylls of those lycopods originated. It can be assumed that the wider branch of the unequal dichotomy of *Konioria* would change into the main axis, as a result of the process of overtopping. The other narrower branch of *Konioria* consisting of ends of axes with a sporangium attached at the basis of the dichotomy, could be transformed into the lycopod sporophyll by the processes of planation and reduction. In *Konioria* there are unequal dichotomies of the hook-like apices under which the sporangia are attached. Therefore, it is possible to derive the sporophylls of *Colpodexylon* directly from *Konioria*, because in *Konioria* there are apices with three or four branches above the sporangium. It is more difficult to derive the sporophyll of the lycopod *Leclercqia complexa*, which ends with five segments, from *Konioria*, because five times divided apices of *Konioria* were not found. In theory, however, such branching is also possible.

There is also the theoretical possibility of deriving the undivided sporophylls of *Cyclostigma* (Chaloner 1968) and similar lycopods by a reduction from sporophylls showing more than one division.

As a result of those considerations, the explanation by Zimmermann (1930) of the origin of the lycopod sporophyll from sterile and fertile axes by overtopping and reduction appears justified, and can be envisaged directly from the Zosterophyllophytina, but not from the Rhyniophytina. The sequence proposed in the present paper appears to confirm the axial origin of the lycopod sporophyll.

In the light of new facts established about the position of sporangia in *Drepanophycus* and *Protolopododendron*, these two genera are excluded from the sequence. *Drepanophycus* (*Protolycopodites*) *devonicus* is not placed here, because Schweitzer and Giesen (1980) established that sporangia of this plant do not occur on sporophylls, but on the axis among microphylls. According to Schweitzer and Giesen, the sporangia in *D. spinaeformis* Goepp. also have a similar position, and do not occur on the sporophyll as described by Kräusel and Weyland (1930). Also, *Protolopododendron scharianum* Potonič and Bernard which according to Kräusel and Weyland (1932) possessed bifurcating sporophylls is not shown in the sequence. According to Schweitzer and Giesen (1980), its sporophylls show a double dichotomy with a sporangium present below each dichotomy. Schweitzer and Giesen think that *P. wahnbachense* Kräusel and Weyland also shows this type of sporophyll (see their reconstruction (text-fig. 12, p. 15)). However, there exists a controversy about this reconstruction, because according to Fairon-Demaret (1979) these sporophylls bear several sporangia, and she tentatively attributes this plant to the Sphenopsida and not to the Lycopsidea.

In summary, the above considerations demonstrate the possibility that the lycopod sporophyll may have originated through a change in the ends of axes into sporophylls divided into segments, and to a reduction of the number of these segments (text-fig. 5).

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TWO SALENIROID ECHINOIDS IN THE DANIAN OF THE MAASTRICHT AREA

by J. F. GEYS

ABSTRACT. Two species of salenioid echinoids, *Salenia minima* Agassiz and Desor, 1846 and *Hyposalenia heliophora* (Agassiz and Desor 1846) from the Danian strata in the Maastricht area, are described and discussed. Biometrical parameters are statistically treated and compared with those of some other salenioids. It is shown that both species are probably good index fossils for strata of Danian age.

PREVIOUS systematic treatments of the Danian echinoderm fauna in the Maastricht area were made exclusively by investigators studying the Cretaceous Maastricht Chalk. Lambert (1911) was the first to study the echinoid fauna of the Maastricht Cretaceous as a whole. The fauna was systematically revised by Smiser (1935). Both these authors essentially studied the important collections of the Koninklijk Belgisch Instituut voor Natuurwetenschappen in Brussels (K.B.I.N.). The so-called post-Maastrichtian (or Danian) echinoids from the Maastricht area, are less well represented in these collections, which may explain why the characteristic Danian species were not revised by both these authors. The collections of the K.B.I.N., as well as those of the Natuurhistorisch Museum at Maastricht (N.H.M.M.), were revised by M. Meijer. Unfortunately, his results were only partly published, but Meijer (1965) was the first to draw attention to the important differences between the echinoid faunas of the Houthem Formation (post-Maastrichtian) and the underlying chalk beds (Ma to Md), belonging to the Maastricht Chalk. As a result he separated his 'zone III' from the echinoid assemblages of the Maastricht Chalk, and he presumed that this zone was of Dano-Montian age. Meijer's view proved to be correct when Moorkens (1972) correlated the post-Maastrichtian Geulhem Chalk (Houthem Formation) with the Cipy Tuffaceous Chalk, which had been previously correlated with the type Danian at Fakse (Denmark) by Rasmussen (1965).

Two of the most characteristic species from the post-Maastrichtian Houthem Formation in the Maastricht area are discussed in this paper. They occur in the Cipy Tuffaceous Chalk, in the vicinity of Mons (Belgium), but they are absent in overlying and in underlying strata. In the Maastricht area, both species seem to be confined to strata which Felder (1975) termed the Geulhem Chalk of the Houthem Formation. A correlation between the Geulhem Chalk and the Cipy Tuffaceous Chalk is thus confirmed.

The specimens studied belong to the collections of the Natuurhistorisch Museum at Maastricht (N.H.M.). In some specimens, a few dimensions were measured by means of calipers (absolute error: 0.1 mm). Statistical calculations were carried out, using the formulas and symbols proposed by Till (1974).

The following abbreviations are used:

D: ambital diameter of the test III-5;

h: total height of the test;

ds: diameter of the apical system, taken between the centres of the distal borders of ocular III and genital 5;

dp: diameter of the peristome III-5.

SYSTEMATIC DESCRIPTIONS

Class ECHINOIDEA Leske, 1778
 Subclass EUECHINOIDEA Bronn, 1860
 Superorder ECHINACEA Claus, 1876
 Order SALENOIDA Delage and Herouard, 1903
 Family SALENIIDAE Agassiz, 1838
 Subfamily SALENIINAE Agassiz, 1838
 Genus SALENIA Gray, 1835

(= *Cidarelle* Desmoulins, 1835; = *Bathysalenia* Pomel, 1838)

Type species. *Cidarites scutigera* Münster in Goldfuss 1826, by original designation.

Salenia minima Agassiz and Desor, 1846

Plate 29, figs. 1-4

- *.1846 *Salenia minima*, Agassiz and Desor, p. 342.
- .1850 *Salenia minima*, d'Orbigny, p. 273.
- .1857 *Salenia minima*, Desor, p. 151.
- 1857 *Salenia minima*, Bosquet, no. 839.
- 1859 *Salenia minima*, Binkhorst van den Binkhorst, p. 120.
- .1864 *Salenia minima*, Cotteau, pp. 171-173, pl. 1040, figs. 1-10.
- 1879 *Salenia minima*, Ubaghs, p. 228.
- 1881 *Salenia minima*, Mourlon, p. 125.
- .1910 *Salenia minima*, Lambert and Thiery, p. 211.
- .1935 *Salenia minima*, Mortensen, p. 369, fig. 195d.
- v.1965 *Salenia minima*, Meijer, p. 23.
- .1979 *Salenia minima*, Geys, p. 320.
- non 1935 *Salenia minima*, Smiser, p. 28, pl. 2, fig. 6a-d.

Type locality. Ciplu, Hainaut, Belgium. Ciplu Tuffaceous Chalk, Danian.

Studied specimens from the Maastricht area (Geulhem Chalk). Vroenhoven, Belgian Limburg: 88 specimens; Geulhem, Dutch Limburg: 18 specimens.

Dimensions. D: 1.7-9.2 mm; h: 0.9-6.0 mm; h/D ratio: 0.48-0.70; ds: 1.7-6.8 mm; ds/D ratio: 0.60-1.00; dp: 0.8-4.8 mm; dp/D ratio: 0.36-0.63.

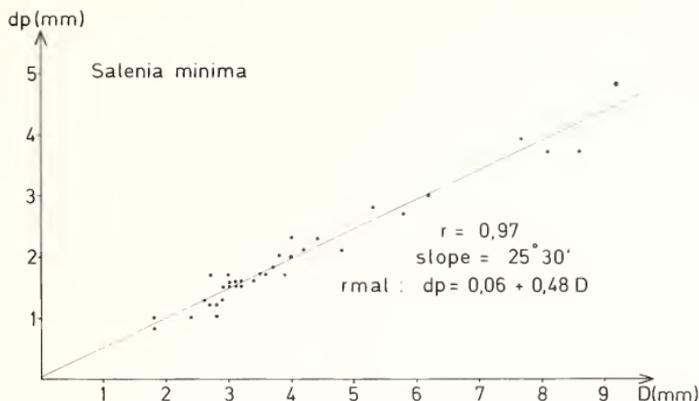
Description. The adoral side of the test is flat; the peristome is circular to subpentagonal, not sunken. Gill slits are very small. The perignathic girdle consists of small, spatulate auricles, not in contact with each other, and low arcuate apophyses.

The apical system is large and covers most of the aboral side of the test in young specimens. It is slightly convex and consists of eleven smooth plates, separated by distinct sutures. Sutural depressions are very small or absent. The ocular plates are triangular and a little concave. The genital plates and the suranal plate are nearly flat. The genital pores have an excentric position in the genital plates, being nearer to the apex. The madreporite can easily be distinguished by its irregular, more or less triangular poriferous depression. The periproct is oval or subtrigonal.

Each ambulacral series shows ten to twelve crenulate, non-perforate primary tubercles. The ambulacra are straight. The bigeminate character of its plates is very regular. The tubercles are close together and extrascrobicular granulation is almost completely absent. The axes of the pore pairs have an inclination of about 45°.

Interambulacral tubercles are crenulate, non-perforate. Five of them make a series. The areoles are smooth, large, and close together. Sometimes they are confluent, in the vicinity of the ambitus. A ring of six to eight scrobicular tubercles surrounds them on all but the adradial sides. Interradial extrascrobicular surfaces are coarsely granulated.

Variability. dp, ds, and h were plotted against D. Some parameters and the reduced major axis lines (rml) were computed for each of these graphs, using the formulas proposed by Till (1974).



TEXT-FIG. 1. dp-D plot of *Salenia minima*, with reduced major axis line (r mal).

a. The r mal of the dp-D plot is given by

$$dp = 0.06 + 0.48 D \quad (1) \text{ (Text-fig. 1).}$$

The 95% confidence intervals of intercept and slope are respectively

$$1.96 s_a(D/dp) = \pm 0.16 \text{ mm} \quad (2)$$

$$1.96 s_b(D/dp) = \pm 0.04 \quad (3).$$

From (1) and (2) one can conclude that the origin of the plot is included in the confidence band of the r mal, and that the dp/D ratio can be considered constant. Moreover, the slope ($b = 0.48 \pm 0.04$) does not differ significantly from the mean dp/ratio ($= 0.50$), as follows from (1) and (3). The relative size of the peristome is not influenced by over-all size or age of the specimen.

b. The r mal of the h-D plot is given by

$$h = -0.31 + 0.68 D \quad (4) \text{ (Text-fig. 2)}$$

The 95% confidence intervals of intercept and slope are respectively

$$1.96 s_a(D/h) = \pm 0.13 \text{ mm} \quad (5)$$

$$1.96 s_b(D/h) = \pm 0.03 \quad (6).$$

Obviously the origin is not included in the confidence band of the r mal, as follows from (4) and (5). (6) indicates that the slope ($b = 0.68 \pm 0.03$) differs significantly from the mean h/D ratio ($= 0.59$). One can thus conclude that the h/D ratio is not constant, though the relationship between h and D is linear. Larger specimens tend to be less flattened than smaller individuals.

c. The r mal of the ds-D plot is given by

$$ds = 0.62 + 0.64 D \quad (7) \text{ (Text-fig. 3),}$$

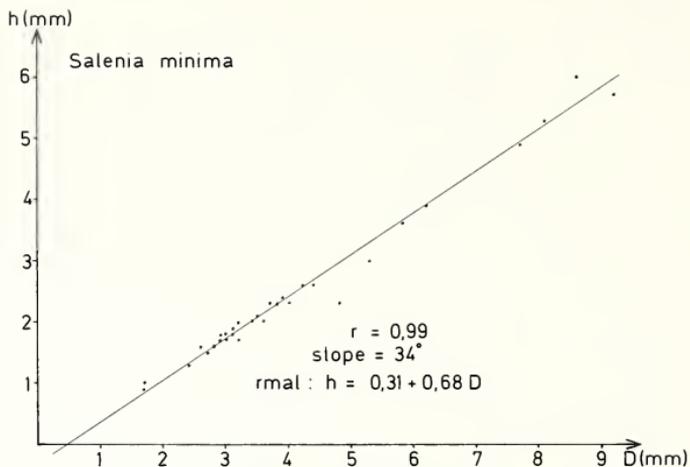
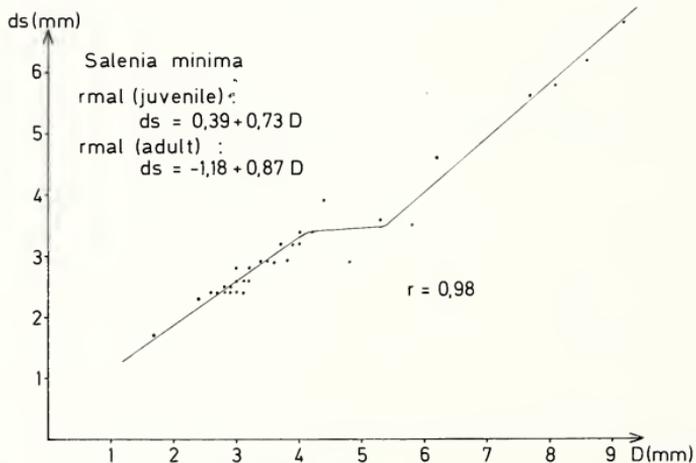
with 95% confidence intervals of intercept and slope respectively

$$1.96 s_a(D/ds) = \pm 0.18 \text{ mm} \quad (8)$$

$$1.96 s_b(D/ds) = \pm 0.02 \quad (9).$$

On one hand, one can conclude from (7) and (8) that the origin is not included in the confidence band of the r mal; on the other, (7) and (9) indicate that the slope ($b = 0.64 \pm 0.02$) differs significantly from the mean ds/D ratio ($= 0.82$). Larger individuals are shown to have a relatively smaller apical system than smaller individuals. This could be put as follows: the apical system seems to grow less fast than the entire animal.

The relationship is clearly linear for specimens with $D > 4.5$ mm and for specimens with $D < 4.5$ mm

TEXT-FIG. 2. h-D plot of *Salenia minima* with reduced major axis line (rml).TEXT-FIG. 3. ds-D plot of *Salenia minima*, with reduced major axis line (rml).

separately, but not for the population as a whole. This is clearly demonstrated by computing the rmal for both partial populations separately.

For large specimens ($D > 4.5$ mm) one obtains

$$ds = -1.18 + 0.87 D$$

with 95% confidence intervals

$$1.96 s_a(D/ds) = \pm 0.61 \text{ mm}$$

$$1.96 s_b(D/ds) = \pm 0.04.$$

For small specimens ($D < 4.5$ mm) one obtains analogously

$$ds = 0.39 + 0.73 D$$

with 95% confidence intervals

$$1.96 s_a(D/ds) = \pm 0.23 \text{ mm}$$

$$1.96 s_b(D/ds) = \pm 0.07.$$

From these equations we can conclude that the intercept is significantly different in large and small individuals. The difference in slope between the rmal of both populations is much less important. It seems as if the rate of growth of the apical system is drastically reduced when the specimens attain 4 to 5 mm over-all diameter. After crossing the $D = 5$ mm threshold, the rate of growth of the apical system seems to be more or less restored.

Discussion. *Salenia minima* is superficially similar to other salenioids, such as *Salenidia pygmaea* (Hagenow 1940) and *Salenidia maestrichtensis* (Schlüter 1892). The lack of sutural depressions in its smooth apical system makes *Salenia minima* easy to recognize.

Smiser (1935) confused *Salenia minima* and *Goniopygus minor*. What he figured as *Salenia minima* is in fact a *Goniopygus minor* Sorignet, 1850. This error is discussed in a forthcoming paper of mine (Geys 1981).

A very similar species to *Salenia minima* has been described from the Danian of Denmark: *Salenidia danica* Ravn, 1928. Both species probably differ in the structure of their ambulacra and in the shape of their ocular plates.

For both *Salenidia pygmaea* and *Salenidia maestrichtensis* h-D, ds-D, and dp-D plots were statistically analysed, respectively by Nestler (1965) and by Geys (1979). A comparison with *Salenia minima* is instructive. The flattening in shape of larger, hence older specimens, as demonstrated in *Salenia minima*, exists in *Salenidia pygmaea* but not in *Salenidia maestrichtensis*. The relative shrinking of the peristome, demonstrated in *Salenidia pygmaea* and *Salenidia maestrichtensis*, is not indicated in *Salenia minima*. The growth of the apical system, however, shows similar patterns in all three of the species. Very small, very young specimens have apical systems covering the complete adapical surface. In *Salenidia maestrichtensis* a non-linear relationship between D and ds was demonstrated. For *Salenidia maestrichtensis* it was established that the beginning of the final linear segments in its d-D plot ($D > 4.5$ mm) coincides with the attainment of sexual maturity. It is not clear whether the same is true for *Salenia minima*.

Subfamily HYPOSALENIINAE Mortensen, 1934

Genus HYPOSALENIA Desor, 1856

(= *Peltastes* Agassiz, 1838, non *Peltastes* Rossi, 1807; *Peltosalenia* Quenstedt, 1874)

Type species. *Echinus acanthoides* Desmoulins 1837, by subsequent designation of Mortensen (1935).

Hyposalenia heliophora (Agassiz and Desor, 1846)

Plate 29, figs. 5-8

v*.1846 *Salenia heliophora*, Agassiz and Desor, p. 342.

v.1850 *Salenia heliophora*, d'Orbigny, p. 273.

v.1856 *Hyposalenia heliophora*, Desor, p. 148.

1857 *Hyposalenia heliophora*, Bosquet, no. 842.

v.1864 *Peltastes heliophorus*, Cotteau, pp. 122-124, pl. 1029, figs. 1-7.

- 1874 *Peltastes heliophorus*, Cotteau, p. 642.
 1879 *Hyposalenia heliophora*, Ubaghs, p. 228.
 1881 *Hyposalenia heliophora*, Mourlon, p. 125.
 .1892 *Peltastes* cf. *heliophorus*, Schlüter, pp. 152-154.
 .1910 *Peltastes heliophorus*, Lambert and Thiery, p. 209.
 v.1928 *Hyposalenia heliophora*, Lambert and Jeannot, p. 203.
 .1935 *Peltastes* cf. *heliophorus*, Kongiel, p. 31, pl. 2, fig. 5a-c.
 .1935 *Hyposalenia heliophora*, Mortensen, p. 344, fig. 188g.
 .1939 *Hyposalenia heliophora*, Kongiel, p. 20, pl. 3, figs. 19-21.
 .1966 *Hyposalenia heliophora*, Fell and Pawson, p. U379, fig. 277-1j.
 v.1966 *Hyposalenia heliophora*, Meijer, p. 23.
 .1979 *Hyposalenia heliophora*, Geys, p. 320.

Type Locality. Maastricht, Dutch Limburg, the Netherlands. Geulhem Chalk, Houthem Formation, Danian.

Other occurrences. Cibly, Hainaut, Belgium: Cibly Tuffaceous Chalk, Danian (Agassiz and Desor 1846). Cibly, Hainaut, Belgium: Malogne Gravel, Danian (Cotteau 1874). Berlin, Germany: 'Geschiebe', reworked in Pleistocene (Schlüter 1892). Gora Pulawska, Poland: Siwak, Lower Danian (Kongiel 1935, 1939).

Studied specimens from the Maastricht area (Geulhem Chalk). Vroenhoven, Belgian Limburg: 41 specimens; Geulhem, Dutch Limburg: 225 specimens.

Dimensions. Forty specimens, chosen at random, were measured. D: 1.7-12.0 mm; h: 1.0-7.5 mm; h/D ratio: 0.5-0.7; ds: 1.6-7.7 mm; ds/D ratio: 0.62-1.00; dp: 0.6-5.2 mm; dp/D ratio: 0.26-0.58.

Description. The adoral side is slightly convex, the peristome a little sunken. The peristome is distinctly decagonal and shows rather large gill slits. These slits are surrounded by low, blunt ridges. The auricles are short, rectangular, and spatulate. They are not in contact over the perradial suture.

The apical system is large and pentagonal, covering most of the adapical surface. It is conically convex and consists of eleven plates, separated by very fine, hardly visible sutures. Real sutural depressions are absent. The ocular plates are pentagonal, with more or less straight distal margins. The genital plates are hexagonal, the suranal plate is pentagonal. All the plates are covered by a conspicuous sculpture of ridges and furrows, which radiate from the centres of the plates, and which are perpendicular to the sutures. The genital pores have a central position in the plates. The periproct is oval or subtrigonal. It is situated between the apex and genital plate 5, so that the test is symmetrical with respect to the III-5 plane.

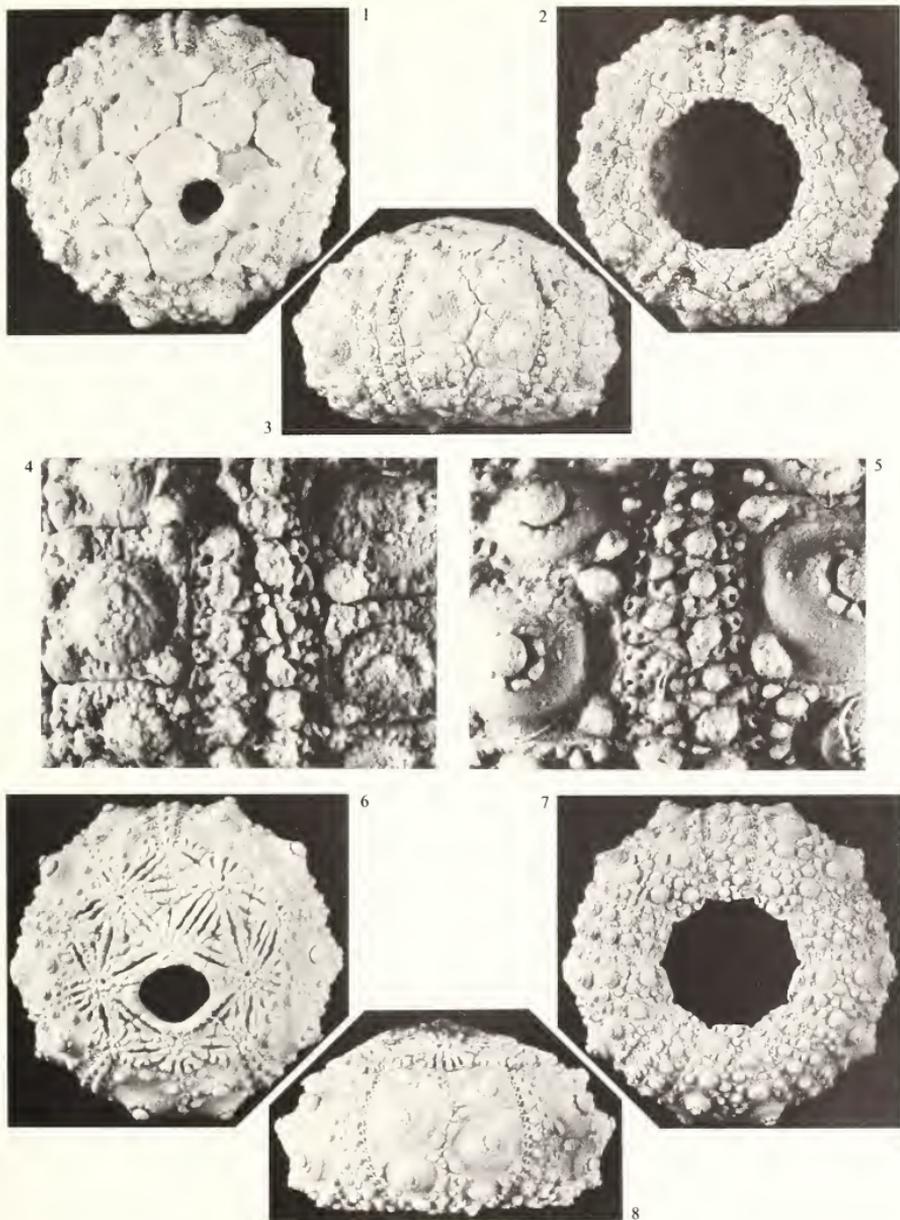
Ambulacral series consist of twelve or thirteen crenulate, non-perforate primary tubercles. The tubercles just below the ambitus are the largest in size. From there upwards, their size diminishes abruptly. The ambulacra are straight. The plates are very regularly bigeminate. The poriferous zones are uniserial throughout. The pores of each pair are separated by a low ridge. The axes of the pore pairs have an inclination of 45° below, and less than 45° above, the ambitus. Very small scrobicular tubercles, or granules, surround the primaries.

The interambulacral tubercles are crenulate, non-perforate. There are four or five in each series. The areoles are smooth, large, and confluent. Scrobicular rings are hence discontinuous. Granulation is coarse on the interradial miliary surfaces.

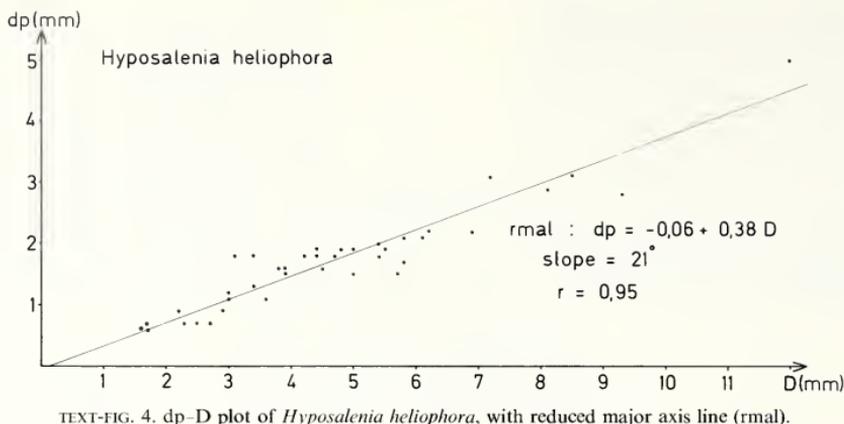
Variability. dp, ds, and h were plotted against D. Reduced major axis lines (rml) and some parameters were computed for each of these graphs.

EXPLANATION OF PLATE 29

Figs. 1-4. *Salenia minima* Agassiz & Desor; NHMM-MM 895; Vroenhoven, Belgian Limburg; Geulhem Chalk. 1, adapical view, $\times 4$. 2, adoral view, $\times 4$. 3, lateral view, $\times 4$. 4, detail of ambulacrum at the ambitus, $\times 12$. Figs. 5-8. *Hyposalenia heliophora* (Agassiz & Desor); NHMM-MM 899; Geulhem, Dutch Limburg; Geulhem Chalk. 5, detail of ambulacrum at the ambitus, $\times 12$. 6, adapical view, $\times 4$. 7, adoral view, $\times 4$. 8, lateral view, $\times 4$.



GEYS, salenioid echinoids



a. The rml of the dp-D plot is given by

$$dp = -0.06 + 0.38 D \quad (\text{text-fig. 4})$$

with 95% confidence intervals of intercept and slope, respectively

$$1.96 s_a(dp/D) = \pm 0.19 \text{ mm}$$

$$1.96 s_b(dp/D) = \pm 0.04.$$

From these equations can be concluded that the origin of the plot is included in the confidence band of the rml, and that the mean dp/D ratio (= 0.37) does not differ significantly from the slope ($b = 0.38 \pm 0.04$). Hence, there is no difference in relative size of the peristome, between young (small) and old (large) specimens. The dp/D ratio is constant.

b. The rml of the h-D plot is given by

$$h = 0.16 + 0.57 D \quad (\text{text-fig. 5})$$

with 95% confidence intervals

$$1.96 s_a(h/D) = \pm 0.11 \text{ mm}$$

$$1.96 s_b(h/D) = 0.01.$$

The origin of the plot is clearly not included in the confidence band of the rml. Moreover, the mean h/D ratio (= 0.62) differs significantly from the slope ($b = 0.57 \pm 0.01$). Though the relationship between h and D is linear, the h/D ratio is not constant. Older (larger) specimens are slightly more flattened than young (small) ones.

c. The rml of the ds-D plot is given by

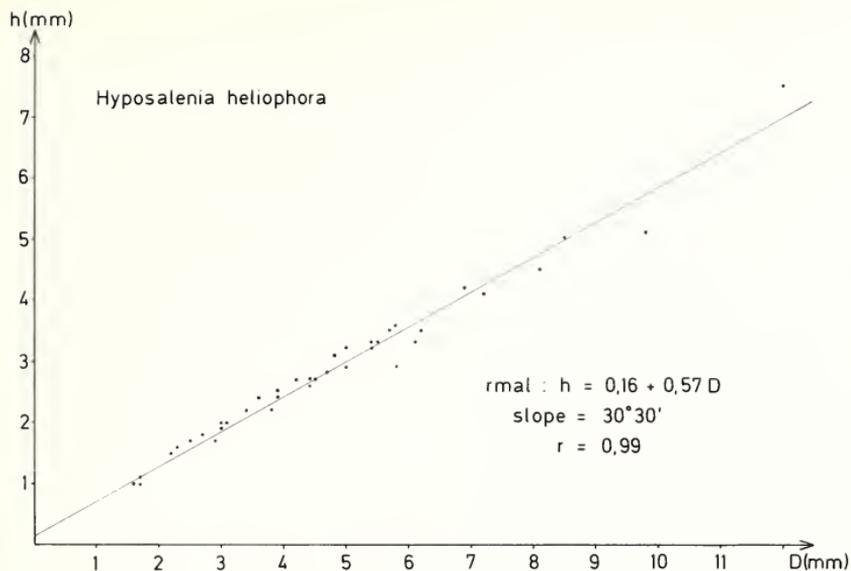
$$ds = 0.60 + 0.62 D \quad (\text{Text-fig. 6})$$

with 95% confidence intervals

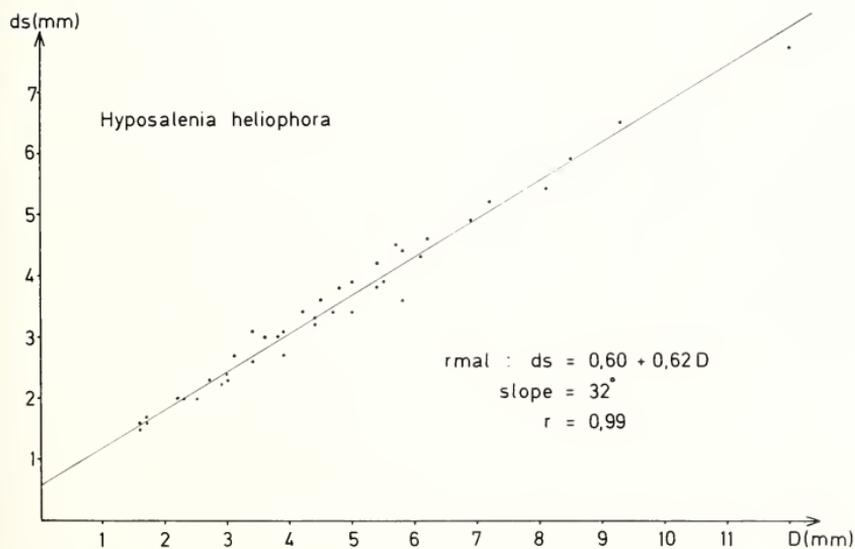
$$1.96 s_a(ds/D) = \pm 0.12 \text{ mm}$$

$$1.96 s_b(ds/D) = \pm 0.01.$$

Obviously the origin of the graph is not included in the confidence band of the rml. The mean ds/D ratio (= 0.78) differs significantly from the slope ($b = 0.62 \pm 0.01$). The ds/D ratio is thus not constant. The apical system, covering the entire adapical surface in very young individuals, grows relatively smaller in older specimens. One could say that the apical system has a rate of growth less fast than that of the animal as a whole. Unlike the other salenioids, discussed above, the relationship between ds and D is linear in *Hyposalenia heliophora*.

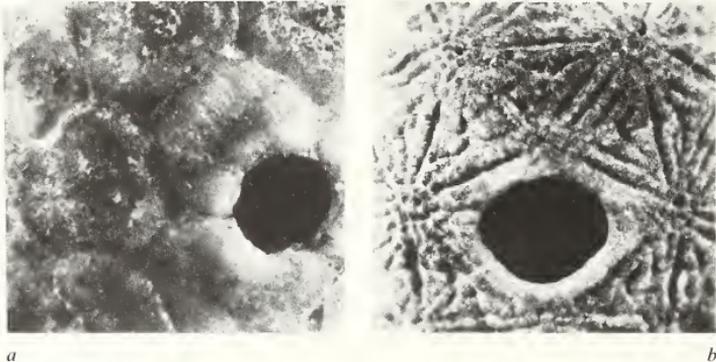


TEXT-FIG. 5. h-D plot of *Hyposalenia heliophora* with reduced major axis line (rmal).



TEXT-FIG. 6. ds-D plot of *Hyposalenia heliophora* with reduced major axis line (rmal).

Discussion. It is clear from the synonymy list that little confusion has arisen with respect to *H. heliophora*. Cotteau (1864) describes this species as being easily recognized, owing to the characteristic structure of its ambulacra and of its apical system. Little can be added to that statement. Like *Salenia minima* Agassiz and Desor, 1846, and *Salenidia pygmaea* (Hagenow 1840), *H. heliophora* shows a slight tendency to flatten in shape with age. Like *Salenia minima*, but unlike *Salenidia pygmaea* and *Salenidia maestrichtensis* (Schlüter 1892), *H. heliophora* has a constant dp/D ratio: the relative size of its peristome does not change with over-all size or age. The growth pattern of the apical system in *H. heliophora* shows some characteristics, common to most, if not all, Salenioids: a strong reduction in relative size with age or with over-all size. Unlike the other species which were statistically analysed, *H. heliophora* has a constant rate of growth in its apical system.



TEXT-FIG. 7. Detail of the apical system, with periproct, suranal plate and surrounding genital plates in *Salenia minima* (a) and *Hyposalenia heliophora* (b). Enlarged, $\times 8$.

CONCLUSIONS

On various occasions *Salenia minima* and *H. heliophora* have been reported from the Upper Cretaceous in Belgium and in the Netherlands (Bosquet 1857; Binkhorst 1859; Ubaghs 1879; Mourlon 1881). These reports are not really erroneous, because the Houthem Formation, as well as the Ciply Tuffaceous Chalk, were included within the Maastrichtian or 'Senonian' at that time. The stratigraphical ranges of both species were precisely documented by Meijer (1966) in Dutch Limburg: the 'uppermost part of the Maastricht Chalk' (now called Houthem Formation), which he called 'zone III' and was then considered to be of Danio-Montian age. Among Cretaceous salenioids in various Dutch and Belgian collections (Geys 1979), I could not trace any specimen of either of the species described here, which was of true Cretaceous age.

Specimens of *Salenia minima* and of *H. heliophora*, in the Natuurhistorisch Museum at Maastricht, were collected exclusively in the so-called 'post-Maastrichtian'. These strata, included in zone III of Meijer (1966), and called Geulhem Chalk of the Houthem Formation by Felder (1975), were considered of Danian age by Meijer (1959). In the Mons Basin the same two species seem to be restricted to the Ciply Tuffaceous Chalk and the underlying Malogne Gravel. The Ciply Tuffaceous Chalk was shown to be of Danian age by Rasmussen (1965).

The debate whether the Mesozoic-Cenozoic boundary is situated at the base or at the top of the Danian is not yet completely resolved. Some authors still include the Danian with the Upper Cretaceous (e.g. Davies 1975). By far the most widespread point of view is to include the Danian into the Lower Tertiary (Berggren 1963; Moorkens 1972). The evidence is mainly based on various

palaeontological arguments: foraminifera and calcareous nannoplankton (Čepek and Moorkens 1979), ostracods (Deroo 1966), brachiopods (Krutzler and Meijer 1958). Both *Salenia minima* and *H. heliophora* seem to be index fossils for Danian strata. Their presence in Maastrichtian or in Montian deposits has not yet been demonstrated.

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DEVONIAN MIOSPORE ASSEMBLAGES FROM FAIR ISLE, SHETLAND

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ABSTRACT. Miospore assemblages have been isolated from a Devonian sequence of Old Red Sandstone facies, on Fair Isle, Shetland. The special problems encountered in processing these palynomorphs with their high carbonization levels and subsequent darkening are mentioned. Thirty miospore species are recorded and their taxonomic problems and stratigraphical significance are discussed. Comparisons with similar assemblages from the northern hemisphere indicate a Givetian (in parts specifically late Givetian) age for the Fair Isle material. The genus *Rhabdosporites* Richardson 1960 is emended, and *R. langii* Richardson 1960 and *R. parvulus* Richardson 1965 are combined. The ecological significance of *Geminspora* (Balme) Owens 1971 is discussed.

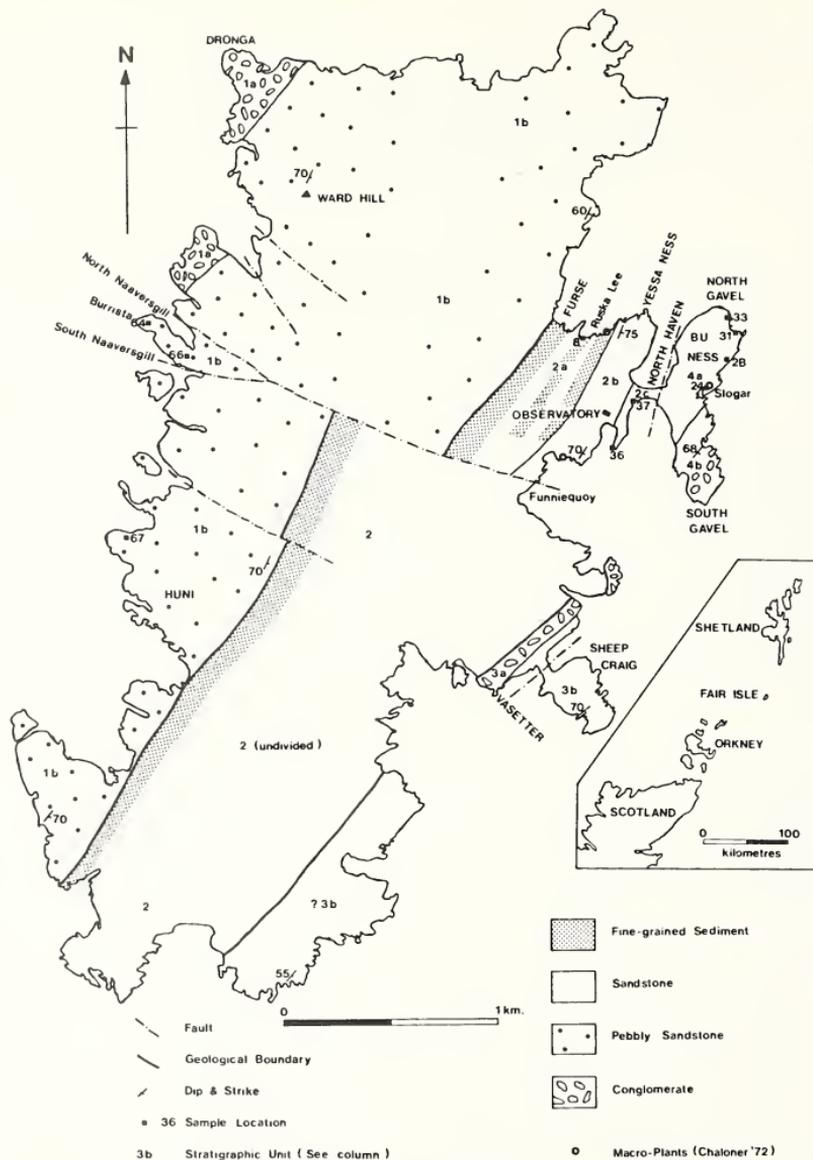
SHETLAND contains one of the most complex set of continental Devonian rocks in Britain, with different rock sequences juxtaposed by major transcurrent faults. These complex structural relationships have proved very difficult to elucidate, and this has not been helped by the poor biostratigraphic control between the different basins. It is hoped that palynological contributions will give the biostratigraphic basis for a comparison of the time relations in these sedimentary basins, and will yield information on the timing of the movements along the major transcurrent faults, about which there is still much controversy (Smith 1977). This paper deals with the sequence found in the small (5 km × 3 km), isolated Devonian outlier of Fair Isle, which lies 39 km south-west of the southern tip of mainland Shetland (text-fig. 1). Emphasis is placed on stratigraphic palynology; little attempt has been made to formally modify, or add to existing taxonomy. This is because of serious preservational problems encountered in the palynological studies, which are discussed later.

THE DEVONIAN SUCCESSION ON FAIR ISLE

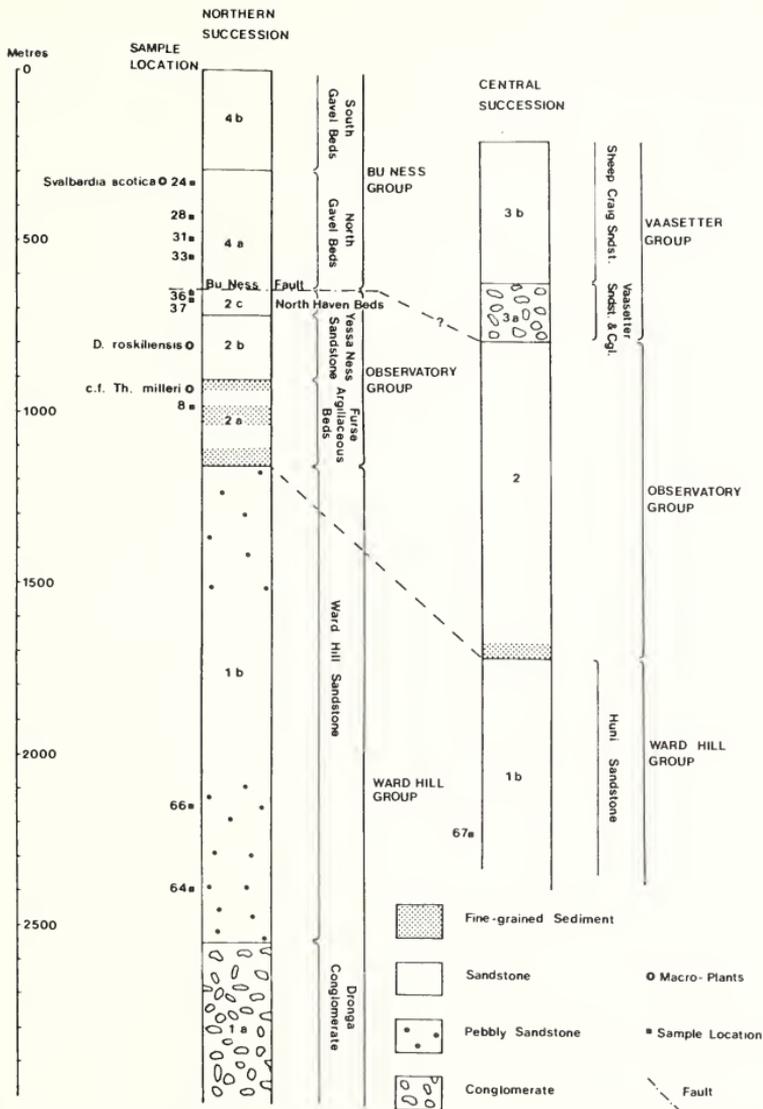
Although Fair Isle has a relatively small Devonian outcrop, its geographical position (text-fig. 1) is of importance because it is generally considered (Mykura and Young 1969; Mykura 1972a) to lie just to the east of the Walls Boundary Fault, which is a possible extension of the Great Glen Fault. It has also been suggested (Mykura 1976; Donovan, Archer, Turner, and Tarling 1976) that it is part of the same sedimentary basin as that in which the Walls Sandstone was deposited, and movements along this fault have placed it in its present position. Any indication therefore of the precise age could help clarify these palaeogeographic relationships.

The most recent and complete accounts of the geology of Fair Isle are those of Mykura (1972a, 1972b, 1976), and this brief synopsis is drawn from them. The Fair Isle sedimentary sequence (for which neither the top nor the base is seen), is composed of over 3000 m of dominantly clastic terrigenous sediments, all steeply dipping east-south-east. The rocks have been subdivided (Mykura's nomenclature and notation followed here) into four stratigraphic subdivisions (see text-figs. 1, 2), on the basis of lithological differences. These units can be traced with varying degrees of accuracy across the island, but the presence of two major east-north-east trending faults create local correlation difficulties which are only partially solved by lithological mapping.

The lowest unit is the Ward Hill Group (1a and 1b in Mykura's notation), composed of over 1600 m of conglomerates and sandstones. This is succeeded by the Observatory Group (2a, 2b, and 2c) with over 900 m of sandstones and finer sediments including dolomitic siltstones and mudstones. Above this, the Vaasetter Group (3a and 3b) which is only exposed in the central fault block, is composed of about 600 m of conglomerates and sandstones, most of which are inaccessible. The top



TEXT-FIG. 1. Geological map of Fair Isle (after Mykura), showing location of palynological samples and plant macrofossil sites.



TEXT-FIG. 2. Stratigraphical section of Fair Isle (after Mykura) showing position of palynological samples.

unit, the Bu Ness Group (4a and 4b), consists of approximately 600 m of conglomerates, sandstones, and siltstones; is seen only in the northern succession of the island where it is faulted against the Observatory Group (2a, 2b, and 2c).

Increasing tectonic disturbance is seen in the rocks towards the southern end of the island where they exhibit prominent cleavage, minor folding, mineralization, and the emplacement of small dyke intrusions. The cause of this disturbance has been discussed by Mykura (1972a) who suggested a possible granitic intrusion lying off the south-east coast of the island.

Previous palaeontological records are very restricted, and largely limited to the plant macrofossil remains described by Chaloner (1972), for which the localities are shown on text-fig. 1. The fossil plants clearly indicate a Devonian age. Chaloner tentatively suggests an age not older than middle Siegenian for the Observatory Group (Unit 2a) based on the presence of *Dawsonites roskiliensis* Chaloner 1972, and an age not older than Eifelian, but more likely Middle Devonian, for the Bu Ness Group (Unit 4a), based on the occurrence of *Svalbardia scotica* Chaloner 1972. Other plants include cf. *Thursophyton milleri* (Salter) Nathorst 1915 in the Observatory Group and hostinellid axes and cf. *Prototaxites* Dawson 1859 in the Bu Ness Group.

The Bu Ness Group yields the only animal fossils yet found, which include dipnoan scales, an arthrodire plate (?*Cocosteus* Agassiz 1844) and the branchiopod *Asmussia* Pacht, 1849. These also favour a Middle Devonian age for this group.

MATERIAL AND METHODS

Four samples were initially provided by the Institute of Geological Sciences (Edinburgh), and when two of these were found to contain miospores a field trip was made to the island, and seventy-eight samples were collected from fine-grained dark-grey to black clastic rocks for palynological analysis. Of these, sixty-one were processed, but only ten gave assemblages of sufficient quantity and preservation to merit further study. The best-preserved assemblages were from the Observatory Group; followed by the Bu Ness and Ward Hill Groups. Very poor preservation was found in the argillaceous units (2a) of the Furse Argillaceous Beds where there was some cleavage development. The lack of miospores in the southern part of the island is of interest, as it is in accord with the increased deformation reported by Mykura (1972a). Megaspores were also rare and usually fragmentary. This can be related to the orthogonal crack sets seen on some of the larger specimens, which may result from an incipient cleavage (or shrinkage), causing their fragmentation during deformation or in the processing (Burmman 1969).

The samples were firstly demineralized with hydrochloric and hydrofluoric acids, then screen-washed through a twenty micron nylon sieve, before being cleaned of insoluble fluorides with repeated hot HCl treatments to give a kerogen concentrate. The miospore assemblages were very highly carbonized (black in colour), and the only oxidizing medium found capable of clearing them was a fuming Schulze mixture. The oxidations were carried out in a porosity-2 sinter funnel/buchner flask system linked with a low-pressure air line to give continuous aeration (Neves and Dale 1963). The Schulze mixture was made up with fuming nitric acid either at full strength or freshly diluted with water, but always at a concentration greater than 70%. The time taken for the miospores to be oxidized to a level suitable for transmitted light microscopy varied from 5 to 30 minutes. In addition, a marked preferential clearing was seen, with some of the thicker walled (e.g. *Hystricosporites* spp.) miospores never attaining more than a low level of translucency. Samples from different horizons showed very different oxidation characteristics. Those from the Furse Argillaceous Beds (2a), required only 5 minutes' oxidation time and a relatively weak fuming Schulze, to reveal a poorly preserved assemblage; whilst samples from the Bu Ness Group needed stronger and longer oxidation, but gave much better-preserved assemblages.

After oxidation the miospores showed the phenomenon of redarkening (to opacity) in 1 to 3 days, with the thicker-walled miospores deteriorating much more rapidly. This degradation was accelerated by heating and water removal, so that an inert non-water miscible plastic mounting medium could not be used, as dehydration was impossible under normal conditions. Silicone oil was

also tried, but the dehydration step involving tertiary butyl alcohol, produced a rapid darkening reaction in the cleared sample. Eventually, glycerol jelly was used as the mounting medium, and this gave assemblages which could be studied for up to 3 days. The breakdown and darkening of the exines when mounted in glycerol jelly was noticeable, with degradational products imparting a yellow stain to the mounting medium. Miospores with thicker exines (e.g. *Hystricosporites*, *Geminospora*) showed a more rapid return to opacity, and had to be studied during the first day.

A subsequent study of palynological assemblages from the Devonian of the south-east mainland of Shetland also showed this oxidation problem. There, it was much more serious, with viability times of about 5 minutes in glycerol jelly. During this time the miospores could be seen to redarken and start to dissolve. It was then that a special technique was developed which involved a matching of the oxidizing media strength to a miospore assemblage preservation, and the use of a rapid drying technique which dehydrated the miospores faster than they could redarken, so that an inert plastic mountant could be used (Marshall 1980).

The assemblages from Fair Isle were all studied from repeated oxidation, with fresh assemblage slides being made up every 2 to 3 days. The study was therefore limited by the amount of organic residue per sample; some giving enough material for seventy to eighty slides, others only having sufficient for four or five. All the slides have been kept, and co-ordinates given for illustrated specimens in the event that advances in techniques, such as infra-red microscopy, will enable palynomorphs to be studied without further recourse to oxidative clearing.

One difficulty in dealing with such highly carbonized assemblages ('vitrinite' reflectance measurements from Fair Isle give values of approx. 4 to 5%, pers. comm. Dr. J. M. Jones), is that the identification of reworked components by colour differences is not possible. Three species are described (*Emphanisporites rotatus*, *Camptozonotriletes aliquantus*, and *Grandispora ?naumovii*) which occur in a very low proportion, and it is possible that these may represent reworked components (see Clayton, Higgs, and Keegan 1977 for a discussion of *Emphanisporites*). However, until one is better able to recognize features of reworking such as breakage and erosion (as in Birks 1970), both this possibility and that of their continued presence as minor and rare elements in the flora must be considered.

PREVIOUS PALYNOLOGICAL STUDIES FROM SHETLAND AND ADJACENT AREAS

The pioneer work on Old Red Sandstone palynology in Britain was carried out by Lang (1925) as part of his study of the Orcadian Basin flora. Later, Richardson produced a series of papers (1960, 1962, 1965) on the classical Orcadian area. Since then, very little work has been published except for brief taxonomic lists as, for example, Donovan, Collins, Rowlands, and Archer (1978), who give an account of a miospore assemblage from the island of Foula (western Shetland). Two doctoral theses have included a certain amount of Orcadian palynology. Fannin (1970), in conjunction with Richardson, has tabulated information on the palaeoecology and stratigraphic distribution of miospore assemblages from Orkney, whilst Fletcher (1976) studied the megaspores of the Melby Fish Beds. Although a useful amount of data has accumulated on the taxonomy of Devonian spores from the Orcadian Basin, very little is known of their detailed stratigraphic distribution, and this has been a major handicap to any precise correlation.

STATISTICS AND DATA HANDLING

The treatment of the simple bivariate statistical data, such as the exoexine and intexine diameters of miospores, presents problems for data handling and statistical testing. Classical regression analysis is not applicable, as there are no dependent and independent variates; furthermore, there is no easy solution to fit a best line to this type of two-error data. Various iterative methods such as those described by Williamson (1968), York (1966), and comparatively reviewed by Brooks, Hart, and Wendt (1972),

demand statistical estimates for the variances of each data point. These are certainly not worth the extra time involved for the quality of data produced on the Fair Isle material. An approximate method is the Reduced Major Axis line as described by Kermack and Haldane (1950), and further documented by Till (1974) and others. The statistical validity of the line produced is in doubt, but as it appears correct (i.e. passes through the centre of the experimental scatter), it is a useful means of comparing populations, providing not too much reliance is placed on any subsequent statistical tests based upon it.

The data in the bivariate plots were in fact computed for logarithmic and linear fits, using both classical regression and the reduced major axis line to find the best fit. The latter was found to be more successful in describing a line through a set of data points. However, the logarithmic fit did not give much advantage over the linear model. When data values were taken from published graphical plots (Richardson 1965), an electronic digitizing machine (D-MAC) was used to provide more accurate results and known estimates of error.

NOMENCLATURE AND SYSTEMATICS

The morphological terminology used is that of Smith and Butterworth (1967), and their classification system is followed except for the inclusion of *Hystricosporites*, *Ancyrospora*, and *Geminospora* in an *incertae sedis* group, following the practice of Strel (in Becker, Bless, Strel, and Thorez 1974). No categories higher than infraturmae are used, and the retusoid miospores are retained in the *Laevigati* and *Apiculati*, because haptotypic features are not here regarded as being of major classificatory importance.

Figured material is housed in the palaeobotanical collection of the Department of Botany, Bristol University. Co-ordinates given refer to a Leitz Orthoplan microscope no. 715334. A ringed reference slide is also provided. Each sample number (i.e. Fair 66) is followed by a strew slide number and then the appropriate co-ordinates.

Infraturma LAEVIGATI Bennie and Kidston emend. Potonić and Kremp 1954

Genus TRILEITES Erdtman ex Potonić 1956

Type species. Trileites spurius Dijkstra emend. Potonić 1956

Trileites langii Richardson 1965

Plate 30, fig. 1

Dimensions (two specimens). Maximum equatorial diameters 141 and 160 μm .

Lithostratigraphic Range. Ward Hill Sandstone (1b); sample Fair 66 (see text-fig. 2).

EXPLANATION OF PLATE 30

All figures $\times 400$ unless otherwise stated.

Fig. 1. *Trileites langii* Richardson 1965. Fair 66.2, 48.9, 98.7

Figs. 2, 5. *Acinosporites lindlarensis* Riegel 1968 var. *minor* McGregor and Camfield 1976. Fair 37.80, 37.4, 104.8, $\times 1000$ Distal and proximal surfaces respectively.

Figs. 3, 4. *Camptozonotriletes aliquantus* Allen 1965. 3, Distal view. 4, $\times 1000$ Distal surface showing sculpture. Both Fair 66.2, 17.5, 109.8

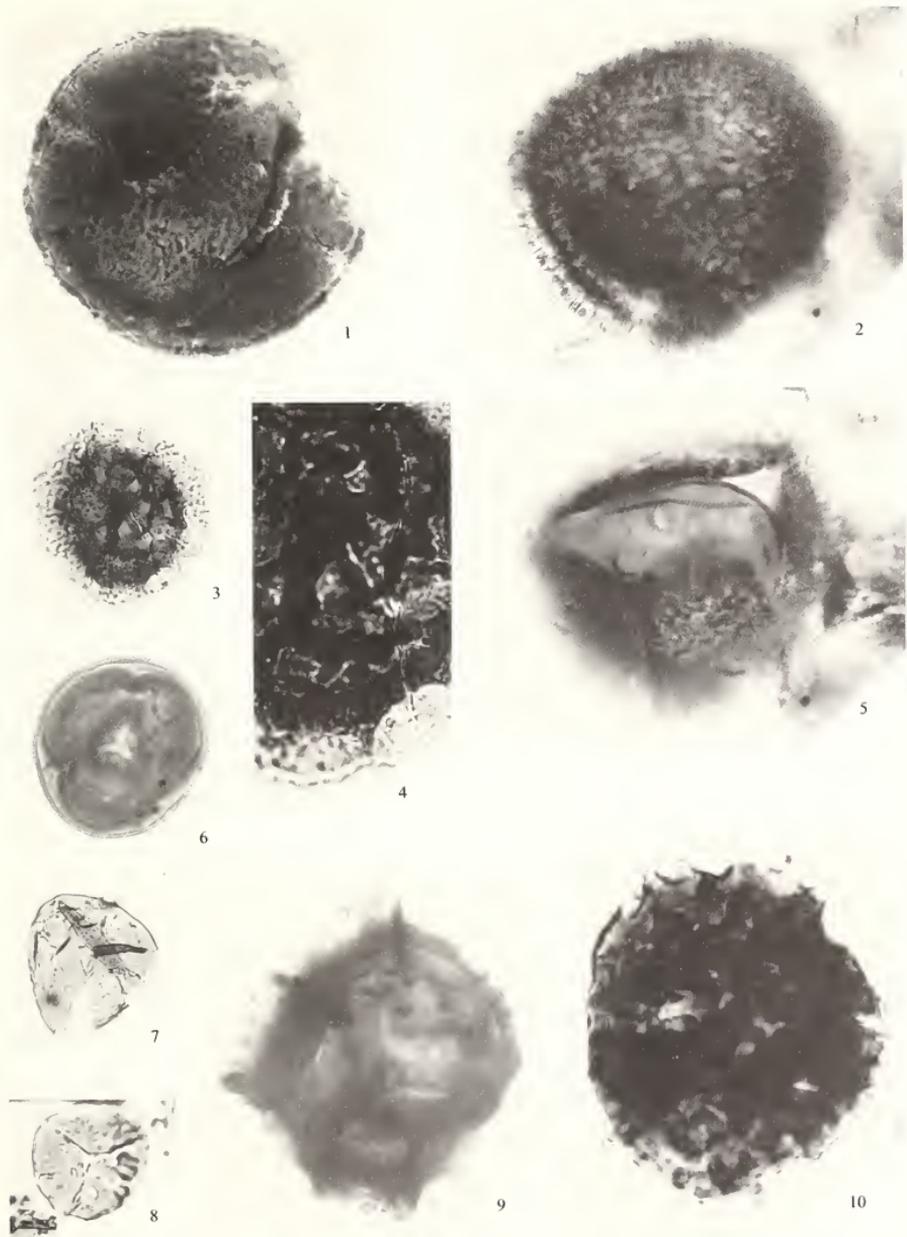
Fig. 6. *Retusotriletes rotundus* (Strel) Lele and Strel 1969. Fair 37.79, 19.9, 106.0.

Fig. 7. *Calamospora atava* (Naumova) McGregor 1964. Fair 37.79, 26.9, 96.5

Fig. 8. *Emphanisporites rotatus* (McGregor) McGregor 1973. Fair 28.32, 114.6, 27.2

Fig. 9. *Chelinospora concinna* Allen 1965. $\times 1000$. Fair 37.1, 25.9, 115.3

Fig. 10. *Convolutispora disparalis* Allen 1965. $\times 1000$ Fair 24.40, 50.0, 100.3



MARSHALL and ALLEN, Devonian miospores

Remarks. Similar to the population described by Richardson (1965), but smaller in over-all diameter. However, it is comparable with the miospores described by Chi and Hills (1976), and is here referred to *Trileites langii*.

Genus *RETUSOTRILETES* Naumova 1953 emend. Streele 1964

Type species. *Retusotriletes simplex* Naumova 1953

Retusotriletes rotundus (Streele) Lele and Streele 1969

Plate 30, fig. 6

Synonymy, see McGregor (1973, p. 20).

Dimensions (eighteen specimens). Maximum equatorial diameter 56–80 μm (mean 67 μm).

Lithostratigraphic range. Ward Hill, Observatory, and Bu Ness Groups (1b to 4a). Found in all samples examined.

Remarks. This is an example from the wide variety of retusoid forms which occur in the Fair Isle assemblages.

Genus *CALAMOSPORA* Schopf, Wilson, and Bentall 1944

Type species. *Calamospora hartungiana* Schopf, Wilson, and Bentall 1944

Calamospora atava (Naumova) McGregor 1964

Plate 30, fig. 7

Dimensions (twenty-four specimens). Maximum equatorial diameter 27–71 μm (mean 56 μm).

Lithostratigraphic range. Ward Hill Group to Bu Ness Group (1b to 4a). In all samples examined except Fair 33 (see text-fig. 2).

Remarks. Compares well with the emended species described by McGregor (1964), but exhibits a slightly greater size range.

Infraturma *MURORNATI* Potonić and Kremp 1954

Genus *CONVOLUTISPORIS* Hoffmeister, Staplin, and Malloy 1955

Type species. *Convolutispora florida* Hoffmeister, Staplin, and Malloy 1955

Convolutispora disparalis Allen 1965

Plate 30, fig. 10

Dimensions (six specimens). Maximum equatorial diameter 36–54 μm (mean 46 μm).

Lithostratigraphic range. Bu Ness Group (4a); samples Fair 24 and 28.

Remarks. As stated in Allen (1965) it is thought likely that sculptural elements of this type result from corrosion of the exine. It is noticeable that a wide range of sculpture is present, with transitional forms resembling *Raistrickia* Potonić and Kremp 1954.

Genus *EMPHANISPORITES* McGregor 1961

Type species. *Emphanisporites rotatus* McGregor 1961

Emphanisporites rotatus McGregor emend. McGregor 1973

Plate 30, fig. 8

Synonymy, see McGregor (1973, p. 46).

Dimensions (three specimens). Maximum equatorial diameter 33, 38, and 50 μm .*Lithostratigraphic range*. Observatory and Bu Ness Groups (4a and 2c); samples Fair 28 and 37.*Remarks*. Clayton *et al.* (1977) have documented a series of sporadic occurrences of *Emphanisporites* spp. from the later Devonian and early Carboniferous of southern Ireland. Similar sporadic occurrences were also noted by Richardson (1965) from the Eday Flags of the Orcadian Basin. It seems likely that the Fair Isle occurrences are only rare examples of a minor but persistent element in the flora. The decision when to regard elements of an assemblage as reworked or rare is often difficult (see *Captozonotrilites aliquantus*), and should be based on features such as stratigraphic persistence, association with other possible reworked elements, and obvious signs of physical reworking (see Birks 1970).

GENUS ACINOSPORITES Richardson 1965

Type species. *Acinosporites acanthomammillatus* Richardson 1965*Acinosporites lindlarensis* Riegel 1968 var. *minor* McGregor and Camfield 1976

Plate 30, figs. 2, 5

Dimensions (one specimen). Maximum equatorial diameter 48 μm .*Lithostratigraphical range*. Observatory Group (2c); sample Fair 37.*Remarks*. The Fair Isle miospore closely resembles specimens described by McGregor and Camfield (1976) from sediments of Emsian to Givetian age from the Moose River Basin, Ontario. Although this species has a *Geminospora* organization, the authors follow McGregor and Camfield (1976), by placing it in *Acinosporites*.

Infraturma CRASSITI Bharadwaj and Venkatachala 1962

GENUS ANEUROSPORA (StreeI) StreeI 1967

Type species. *Aneurospora goensis* Steel 1964*Aneurospora greggsii* (McGregor) StreeI in Becker *et al.* 1974

Plate 31, fig. 1

Synonymy, see StreeI in Becker *et al.* (1974, p. 24).*Dimensions* (eight specimens). Maximum equatorial diameter 68–116 μm (mean 84 μm)*Lithostratigraphic range*. restricted to the Bu Ness Group (4a); samples Fair 24, 28, 31, and 33.*Comparisons*. Similar problems to those noted by Lele and StreeI (1969) and StreeI (1972) were encountered in separating this genus from *Geminospora*. A possible synonymy is with *Archaeozonotrilites nalivkini* Naumova as figured by Chibrikova (1977, pl. XIX, fig. 11), but since no description was given, it is impossible to make a detailed comparison. Certain specimens also show similarities with *Geminospora svalbardiae* Allen 1965.

Infraturma CINGULICAVATI Smith and Butterworth 1967

GENUS CAMPTOZONOTRILETES Staplin 1960

Type species. *Camptozonotrilites vermiculatus* Staplin 1960

Camptozonotriletes aliquantus Allen 1965

Plate 30, figs. 3, 4

Dimensions (one specimen). Maximum exoexine diameter 77 μm , maximum intexine diameter 57 μm .

Lithostratigraphic range. Ward Hill Group (1b), sample Fair 66.

Remarks. The known stratigraphic occurrences for this species are Siegenian to Lower Eifelian (Allen 1967); Upper Siegenian to Lower Emsian (Massa and Moreau-Benoit 1976), and lower Eifelian (Riegel, 1973, 1974). These occurrences are significantly different from the Givetian age assigned to the Fair Isle succession, and its appearance may be the result of reworking.

Genus *DENOSPORITES* Berry emend., Potonić and Kremp 1954

Type species. *Densosporites covensis* Berry 1937

Remarks. Butterworth *et coll.* 1964 (and in Staplin and Jansonius 1964) in an emendation of the densospora group of miospores, provided unified limits (based largely on Carboniferous material) for the subdivision of generic groups. These genera have not proved applicable for the Devonian densosporites from Fair Isle, but until a more unified revision is carried out, we feel they should be retained.

Densosporites devonicus Richardson 1960

Plate 31, fig. 12

Dimensions (thirty-six specimens). Maximum equatorial diameter 55–120 μm (mean 85 μm).

Lithostratigraphic range. Ward Hill to Bu Ness Group (1b to 4a). In all samples examined.

Remarks. Richardson (1965), in his study of Middle Devonian miospores from the Orcadian Basin, gave the sculptural details, and the relative widths of the light and dark zones of the cingulum as criteria for distinguishing *Densosporites devonicus* from *D. orcadensis*. These same criteria were used in Fair Isle in an attempt to substantiate the differences between the two species, but no systematic variation of these characters, as claimed by Richardson (1965, p. 581), was found. McGregor and Camfield (1976) and McGregor (1979*b*) also had difficulty in distinguishing between the two species. This raises doubts as to the significance of the stratigraphic distribution of the two species as recorded by Richardson (1965).

Genus *SAMARISPORITES* Richardson 1965

Type species. *Samarisporites orcadensis* (Richardson) Richardson 1965.

EXPLANATION OF PLATE 31

All figures $\times 400$ unless otherwise stated.

Fig. 1. *Aneurospora greggsii* (McGregor) Streef 1974. Fair 31.8, 28.5, 100.6

Fig. 2. *Cirratriradites avius* Allen 1965. Fair 66.2, 12.8, 95.2

Fig. 3. *Samarisporites orcadensis* (Richardson) Richardson 1965. Fair 31.5, 12.1, 104.5

Figs. 4, 7. *Cirratriradites* sp. A. 4, $\times 1000$. Detail of distal sculpture. 7, $\times 400$. Fair 66.9, 13.9, 110.6

Figs. 5, 6. *Samarisporites mediconus* (Richardson) Richardson 1965. 5, Proximal view. 6, Distal view. Fair 37.71, 13.5, 101.2

Figs. 8, 9. *Samarisporites conannulatus* (Richardson) Richardson 1965. 8, Distal view. 9, Proximal view. Fair 37.80, 5.1, 100.3

Fig. 10. *Auroraspora macromanifestus* (Hacquebard) Richardson 1960. Fair 37.82, 14.8, 112.4

Fig. 11. *Auroraspora micromanifestus* (Hacquebard) Richardson 1960. Fair 37.82, 7.1, 111.0

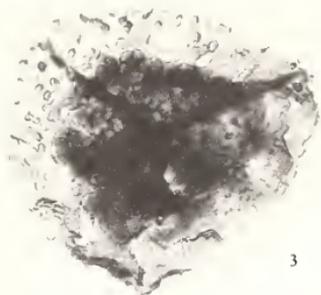
Fig. 12. *Densosporites devonicus* Richardson 1960. Fair 66.3, 4.0, 95.7



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2



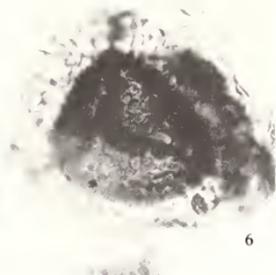
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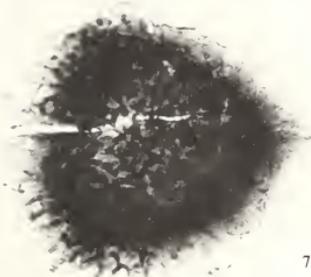
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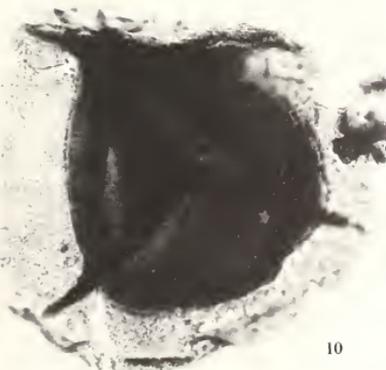
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12

Remarks. The generic status of *Samarisporites* is similar to that of the Devonian *Densosporites*, in being an element of the densospore complex. The genus *Samarisporites*, as originally proposed by Richardson (1965), was to accommodate zonate spores with a variety of solely distal sculptural elements. The justification for the erection of this genus was that its initial assignation to *Cristatisporites* (Potonié and Kremp 1954) was invalid, because the latter has both proximal and distal sculpture. However, it was suggested by Playford (1971), that with the emendation of *Cristatisporites* (Butterworth *et coll.* 1964) as part of a general reorganization of the densospore group, that the use of *Samarisporites* as a distinct generic category could be abandoned. The emendation, however, still includes the possible presence of a proximal sculpture in the form of a ring of setae. It also restricts the distal sculpture to being dominantly mammoid in type, and showing no differentiation in form. The present usage of *Samarisporites* includes forms with a wide variety of distal sculpture (e.g. conical, cristae, verrucae) which cannot be accommodated within *Cristatisporites* (*sensu* Butterworth *et coll.* 1964). It is proposed therefore to use *Samarisporites* for these species, until a more unified set of limits for the densospore group is proposed, which accommodates both Devonian and Carboniferous representatives.

Richardson (1960, 1965) erected three species of *Samarisporites* based largely on sculptural differences and their distribution on the distal surface (e.g. central packing in *S. mediconus*, ring development in *S. conannulatus*). The Fair Isle populations contain intermediate forms, and there is a complete morphological transition series between Richardson's *S. mediconus*, *S. orcadensis*, and *S. conannulatus*, which can be considered as occupying distinct positions on the various trends. It would be interesting to speculate whether the continuous variation this plexus of species exhibits, could be treated in the same way as in the morphon concept recently outlined by Van der Zwan (1979, 1980). However, not enough individuals have yet been found to systematically describe the variation both in a morphological and stratigraphical sense, either to record separate species or varieties in a morphon, or to combine them as a single species.

Samarisporites mediconus (Richardson) Richardson 1965

Plate 31, figs. 5, 6

Dimensions (eight specimens). Maximum equatorial diameter 73–130 μm (mean 108 μm), cingulum 10–26 μm wide (mean 17 μm).

Lithostratigraphic range. Ward Hill to Bu Ness Group (1b to 4a); samples Fair 31, 37, and 66.

Remarks. Closely resembles the type species, except that there is a greater variety of labra morphology.

Samarisporites orcadensis (Richardson) Richardson 1965

Plate 31, fig. 3

Dimensions (three specimens). Maximum equatorial diameter 88, 97, and 146 μm . Cingulum width 15–20 μm .

Lithostratigraphic range. Observatory and Bu Ness Groups (2c and 4a); samples Fair 31, 33, and 36.

Remarks. The three individuals found compare closely with Richardson's holotype. However, they show greater variety of labra morphology in both length and height.

Samarisporites conannulatus (Richardson) Richardson 1965

Plate 31, figs. 8, 9

Dimensions (five specimens). Maximum equatorial diameter 104–120 μm (mean 113 μm). Cingulum 14–21 μm wide, maximum width interradially.

Lithostratigraphic range. Ward Hill to Bu Ness Groups (1b to 4a); samples Fair 31, 36, 37, and 64.

Remarks. Compares closely with the type species except that the labra show a greater amount of variation in length and height.

Genus *CIRRATRIRADITES* Wilson and Coe 1940.

Type species. *Cirratriradites saturnii* (Ibrahim) Schopf, Wilson, and Bental 1944

Cirratriradites avius Allen 1965

Plate 31, fig. 2

Dimensions. Maximum equatorial diameter 80–130 μm (mean 105 μm), twenty-eight species measured. Maximum intexine diameter 58–78 μm (mean 67 μm), eight specimens measured.

Lithostratigraphic range. Bu Ness and Ward Hill Groups (4a and 1b); samples Fair 24, 28, 33, 64, and 66.

Remarks. Although the type species of this genus is characterized by having distinctive fovea, the formal designation of the genus considered this feature to be of little importance. The assignment by Allen (1965) of *Cirratriradites avius* to this genus, was made on the presence of the reduced sculpture and apparently thin equatorial flange. As it may seem desirable to restrict the use of *Cirratriradites* to miospores with distinctive fovea, it may in the future be necessary to refer this, and other species of similar organization, to a new genus within the densospore complex. The intexine is only seen in overmacerated specimens. *Hymenozonotriletes punctomonogrammos* Arkhangelskaya (in Filimonova and Arkhangelskaya 1963), from the Mosolovian of the Central Devonian Field is clearly similar.

Cirratriradites sp. A

Plate 31, figs. 4, 7

Description. Miospores trilete; camerate; amb triangular. Suturae indistinct. Exine two-layered, intexine thin and closely appressed to the exoexine. Exoexine infrapunctate, distally sculptured with muri (2–6 μm high) fused into a cristoreticulate pattern, more dense in central area. Cingulum with an apparent thin margin, but possessing a thicker inner zone.

Dimensions (two specimens). Maximum equatorial diameter 125 and 135 μm .

Lithostratigraphic range. Ward Hill Sandstone (1b); sample Fair 66 only.

Remarks. Differs from *Cirratriradites avius* in having a dense distal sculpture of muri. *Hymenozonotriletes monogrammos* Arkhangelskaya (1963) recorded from the Vorobyevskian, Starskoolian, Chernoyarian, and Mosolovian beds (Eifelian to Givetian) of the Russian Platform, Volga-Urals, and Karatau (Filimonova and Arkhangelskaya 1963, Arkhangelskaya 1974, Raskatova 1969, Chibrikova 1977) is very similar, having a distal network of muri and may prove to be synonymous.

Infraturma *PATINATI* Butterworth and Williams emend. Smith and Butterworth 1967

Genus *CHELINOSPORA* Allen 1965

Type species. *Chelinospora concinna* Allen 1965

Chelinospora concinna Allen 1965

Plate 30, fig. 9

Dimensions (eight specimens). Maximum equatorial diameter 36–65 μm (mean 45 μm).

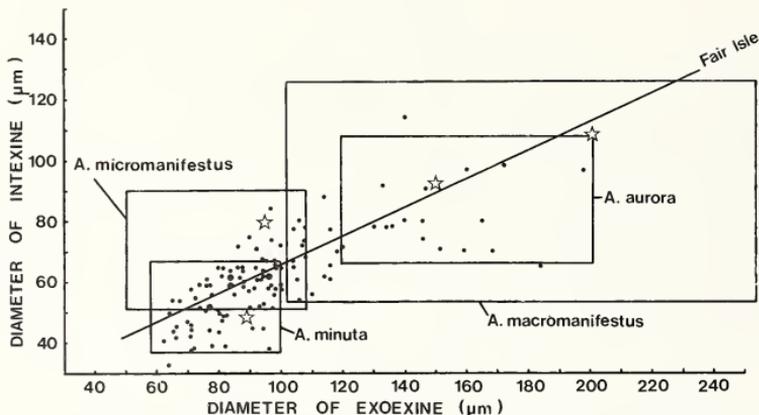
Lithostratigraphic range. Observatory Group (3c); samples Fair 36 ad 37.

Infraturma *MONOPSEUDOSACCITI* Smith and Butterworth 1967

Genus *AURORASPORA* Hoffmeister, Staplin, and Malloy 1955

Type species. *Auroraspora solisortus* Hoffmeister, Staplin, and Malloy 1955.

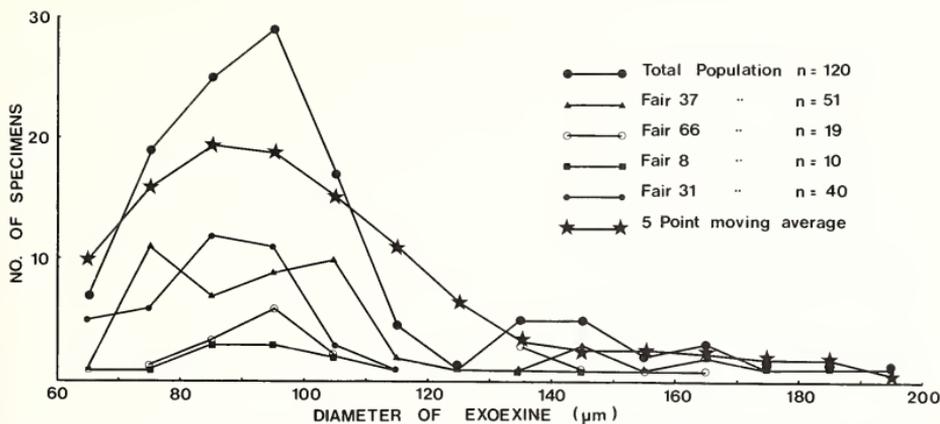
Population variation in Auroraspora. Four species of *Auroraspora* have been described from the Middle Devonian of the Orcadian Basin, separated on features such as size, shape, and the relative dimensions of the intexine and exoexine layers. The exoexine and intexine diameters for the type-species populations of *Auroraspora micromanifestus* Richardson 1960, *A. macromanifestus* Richardson 1960, *A. minuta* Richardson 1965, and *A. aurora* Richardson 1960 (with holotype positions



TEXT-FIG. 3. Graphical plot of exoexine and intexine diameters for *Auroraspora* spp. from Fair Isle. The stars mark the holotype positions of species recorded by Richardson 1960, 1965. The regression line is for all *Auroraspora* from Fair Isle.

marked), are plotted in text-fig. 3, and as can be readily seen, the degree of separation is not sufficient to delimit the species purely by this method. The differences could be related to ontogenetic variation in a sporangium, with a changing ratio of exoexine to intexine diameters as the miospores increase in size. Other characters cited as important in delimiting species, such as shape and eccentricity, are probably not mutually exclusive, and can be related to the presence or absence of labra and their degree of development, which are again themselves a poor classificatory character. Prominent labra on a small miospore will give a triangular shape, whereas small labra on a large miospore often results in a circular shape which, when compressed, can increase the eccentricity of the two exine layers. A histogram of the exoexine size distribution (text-fig. 4) also provides valuable information, as a skewed population is seen, which is reminiscent of the pattern produced during the development of heterospory (see Chaloner 1967). Size distribution is also given for individual collection samples, and this shows the effects of some sedimentary sorting. However, bimodal populations are apparent in three of the four assemblages, as well as in the five point moving average line.

It is believed that the species differences are ontogenetic and perhaps reinforced by an incipient heterospory, but more information is needed on miospore populations found both dispersed and *in situ* from single sporangia, before combining certain miospore species. A note of caution is also necessary in case the lumping of species causes the loss of potentially valuable morphological data which may be of stratigraphic value as populations of *Auroraspora* succeed each other, with slightly different degrees of size distribution (viz. the possible biostratigraphic value of changing over-all diameters in *Retusotriletes* from the Russian Platform as shown by Naumova 1953, p. 18, text-fig. 6). A sensible course in handling species such as those of *Auroraspora*, is to give precise descriptions and details of dimensions as illustrated in text-figs. 3 and 4.



TEXT-FIG. 4. Frequency distribution plot for *Auroraspora*. Note skewed distribution present in different samples and remains on five point moving average lines.

Auroraspora macromanifestus (Hacquebard) Richardson 1960

Plate 31, fig. 10

Dimensions (seventeen specimens). Maximum exoexine diameters 120–200 μm (mean 153 μm), maximum intexine diameters 60–115 μm (mean 83 μm). See text-fig. 3 for size distributions and ratios of central-body diameter to whole-body diameter (mean 1:4).

Lithostratigraphic range. Ward Hill Group to Bu Ness Group (1b to 4a); samples Fair 8, 31, 37, and 66.

Remarks. Differs from specimens described by Richardson (1960) from the Middle Devonian of the Cromarty area (Scotland) only in size range.

Auroraspora micromanifestus (Hacquebard) Richardson 1960

Plate 31, fig. 11

Dimensions (one hundred and two specimens). Maximum exoexine diameter 65–120 μm (mean 89 μm), maximum intexine diameter 35–85 μm (mean 56 μm). See text-fig. 3 for size distribution and ratio of central-body diameter to whole-body diameter (mean 1:2).

Lithostratigraphic range. Ward Hill to Bu Ness Group (1b to 4a); samples Fair 8, 24, 28, 31, 33, 36, 37, 64, 66, and 67.

Genus GRANDISPORA (Hoffmeister, Staplin, and Malloy) Neves and Owens 1966 *sensu* Playford 1971

Type species. *Grandispora spinosa* Hoffmeister, Staplin, and Malloy 1955.

Grandispora ?naumovii (Kedo) McGregor 1973

Plate 32, fig. 5

Description. Miospore trilete, camerate, amb ovate. Suturae accompanied by wavy labra up to 6.5 μm in height and individually 2 μm wide. Exine two-layered, intexine laevigate, indistinct, exoexine 1 μm thick, shagrenate, distally sculptured with sparse, gently tapering spines. There are eleven spines around the equatorial periphery which measure up to 20 μm in length.

Dimensions (one specimen). Exoexine diameter $130 \times 106 \mu\text{m}$, intexine diameter $80 \times 62 \mu\text{m}$.

Lithostratigraphic range. Observatory Group (2c); sample Fair 37.

Comparisons. This miospore closely resembles *Grandispora ?naumovii* described by McGregor and Camfield (1976) from the Middle Devonian of the Hudson Bay area (Canada) and by McGregor (1973) from the Middle Devonian of Gaspé (Canada).

Grandispora velata (Eisenack) Playford 1971

Plate 32, fig. 2

Synonymy, see Owens 1971, p. 46

Dimensions (nine specimens). Maximum exoexine diameter $94\text{--}123 \mu\text{m}$ (mean $111 \mu\text{m}$), maximum intexine diameter $57\text{--}80 \mu\text{m}$ (mean $70 \mu\text{m}$).

Lithostratigraphic range. Ward Hill to Bu Ness Groups (1b to 4a); samples Fair 24, 36, 37, and 66.

Comparisons. The Fair Isle population differs from the type population in having a slightly smaller sculptural size range.

Grandispora protea (Naumova) Moreau-Benoit 1980

Plate 32, figs. 3, 4

Dimensions (ten specimens). Maximum exoexine diameter $84\text{--}184 \mu\text{m}$ (mean $136 \mu\text{m}$), maximum intexine diameter $39\text{--}97 \mu\text{m}$ (mean $70 \mu\text{m}$).

Lithostratigraphic range. Ward Hill to Bu Ness Groups (1b to 4a); samples Fair 24, 36, 37, and 66.

Genus VELAMISPORITES Bharadwaj and Venkatachala 1962

Type species. *Velamispories rugosus* Bharadwaj and Venkatachala 1962.

Remarks. Evans (1970) has interpreted the organization of the genus *Perotrilites* Erdtman ex Couper 1953 as being zonate and not perinate as previously supposed (see Playford 1971). Prior to this, Palaeozoic perinate miospores were placed in *Perotrilites*, but these are now removed to *Velamispories*, which was originally thought to be a junior synonym, but now forms a satisfactory genus for miospores with such an organization.

Velamispories sp. A

Plate 32, fig. 1

Description. Miospores trilete, camerate, amb triangular to rounded. Suturae accompanied by labra commonly $1.5\text{--}2.5 \mu\text{m}$ high (maximum $4 \mu\text{m}$) which continue as folds on to the perine layer. Exine three-layered; intexine

EXPLANATION OF PLATE 32

All figures $\times 400$ unless otherwise stated.

Fig. 1. *Velamispories* sp. A. $\times 1000$. Fair 66.2, 19.5, 102.2

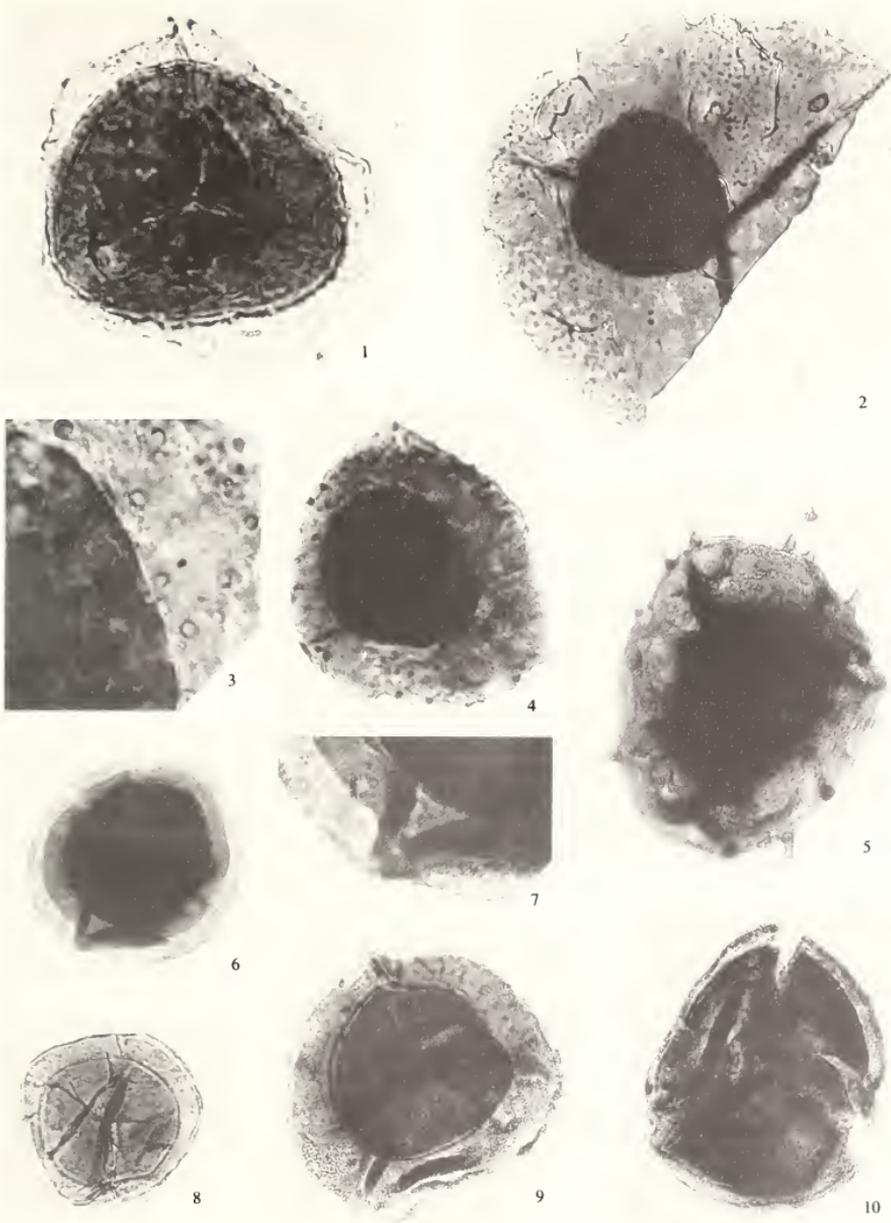
Fig. 2. *Grandispora velata* (Eisenack) Playford 1971. Fair 37.64, 14.3, 100.7

Figs. 3, 4. *Grandispora protea* (Naumova) Moreau-Benoit 1980. 3, detail of distal sculpture $\times 1000$. 4, $\times 400$. Fair 37.71, 49.5, 108.1

Fig. 5. *Grandispora ?naumovii* (Kedo) McGregor 1973. Fair 37.80, 12.5, 93.2

Figs. 6, 7. *Rhabdosporites* sp. A. 6, $\times 400$. 7, $\times 1000$: detail showing three wall layers. Fair 37.71, 44.4, 95.1

Figs. 8-10. *Rhabdosporites langii* (Eisenack) comb. nov. 8, 'parvulus' type Fair 37.62, 19.4, 94.60. 9, 'langii' type Fair 37.80, 40.2, 105.5. 10, 'parvulus' type, compare with *Geminispora*. Fair 37.82, 40.2, 105.5



MARSHALL and ALLEN, Devonian miospores

laevigate, often indistinct, closely appressed to the exoexine. Exoexine commonly infrapunctate, 1.5–4 μm thick, with an interradial maximum. Perine wrinkled (especially on the contact areas, where it forms muroid folds) 0.25–0.5 μm thick, sparsely sculptured with parallel sided, flat-topped rods (up to 1 μm high) mixed with grana and coni (up to 0.5 μm high).

Dimensions (seven specimens). Maximum perine diameter 61–76 μm (mean 66 μm), maximum exoexine diameter 46–67 μm (mean 55 μm). Separation between these two layers 5–17 μm (mean 11 μm).

Lithostratigraphic range. Ward Hill to Bu Ness Groups (1b to 4a); samples 31, 37, and 66.

Remarks. Many of the described species of Devonian *Perotrilites* resemble the Fair Isle material. However, all differ in size and minor sculptural details. *Perotrilites pannosus* Allen 1965 has a thick perine with more folds, and coni with bifurcating tips. *P. conatus* Richardson 1965 has a denser sculpture of cones and a different ratio of wall-layer dimensions. *P. aculeatus* Owens 1971 has a thinner perine and a sculpture of cones. *P. selectus* (Arkhangelskaya) McGregor and Camfield 1976 is larger and has cones.

GENUS RHABDOSPORITES Richardson emend.

Type species. *Rhabdosporites langii* (Eisenack) Richardson 1960.

Emended diagnosis. Miospores radial, trilete, amb circular to triangular. Camerate, with separate exoexine and intexine attached at the proximal pole. Exoexine with or without limbus, sculptured with low rods, coni, and grana. Intexine laevigate.

Discussion. In 1960 the genus *Rhabdosporites* was erected to accommodate certain distinctive pseudosaccate miospores previously described by Eisenack (1944), Lang (1925), and others. Its main distinguishing features according to Richardson (1960) were the proximally attached non-limbate bladder and the evenly distributed over-all sculpture of closely packed rods with parallel sides and flat tops. Subsequently, the genus, and particularly the type species *Rhabdosporites langii*, has proved to be one of the most common Devonian miospores, showing a wide stratigraphic range and geographic distribution. Later workers, however, have not kept to the original diagnosis, placing in *Rhabdosporites* limbate miospores as well as those with sculptural elements containing grana and coni. There have been some good arguments for this; Owens (1971) pointed out a discernible limbus in the illustration of the type species, and Lele and Streele (1969, p. 102) commented on some well-preserved specimens from the same horizons as Richardson's material, with coni often as a dominant element, as well as rods with truncated tips. It would seem sensible therefore to widen the scope of the genus to include similar spores, with both a limbus and a more variable ornament of reduced size. Camerate spores with coarser sculpture are included in other genera (e.g. *Grandispora*). In widening the generic concept of *Rhabdosporites*, we are aware of the close similarity between small specimens of *Rhabdosporites* and *Geminispora* (Balme) Owens 1971, which has been mentioned by previous authors (e.g. Lele and Streele 1969, p. 103). *Geminispora* is typified by a thin-walled intexine either closely appressed to, or showing a variable degree of separation from, a sculptured exoexine with a thickened distal surface. This organization is difficult to distinguish (without recourse to microtome sections) from a limbate pseudosaccate miospore (see Pl. 32, fig. 8) with a high intexine–exoexine cavity ratio as seen in small *Rhabdosporites*. Various indirect criteria were used in attempts to distinguish the forms, based on the presence of the thickened distal surface which is a characteristic of the *Geminispora* group. It might be expected that this would hold the miospore rigid, with the intexine and proximal exoexine positioned in the shaped distal exoexine 'cup', thus limiting the eccentricity between the two bodies when compressed. The thickened distal exoexine would also deflect and restrict exoexine folding, to give different folding characteristics on the proximal and distal surfaces. Further evidence for the similarity (or inability to easily distinguish) between *Rhabdosporites* and *Geminispora* comes from the study of *in situ* spores (see Allen 1980), where spores assignable to *Rhabdosporites* and *Geminispora* are recorded from closely related progymnosperms.

Rhabdosporites langii (Eisenack) comb. nov.

Plate 32, figs. 8-10

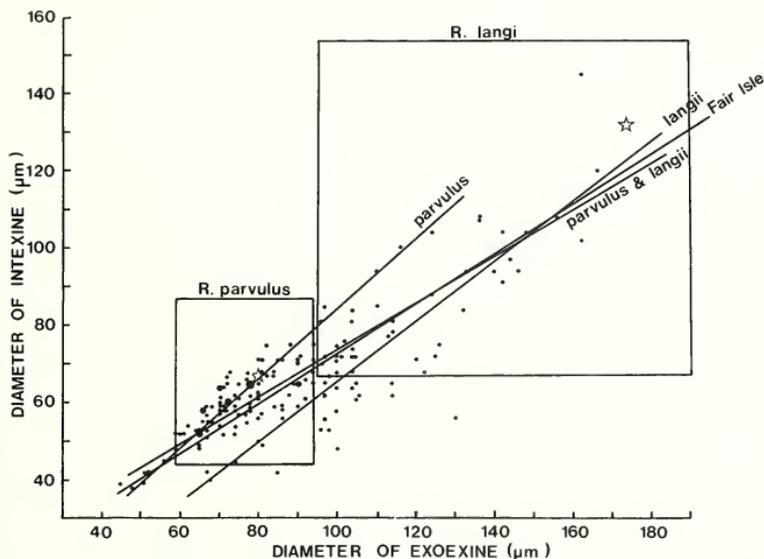
- 1925 Type B Lang, p. 256, pl. 1, figs. 3-6.
 1944 *Triletes langii* Eisenack, p. 112, pl. 12, fig. 4.
 1960 *Rhabdosporites langii* (Eisenack) Richardson, p. 54, pl. 14, figs. 8, 9.
 1963 *Rhabdosporites firmus* Guennel, p. 256, fig. 12.
 1965 *Rhabdosporites parvulus* Richardson, p. 588, pl. 93, figs. 5-7.
 1971 *Rhabdosporites micropaxillus* Owens, p. 49, pl. 15, figs. 3-7.
 1973 *Rhabdosporites* sp. Hamid, p. 202, pl. 10, no. 1.

For additional synonymies, see Moreau-Benoit, 1980, pp. 29 and 30.

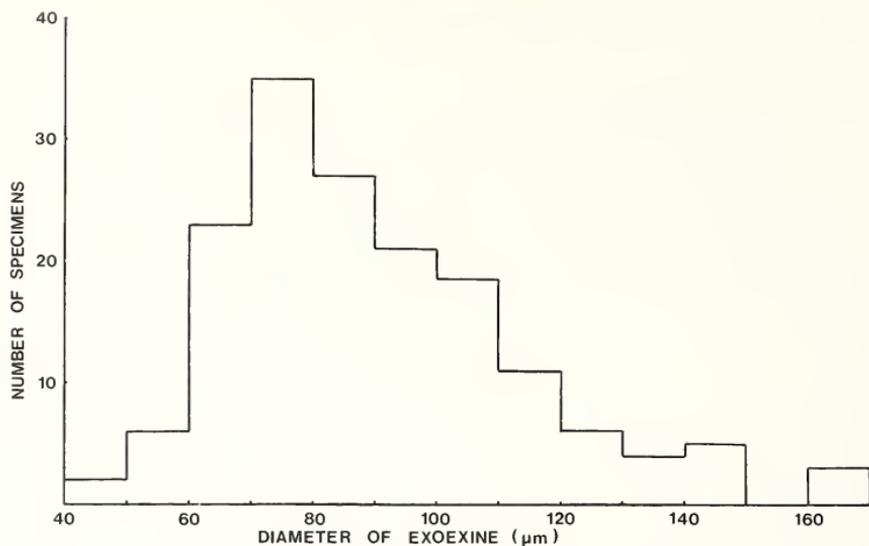
Dimensions (one hundred and sixty-five specimens). Maximum exoexine diameter 45-166 μm (mean 90 μm), maximum intexine diameter 39-146 μm (mean 65 μm).

Lithostratigraphic range. Ward Hill to Bu Ness Group (1b to 4a)—samples Fair 8, 24, 28, 31, 33, 36, 37, 64, 66, and 67.

Remarks. *Rhabdosporites parvulus* Richardson 1965 was associated with *R. langii* in all the samples studied, and attempts were made to discriminate between the two species as did Richardson (1965, p. 588), using a graphical plot of exoexine and intexine diameters. A graph of the data from Fair Isle (text-fig. 5) shows no obvious separation into two populations, but a gradual change in the ratio of



TEXT-FIG. 5. Size variation in *Rhabdosporites langii* from Fair Isle compared with published data from the Orcadian Basin. Reduced major axis lines are seen to be closely comparable between Fair Isle and a combined *R. langii* and *R. parvulus* population from the Orcadian Basin. Separate R.M.A. lines for *R. langii* Richardson 1960 and *R. parvulus* Richardson 1965 only apply to parts of the population which is clearly seen to be continuous. The boxes show the limits of the type-species population, and the stars show the holotype position. Larger points refer to two or three individuals.



TEXT-FIG. 6. Frequency plots for *Rhabdosporites* exoexine diameters.

the exoexine and intexine diameters as the spore size increases. Further, the data from Richardson's graph were replotted as a single population, and reduced major axis lines calculated for the combined data. It can be seen from this result that there is no obvious difference between regression lines for combined populations of *R. langii* and *R. parvulus* and similar lines calculated for the separate species as defined by Richardson. A regression line calculated for the Fair Isle population shows a strong similarity to the combined Richardson plot. A frequency distribution plot of the exoexine diameters (see text-fig. 6) gives a smooth population curve and no sign of bimodality, which might be expected if two distinct species were present. The stratigraphic range chart of Richardson (1965, opposite p. 590) shows a disjunct appearance for *R. parvulus* only in the Eday Group, whilst the text (p. 588) does indicate its appearance further down the sequence, such that it is coincident with *R. langii*. *Rhabdosporites* has also been identified as an *in situ* miospore in both *Tetraxylopteris schmidtii* (Beck) Bonamo and Banks 1967 and in *Rellimia thompsonii* Leclercq and Bonamo 1973 (in Leclercq and Bonamo 1971). These occurrences also provide further information on the similarity between *Rhabdosporites langii* and *R. parvulus*, as both of these descriptions also comment on the presence of miospores with a size range including both *R. langii* and *R. parvulus* in the same sporangium. These authors also consider that the differences described by Richardson are ontogenetic, and as miospores matured inside a sporangium, the exoexine expanded more rapidly than the intexine, showing an increasing ratio between the two wall diameters as well as increased sculpture size. It is suggested that the continua seen in the dispersed species can be attributed to this ontogenetic variation, and that with the size distribution data collected for these *in situ* miospores to confirm this similarity there is now no reason to consider *langii* and *parvulus* as separate species. If the enlarged concept of the genus to include limbate spores with sculptural elements of grana and coni as well as rods is accepted, then *R. micropaxillus* Owens 1971 is intermediate between *R. langii* and *R. parvulus* and can be regarded as synonymous; as are *R. firmus* Guenel 1963 and *Rhabdosporites* sp. Hamid 1973, which similarly differ only in the presence of grana and coni amongst the sculptural elements.

Rhabdosporites sp. A

Plate 32, figs. 6, 7

Description. Miospores trilete; amb circular; exine three-layered. Suturae length equal to inner body radius, accompanied by simple labra (each 1 μm wide). The two inner wall layers laevigate, homogeneous; the outer wall infrapunctate, sculptured with conical, rounded-tipped rods, and grana (0.25–1 μm high). The three walls are variable in thickness and carry folds which show them to be separated except on the proximal surface. Outer wall appears limbate.

Dimensions (three specimens). Maximum diameters: outer wall 90 μm , 101 μm , 96 μm ; middle wall 74 μm , 67 μm , 80 μm ; inner wall 58 μm , 43 μm , 61 μm . Optically discernible wall thicknesses: outer wall 2.0 μm , 2.5 μm , 0.5 μm ; middle wall 0.25 μm , 1.0 μm , 0.5 μm ; inner wall 2.0 μm , 1.5 μm , 2.0 μm .

Lithostratigraphic range. Observatory Group (2c); sample Fair 37.

Remarks. *Rhabdosporites* sp. A of Richardson 1965 is similar in having three layers, and differs only on size and minor sculptural features. ?*Calyptosporites* sp. A Mortimer and Chaloner 1972 appears to be conspecific, and these authors also suggest a possible further synonymy with a miospore figured by Ozolin'a (1960a, pl. 1, fig. 29) and identified as *Archaeozonotriletes micromanifestus* var. *minor* Naumova. Hemer and Nygreen (1967) illustrate a trivalved miospore as *Rhabdosporites* sp. but as no description was provided, further comparison is impossible. Massa and Moreau-Benoit (1976) record the presence of *Rhabdosporites* sp. A Richardson, from their palynozones 6 and 7, which are dated as late Givetian and early Frasnian.

Similar *in situ* miospores have been recovered by *Tetraxylopteris schmidtii* Bonamo and Banks 1967, where they occurred in subordinate numbers to specimens similar to *Rhabdosporites langii* and *R. parvulus*. Bonamo and Banks (1967) included a personal communication from Richardson, which expressed the opinion that the extra layer could have arisen by a splitting of one of the two wall layers of *Rhabdosporites*. The middle wall of the Fair Isle specimens appears to be a more definite layer than in similar miospores illustrated from *T. schmidtii*. A possible explanation for this difference is that the third layer may be a teratological feature, and a possible way of showing this, as opposed to the wall splitting hypothesis, is to sum the various thicknesses of the wall layers. It might be expected that any wall splitting would provide a total equal to the mean intexine plus exoexine value of a normal *Rhabdosporites*. Unfortunately the data are not available to show this, as no wall-thickness measurements are provided for the Cromarty populations of these spores. The presence of a limbate wall feature would also create difficulties and uncertainty in measurement.

INCERTAE SEDIS

Genus *HYSTRICOSPORITES* McGregor 1960

Type species. *Hystricosporites delectabilis* McGregor 1960.

Hystricosporites cf. *corystus* Richardson 1960

Plate 33, figs. 7–9

Description. Miospore trilete; amb circular to triangular, ovate in lateral compression. Suturae accompanied by prominent labra (19–36 μm high, 56–116 μm in length as seen in lateral compression). Exine two-layered, intexine laevigate, closely appressed to the exoexine. Exoexine with paired radial muri on the contact areas (length 20–28 μm , width 4–7 μm), proximo-equatorially and distally sculptured with 5–14 grapnel-tipped spines (20–52 μm long).

Dimensions. Maximum equatorial diameter 60–130 μm (mean 96 μm), eleven specimens measured. Maximum height (excluding labra) in lateral compression 65–122 μm , six specimens measured.

Lithostratigraphic range. Ward Hill to Bu Ness Groups (1b to 4d); samples Fair 8, 24, 31, 33, 36, 37, 64, 66, and 67.

Remarks. The Fair Isle population is very similar to *Hystricosporites corystus* Richardson 1962, differing only in gross size. Richardson's *Hystricosporites* cf. *corystus* should not be confused with the Fair Isle miospores.

The proximal radial muri and intexine are seen only in overmacerated specimens. Frequently only the bases of the spines are complete, but when intact the grapnel-tips are of the laterally extended form (see Owens 1971, p. 87). Difficulties were encountered in relating spores with intact spines to those showing proximal lip and intexine detail, because the high maceration levels needed to clear the miospores resulted in severe erosion of the grapnel-tips.

Genus ANCYROSPORA Richardson emend. Richardson 1962

Type species. *Ancyrospora grandispinosa* Richardson 1960.

Ancyrospora ancyrea (Eisenack) Richardson 1962

Plate 33, figs. 3, 10

Dimensions (seventeen specimens). Maximum equatorial diameter 81–165 μm (mean 120 μm).

Lithostratigraphic range. Ward Hill to Bu Ness Groups (1b to 4a), samples 8, 24, 28, 31, 33, 36, 37, 64, 66, and 67.

Remarks. Placed in *Ancyrospora ancyrea* and not *A. ancyrea* var. *ancyrea* Richardson 1962 because it does not show the wide flange development which characterizes the variety. It conforms to text-fig. 5 (p. 178) of Richardson (1962), and is morphologically average for the three described varieties.

The same maceration problems were encountered in studying this species as with *Hystricosporites* cf. *corystus*, in that it was rare to find completely cleared spores in which the grapnel-tipped spines were preserved.

Ancyrospora ancyrea cf. var. *brevispinosa* Richardson 1962

Plate 33, figs. 4–6

Description. Miospores trilete; amb triangular to subtriangular. Suturæ accompanied by labra (1 μm high). Exine two-layered, intexine laevigate, thin, closely appressed to the exoexine. Exoexine shagreenate, with a dark halo, or triangular darkening in the proximal polar area, contact areas often with sinuous folds. Proximo-equatorially and distally sculptured with grapnel-tipped spines (1–10 μm long), the tips 1–2 μm across have little discernible detail (Pl. 33, fig. 6). Flange development variable (0–12 μm wide) with some very narrow forms (Pl. 33, fig. 5) and others interradially.

Dimensions (one hundred and fifty specimens). Maximum equatorial diameter 39–95 μm (mean 65 μm).

Lithostratigraphic range. Ward Hill to Bu Ness Group (1b to 4a); samples 8, 24, 28, 31, 33, 36, 37, 64, 66, and 67.

EXPLANATION OF PLATE 33

All figures $\times 400$ unless otherwise stated.

Fig. 1. *Geminospira* sp. B. Fair 31.5, 6.3, 101.1

Fig. 2. *Geminospira* sp. A. Fair 31.5, 36.6, 101.7

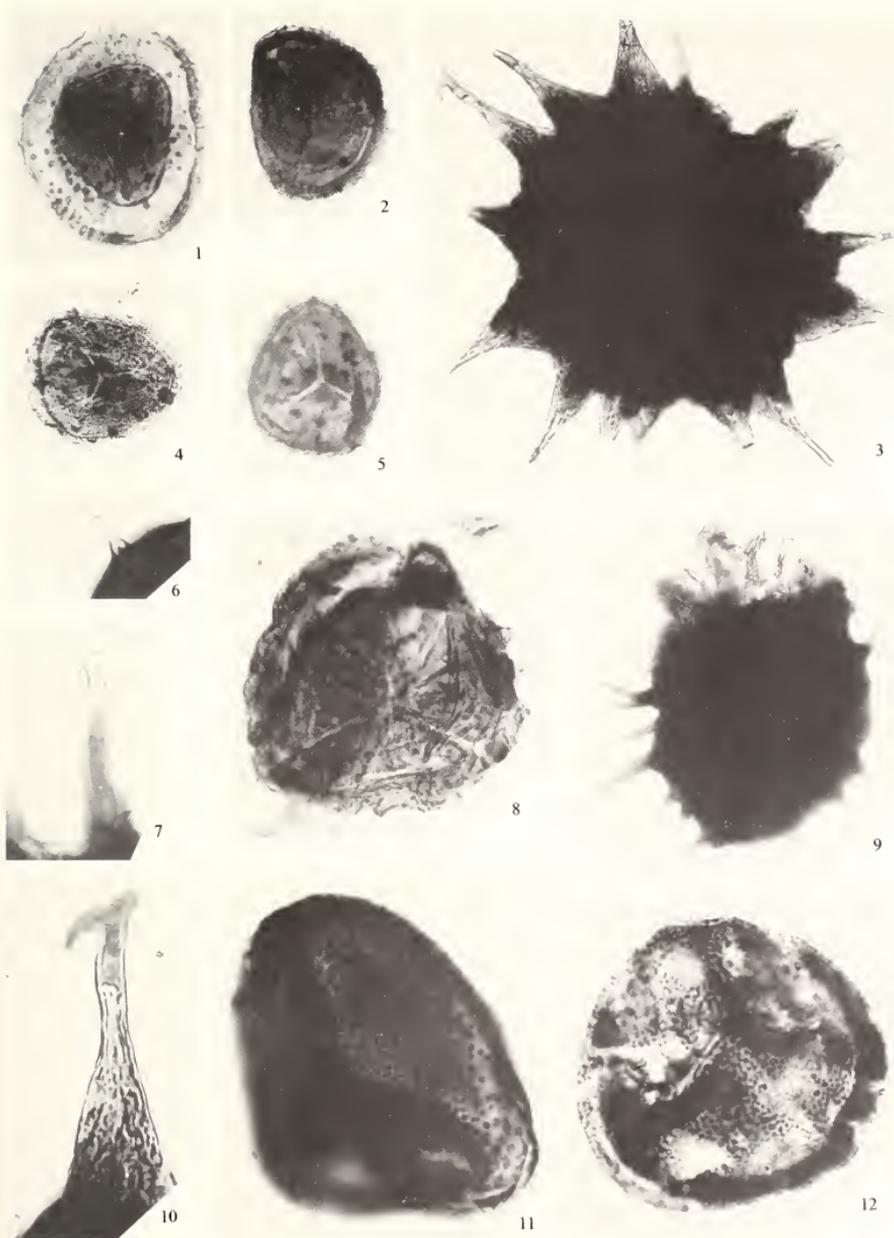
Figs. 3, 10. *Ancyrospora ancyrea* (Eisenack) Richardson 1962. 3, Fair 37.64, 29.3, 107.1. 10, detail of spine process, $\times 1000$.

Figs. 4–6. *Ancyrospora ancyrea* cf. var. *brevispinosa* Richardson 1962. 4, wide flange form. Fair 8.1, 11.4, 106.1. 5, narrow flange form. Fair 37.64, 14.4, 96.9. 6, detail of spine process from 5, $\times 1800$.

Figs. 7–9. *Hystricosporites* cf. *corystus* Richardson 1960. 7, detail of spine process from 9. 8, well oxidized specimen. Fair 67.30, 100.6, 33.4. 9, dark specimen, lateral compression. Fair 37.63, 9.1, 96.9.

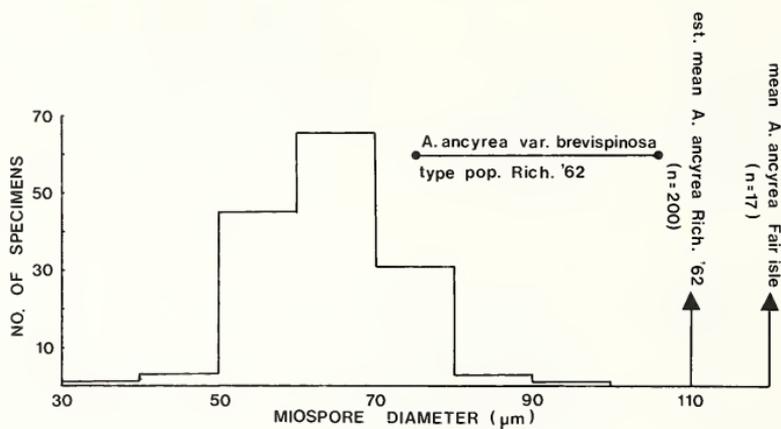
Fig. 11. *Geminospira tuberculata* (Kedo) Allen 1965. $\times 1000$. Fair 37.64, 22.4, 99.2

Fig. 12. *Geminospira svalbardiae* (Vigran) Allen 1965. $\times 1000$. Fair 28.20, 50.2, 114.3



MARSHALL and ALLEN, Devonian miospores

Remarks. This spore is closely similar to *Ancyrospora ancyrea* var. *brevispinosa* Richardson 1962 except in gross diameter, which seems to reflect a genuine difference, as opposed to modifications in the population based in sedimentary sorting processes. The evidence for this (see text-fig. 7) is that whilst the size frequency distributions for *Ancyrospora ancyrea* from both Fair Isle and the Orcadian Basin (see Richardson 1962, p. 185) clearly parallel each other, those for var. *brevispinosa* (this paper) are quite different. It is postulated on a simple model that any sorting process which could modify the size-frequency distributions of the variety *brevispinosa* and cf. *brevispinosa* to this extent, would also show a difference in the *Ancyrospora ancyrea* populations, which is not so.



TEXT-FIG. 7. Frequency plot for *Ancyrospora ancyrea* cf. var. *brevispinosa*. There is a difference in population size range compared with that of Richardson 1962, which is not reflected in *A. ancyrea*.

The much-reduced flange on the exoexine (see Pl. 33, fig. 5) produces some problems in using the genus *Ancyrospora*, which, as defined by Richardson (1962) in his emended diagnosis, has an extended equatorial flange of pseudoflange. The evidence from the Fair Isle sequence suggests that a continua exists from obviously flanged miospores to almost flangeless ones, and therefore in part outside the generic diagnosis. The presence of sinuous surface folds on the exoexine and the occasional appearance of a membranous top exine layer, suggests the possibility that a third layer is developed, similar to *A. fallacia* Urban (1970), and frequently lost on oxidation. Another point of interest is a possible relationship with *Perotrilites bifurcatus* Richardson 1962, which could be interpreted as an overmacrated *Ancyrospora* with the spalling off of a third outer exine layer normally closely appressed to the exoexine.

GEMINOSPORA (Balme) Owens 1971

Type species. *Geminospira lemurata* Balme 1962

Discussion. As well as the difficulties discussed earlier in separating *Rhabdosporites* from *Geminospira*, there is an apparent morphological transition series between *Geminospira* and *Grandispora* in our material. The problem has previously been described in other assemblages by Neves and Owens (1966) and Playford (1971). Where one draws the dividing line between truly camerate miospores such as *Grandispora* which show a clear separation of intexine and exoexine (sensu Playford 1976 and not McGregor 1973), and *Geminospira* which has both widely separated and closely appressed

wall layers in the same population, is at present arbitrary. A further difficulty is that increased separation of wall layers may result from the oxidative processes used in clearing the highly carbonized Fair Isle miospore assemblages.

Geminospora tuberculata (Kedo) Allen 1965

Plate 33, fig. 11

Dimensions (eleven specimens). Maximum equatorial diameter 42–67 μm (mean 56 μm).

Lithostratigraphic range. Ward Hill to Bu Ness Groups (1b to 4a); samples Fair 24, 28, 31, 33, 36, 37, 66, and 67.

Remarks. The Fair Isle material differs only from that described by Allen (1965) in having slightly smaller sculptural elements and greater variation of haplotypic features. The emendation of *Archaeozonotriletes tuberculatus* Kedo by Allen (1965) to accommodate the Spitsbergen population of *Geminospora* is open to some modification as more Soviet miospores of closely related species have now been described, into which parts of the population could be accommodated. We believe that there are problems of synonymy between *Geminospora* and *Archaeozonotriletes* (sensu Naumova) and a thorough separate revision is preferable to minor amendments made here.

Geminospora svalbardiae (Vigran) Allen 1965

Plate 33, fig. 12

Dimensions (nine specimens). Maximum equatorial diameter 47–72 μm (mean 58 μm).

Lithostratigraphic range. Ward Hill to Bu Ness Groups (1b to 4a); samples Fair 8, 31, 33, 36, 37, and 66.

Remarks. The population described by Allen (1965) is very similar to the Fair Isle material, differing only in being of larger over-all size and having a more reduced sculpture. Possible synonymies include *Geminospora maculata* Taugourdeau-Lantz 1967 and *Geminospora plicata* Clayton and Graham 1974 (nomen illeg.—junior homonym for *G. plicata* Owens 1971). Both these forms, as described, are similar, and differ only in minor features of size and type of sculpture.

Geminospora sp. A

Plate 33, fig. 2

Description. Miospore trilete; amb circular to triangular. Suturæ straight and extending to the intexine margin. Exine two-layered; intexine laevigate, thin with conspicuous folds, and of variable separation from the exoexine. Exoexine 5 μm thick, with a sculpture of coni (2 μm high), some of which are arcuate or biform, typical height 2 μm .

Dimensions (one specimen). Maximum equatorial diameter 70 μm .

Lithostratigraphic range. Observatory Group (2c); sample Fair 37.

Remarks. Similar miospores have been described from the Soviet Union as *Archaeozonotriletes visendus* Chibrikova, *A. visendus* var. *echinatus* Chibrikova, *A. egregius* Naumova, *A. tuberculatus* var. *aculeatus* Raskatova, *A. acutus* Raskatova, *A. pensus* Kedo, *A. lasius* var. *minor* Naumova. Unfortunately its single occurrence in the Fair Isle sequence limits its value at present.

Geminospora sp. B

Plate 33, fig. 1

Description. Miospores trilete; amb roughly triangular. Suturæ simple or accompanied by thin labra commonly 1–2 μm high (maximum 5 μm). Exine two-layered with exoexine and intexine layers separate, attached only at the proximal pole. Intexine laevigate, thin, showing a variation in degree of separation. Exoexine 2.5–14 μm thick (mean 6.5 μm) with individuals showing an interradial maximum (up to 2.5 μm thicker). Exoexine sculpture

(except for contact areas) with cones and fine tapering spines 1–5 μm long (mean 2.5 μm), denser and of greater length distally than equatorially or proximo-equatorially.

Dimensions (twenty-seven specimens). Maximum exoexine diameter 65–140 μm (mean 89 μm).

Lithostratigraphic range. Ward Hill and Observatory Groups (1b to 2c); samples. Fair 37 and 66.

Remarks. *Archaeozonotrites comptus* Naumova (1953), *A. comptus* var. *expletivus* Chibrikova (1959) (see also Raskatova 1969 and Chibrikova 1962, 1977), *A. tuberculatus* Kedo var. *minor* Kedo (1976), and *A. tuberculatus* Kedo var. *triangulatus* Kedo 1976 are all miospores of a similar construction, sculpture, and size. However, their descriptions are not detailed enough to confidently place *Geminospora* sp. B into any one of these species.

SEQUENCE AND STRATIGRAPHIC SIGNIFICANCE OF THE MIOSPORE ASSEMBLAGES

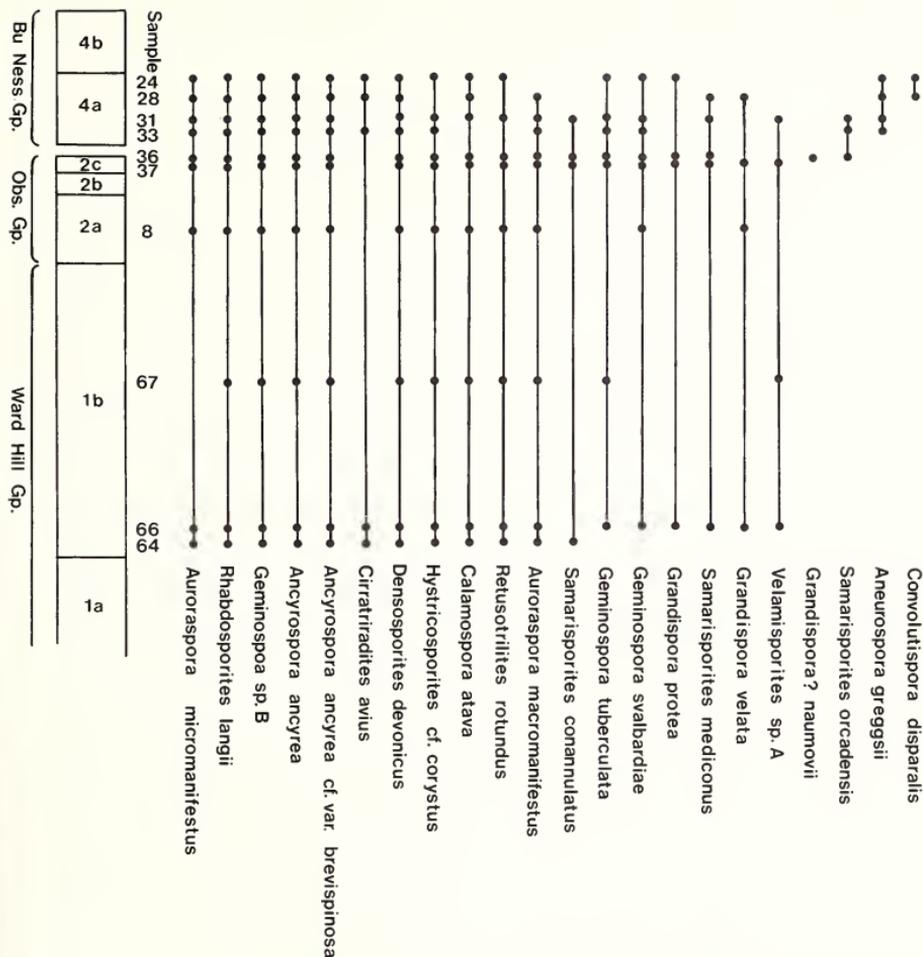
The number of miospore-bearing horizons has proved to be small, but fortunately of wide distribution. This is shown for selected miospore taxa in text-fig. 8. There is no major palynostratigraphic change in the succession until the Bu Ness Group, which is characterized by the incoming of *Aneurospora greggsii* and *Convolutispora disparalis*.

The general problems of Devonian palynostratigraphy have been discussed at length by several authors (Owens and Richardson 1972; Richardson 1974; and McGregor 1979a) so will only be briefly alluded to in this stratigraphical synthesis. The total stratigraphical ranges for some of the taxa from Fair Isle are plotted in text-fig. 9 and show long ranging distributions. This type of compilation suffers from the lack of miospore assemblages securely dated by independent means (notably Ammonoids, Conodonts), which can be compared accurately with the type sections of the traditional stages. The data suggests a Givetian age for the Fair Isle assemblages but does not place reliance on the restricted ranges of several poorly known species. A more precise correlation is possible by drawing comparisons with selected areas containing well-dated assemblages.

Comparisons with European Assemblages (excluding the Soviet Union but including Spitsbergen)

The spore sequences described by Richardson (1965) for the Orcadian Basin are now geographically the closest described Devonian palynofloras to Fair Isle. The abundance in Fair Isle of *Ancyrospora ancyrea* cf. var. *brevispinosa* with the first appearance of *Grandispora ?naumovii* suggest possible equivalence with the Eday Beds. An interesting comparison, and possibly significant, is the very rare occurrences of *Emphanisporites* spp. in both Fair Isle and the Orcadian Basin, which are not thought to be the result of reworking (Clayton *et al.* 1977). A major difference between the Fair Isle beds and the Eday Group on Orkney is the complete absence of *Geminospora* spp. in the latter, compared with its relative abundance and diversity in Fair Isle. It could be argued that this is of stratigraphic importance, except that *Geminospora* spp. is known from independently dated Givetian beds from over a wide area including Illinois (Sanders 1968), Spitsbergen (Allen 1965), and southern England (Mortimer and Chaloner 1972). It has been suggested (Richardson 1967) that the control is ecological, and this will be discussed later.

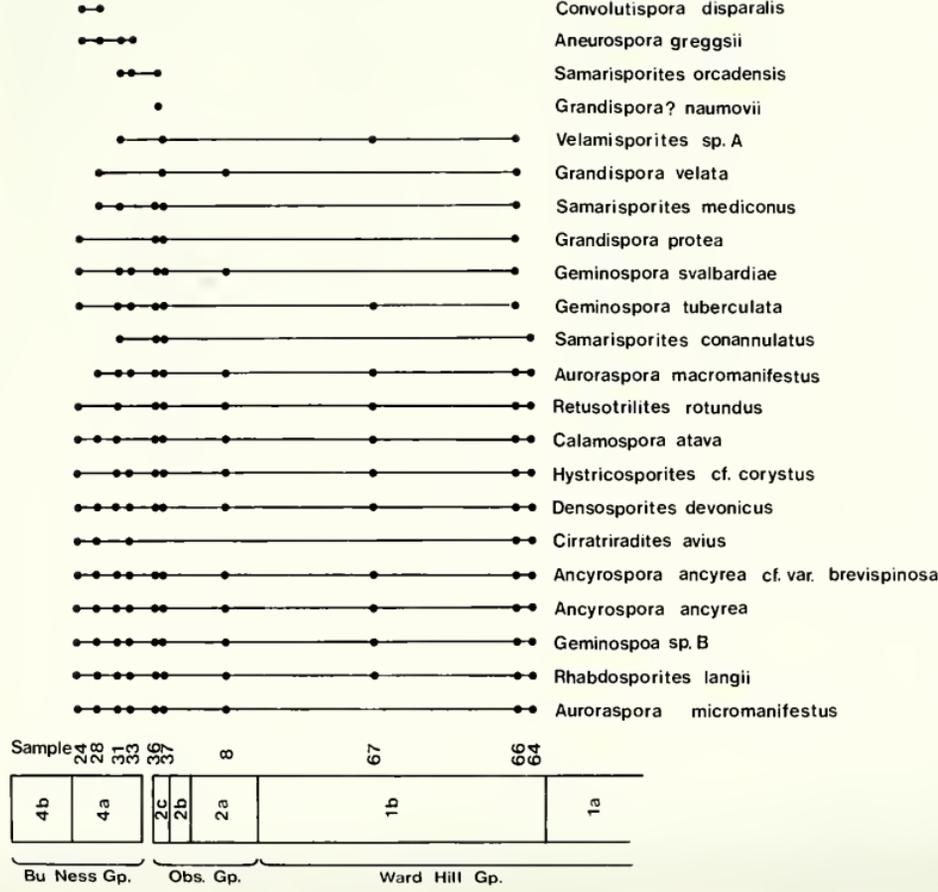
The spore assemblages described from borehole material of southern England by Mortimer and Chaloner (1972) compare quite closely, but add little to the specific age assignment apart from confirming it as Givetian. Detailed comparisons of the Fair Isle spore assemblages can also be made with the sequences described by Streeel and associates (reviewed in Streeel 1972) from Belgium and northern France. Streeel in a discussion of marker spores for the Givetian–Frasnian boundary considers the first appearances of *Aneurospora greggsii*, *Ancyrospora langii*, and *Samarisporites hesperus* to be of major significance. The occurrence of *Aneurospora greggsii* in the Bu Ness Group does suggest that this higher part of the Fair Isle sequence is late Givetian in age and close to the Givetian–Frasnian boundary. Streeel (1972) also gave the range of *Grandispora velata* and *Rhabdosporites langii* (closely comparable with the Fair Isle form) from the Tournai borehole as



TEXT-FIG. 8. Stratigraphical distribution of selected miospores in Fair Isle.

overlapping the range of *Aneurospora greggsii*, but the information was not sufficient to suggest that this was of any widespread stratigraphic value. Loboziak and Streel (1980), in a study of Givetian and Frasnian rocks from Boulonnais (France), considered several species to be of importance in delimiting beds of late Givetian age, including *Chelinospora concinna*, *Ancyrospora ancyrea* var. *brevispinosa*, and *Convolutispora disparalis*, all found in the Fair Isle section.

In Spitsbergen, Allen (1967) described a zonal scheme of three assemblages for the Devonian rocks. The Fair Isle sequence has many similarities to the *triangulatus* assemblage with *Geminospora tuberculata*, *Cirratiradites avius*, *Convolutispora disparalis*, *Densosporites devonicus*, *Chelinospora concinna*, and *Grandispora protea* in common. The *triangulatus* assemblage was assigned to the



TEXT-FIG. 8. Stratigraphical distribution of selected miospores in Fair Isle.

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STAGE \ TAXA																									
		Acinosporites lindlarensis	Ancyrospora ancyrea	Aneurospora greggsii	Auroraspora macromanifestus	A. micromanifestus	Calamospora atava	Chelinospora concinna	Cirratiradites avius	Convolutispora disparalis	Densosporites devonicus	Geminospora svalbardiae	G. tuberculata	Grandispora ?naumovii	G. protea	G. velata	Hystricosporites corystus*	Rhabdosporites sp.A	R. langii	Retusotrilites rotundus	Samarisporites conannulatus	S. mediconus	S. orcadensis		
Famenian			•									•													
Frasnian				•							•														
Givetian		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Eifelian		•	•		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Emsian		•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Siegemian																•					•				
Gedinnian																									

TEXT-FIG. 9. Stratigraphical distribution of selected taxa which occur on Fair Isle. * Refers to comparison record.

Givetian by Allen (1967) although the lower part is without *Densosporites devonicus* and is considered to be of possible Eifelian age (McGregor and Camfield 1976).

A detailed study has been made by Beju (1972) on rocks of Devonian age from the Moesian platform of Romania. The Eifelian subzone (D2a) has the long-ranging *Grandispora protea* and *Calamospora atava* in common with Fair Isle. The Givetian subzone (D2b) is more similar, with *Ancyrospora ancyrea*, *Rhabdosporites langii*, *Grandispora velata*, *Auroraspora macromanifestus*, and *Densosporites devonicus* in common. These last three are considered by Beju to be specifically characteristic of this subzone. The Frasnian zone (D3) contains *Geminospora svalbardiae*, *G. tuberculata*, *Rhabdosporites parvulus*, and *Auroraspora micromanifestus*.

Comparisons with North American Assemblages

The Frasnian Ghost River spore assemblage described from Alberta by McGregor (1964) compares with the Bu Ness Group of the Fair Isle sequence only in the presence of *Aneurospora greggsii*. McGregor (in McGregor and Uyeno 1972) described a sequence of spore assemblages from the Canadian Arctic Archipelago, and of these the closest to the Fair Isle material is assemblage D of late Givetian age, characterized by the appearance of *Grandispora protea* and *Chelinospora concinna*. The disappearance of *Densosporites devonicus* is not held to be of major significance as its replacement by *D. orcadensis* in the Orcadian sequence may be anomalous in view of the apparent synonymy which exists between the two species (see McGregor and Camfield 1976; McGregor 1979a and this paper). Devonian spores described by Owens (1971) from Middle and Upper Devonian rocks of the Canadian Arctic Archipelago, suggest that broad similarities can be drawn, but his work is largely based on new species from a few horizons, and is of limited value for detailed comparisons.

'SPORE TAXA	STAGE																						
	<i>Acinosporites lindlarensis</i>	<i>Ancyrospora ancyrea</i>	<i>Aneurospora greggsii</i>	<i>Auroraspora macromanifestus</i>	<i>A. micromanifestus</i>	<i>Calamospora atava</i>	<i>Chelinospora concinna</i>	<i>Cirratiradites avus</i>	<i>Convolutispora disparalis</i>	<i>Densosporites devonicus</i>	<i>Geminospora svalbardiae</i>	<i>G. tuberculata</i>	<i>Grandispora ? naumovii</i>	<i>G. protea</i>	<i>G. velata</i>	<i>Hystricosporites corystus*</i>	<i>Rhabdosporites sp.A</i>	<i>R. langii</i>	<i>Retusotriolites rotundus</i>	<i>Samarisporites conannulatus</i>	<i>S. mediconus</i>	<i>S. orcadensis</i>	
Famennian		•	•			•					•							•	•				
Frasnian		•	•		•	•	•			•	•	•		•	•	•	•	•	•				
Givetian	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•	•
Eifelian	•	•		•	•	•	•	•		•	•		•	•	•	•			•	•	•	•	•
Emsian	•	•	•	•		•		•			•			•	•			•	•		•		
Siegnian															•				•				
Gedinnian																				•			

TEXT-FIG. 9. Stratigraphical distribution of selected taxa which occur on Fair Isle. * Refers to comparison record.

Givetian by Allen (1967) although the lower part is without *Densosporites devonicus* and is considered to be of possible Eifelian age (McGregor and Camfield 1976).

A detailed study has been made by Beju (1972) on rocks of Devonian age from the Moesian platform of Romania. The Eifelian subzone (D2a) has the long-ranging *Grandispora protea* and *Calamospora atava* in common with Fair Isle. The Givetian subzone (D2b) is more similar, with *Ancyrospora ancyrea*, *Rhabdosporites langii*, *Grandispora velata*, *Auroraspora macromanifestus*, and *Densosporites devonicus* in common. These last three are considered by Beju to be specifically characteristic of this subzone. The Frasnian zone (D3) contains *Geminospora svalbardiae*, *G. tuberculata*, *Rhabdosporites parvulus*, and *Auroraspora micromanifestus*.

Comparisons with North American Assemblages

The Frasnian Ghost River spore assemblage described from Alberta by McGregor (1964) compares with the Bu Ness Group of the Fair Isle sequence only in the presence of *Aneurospora greggsii*. McGregor (in McGregor and Uyeno 1972) described a sequence of spore assemblages from the Canadian Arctic Archipelago, and of these the closest to the Fair Isle material is assemblage D of late Givetian age, characterized by the appearance of *Grandispora protea* and *Chelinospora concinna*. The disappearance of *Densosporites devonicus* is not held to be of major significance as its replacement by *D. orcadensis* in the Orcadian sequence may be anomalous in view of the apparent synonymy which exists between the two species (see McGregor and Camfield 1976; McGregor 1979a and this paper).

Devonian spores described by Owens (1971) from Middle and Upper Devonian rocks of the Canadian Arctic Archipelago, suggest that broad similarities can be drawn, but his work is largely based on new species from a few horizons, and is of limited value for detailed comparisons.

Sanders (1968) described the miospores from an acritarch-dominated assemblage of Givetian age, with *Rhabdosporites langii* (and *R. parvulus*), *Geminospora tuberculata*, and examples of *Ancyrospora* spp. and *Velamispores* spp. (*Perotrilites*).

Comparisons with North African and the Middle-East Assemblages

Massa and Moreau-Benoit (1976) described a series of miospore zones covering the Devonian strata of western Libya, and limited comparisons can be drawn with the Fair Isle succession. Palynozones 4 and 5 are the most similar, having *Auroraspora micromanifestus*, *Emphanisporites rotatus*, *Rhabdosporites parvulus* (*R. langii*), *Grandispora velata*, *Geminospora svalbardiae*, and *Samarisporites mediconus* in common, and these are dated as Couvianian and lower Givetian respectively.

Comparisons with miospore assemblages from the Russian Platform

General comparisons. Table 1 lists some miospore taxa from the Russian Platform together with their stratigraphical ranges, which are considered to be broadly comparable with taxa from Fair Isle. Comparability is variable, ranging from likely direct equivalence to part synonymy or closely similar. Some species, for example *Hymenozonotriletes protea*, can be referred to several western species.

In the compilation of Table 1 it was hoped to keep the stratigraphic information in the form of the local units used over the Russian Platform, but correlation difficulties made it impossible to construct a single table for the data, so that a more generalized scheme was necessarily produced. The placing of the Eifelian-Givetian and the Givetian-Frasnian boundaries is open to question, with some amendments having been made in certain areas. *Hymenozonotriletes punctomonogrammos* and *H. monogrammos* (Arkhangelskaya 1974), for example, are found in the Mosolovian and Chernoyarian beds of the Central and Eastern Russian Platform, and are part of the *polymorphos-monogrammos* zone which has many taxa similar to the Fair Isle material, but is placed in the Eifelian by Arkhangelskaya. A similar problem is seen in the Givetian-Frasnian beds of the Baltic region, where the Soviet workers draw the boundary at the base of the Gauja formation (e.g. Ozolin'a 1963), whereas recently compiled data (Westoll 1979 and pers. comm.), places it at the base of the Snetogor, which gives this succession great importance as being continuous across the Middle/Upper Devonian boundary and containing good vertebrate faunas. Unfortunately although this section appears to be well documented (e.g. Ozolin'a 1955, 1960a, 1960b, 1961, 1963; Kedo 1966) the miospore illustrations and descriptions are poor, making comparisons difficult. The compilation of data presented in Table 1 shows a Givetian age for the Fair Isle assemblages but it is impossible to give greater precision with this type of synthesis.

Comparisons with zonal schemes from the Russian Platform

Several zonal schemes have been published which cover the relevant stratigraphic interval, and specific comparisons are made in an attempt to give a more detailed correlation. Kedo (1966) produced a zonal scheme for the western part of the Russian Platform and although there are some taxa in common, it is very difficult to make a precise correlation, except to record an influx of *Archaeozonotriletes* (sensu Naumova = *Geminospora* spp.) in the upper part of the Givetian, which compares with Fair Isle, but contrasts with the Orcadian Givetian which does not contain *Geminospora*. This indicates either younger Givetian rocks in Fair Isle than in the Orcadian Basin, or the possibility of an ecological control (see below).

Raskatova (1969, 1974) has produced a more compatible scheme which again shows an influx of *Archaeozonotriletes* in the upper Givetian (zones IV to VIII) Vorbyevkian to Staryi' oskolian. *Hymenozonotriletes punctomonogrammos* Arkhangelskaya and *H. monogrammos* Arkhangelskaya are also present, but occur lower down in the uppermost Eifelian as well as the Givetian, so that the age assignment is not clear cut.

From the same horizons, Arkhangelskaya (1974) has also recorded these two species of *Hymenozonotriletes* as well as taxonomic equivalents of *Rhabdosporites langii*, *Densosporites devonicus*, *Grandispora protea*, and *Samarisporites* spp. These were compared with the Weatherall

TABLE 1. Comparative table of selected Soviet and western taxa occurring on Fair Isle. Records include likely synonymies, part synonymies, and close comparisons. Sources include Ozolin'a 1955, 1960a, 1960b, 1961, 1963, Kedo 1955, 1960, 1966, 1967, Chibrikova 1959, 1962, 1972, 1977, Chibrikova and Naumova 1974, Arkhangelskaya 1963, 1974, Naumova 1953, Andreeva 1962, Raskatova 1969, 1974, and Pokrovskaya 1966.

WESTERN TAXA	SOVIET COMPARISONS	EIFELIAN	GIVETIAN	FRANSIAN
Ancyrospora ancyrea	Archaeotriletes sincerus Kedo Archaeotriletes splendidus Kedo Archaeotriletes hamulus Naumova	•	• • •	•
Aneurospora greggsii	Retusotriletes verrucosus (Naumova in litt.) Kedo Retusotriletes punctatus Chibrikova Archaeozonotriletes nalivkini Naumova		• • •	• •
Cirratiradites avius	Hymenozonotriletes punctomonogrammus Arkhangelskaya		•	
Cirratiradites sp. A	Hymenozonotriletes monogrammus Arkhangelskaya		•	
Densosporites devonicus	Hymenozonotriletes meonacanthus Naumova	•	•	•
Geminospora tuberculata	Archaeozonotriletes meonacanthus Nomen nudum Archaeozonotriletes tuberculatus Kedo Archaeozonotriletes plicata (Naumova in litt.) Kedo		• • •	
Geminospora svalbardiae	Retusotriletes parviammatus Kedo Archaeozonotriletes notatus Naumova Archaeozonotriletes rugosus Naumova		• •	• • •
Geminospora sp. A	Archaeozonotriletes visendus Chibrikova Archaeozonotriletes egregius Naumova Archaeozonotriletes tuberculatus var. aculeatus Raskatova Archaeozonotriletes acutus Raskatova Archaeozonotriletes visendus var. echinatus Chibrikova Archaeozonotriletes pensus Kedo Archaeozonotriletes lasius var. minor Naumova		• • • • • • •	• •
Geminospora sp. B	Archaeozonotriletes comptus Naumova Archaeozonotriletes comptus var. expletivus Chibrikova Archaeozonotriletes tuberculatus var. minor Kedo Archaeozonotriletes tuberculatus var. triangulatus Kedo		• • • •	
Grandispora naumovii	Archaeozonotriletes naumovii Kedo	•	•	
Grandispora protea	Hymenozonotriletes curticonicus Kedo Hymenozonotriletes ventosus Kedo Hymenozonotriletes proteus Naumova Hymenozonotriletes versus Naumova Hymenozonotriletes endemicus Chibrikova	•	• •	
Grandispora velata	Hymenozonotriletes echiniformis Naumova Hymenozonotriletes longus Arkhangelskaya Hymenozonotriletes tener var. concinna Chibrikova Hymenozonotriletes proteus Naumova Grandispora velata (Richardson) Playford	• • • • •	• • •	
Rhabdosporites langii	Hymenozonotriletes facetus Arkhangelskaya Hymenozonotriletes polymorphus (Naumova) Kedo Archaeozonotriletes micromanifestus Naumova Hymenozonotriletes varius Naumova Rhabdosporites parvulus Richardson	• • • • •	• • • •	

Formation from Arctic Canada (Givetian), the Thurso and Eday Beds from the Orcadian Basin (Givetian), and the Achanarras Fish Bed (Eifelian-Givetian). The recent zonal scheme produced by Chibrikova and Naumova (1974) is not very detailed with regard to specific taxa, and is largely restricted to generic distribution. The appearance of *Archaeozonotriletes* is considered significant, and is used as a marker for the Givetian stage. The zonal scheme produced by Naumova (1953) is difficult to apply, as the taxa are not often placed in a detailed zonal scheme, but in broad categories

such as Middle or Upper Devonian. The Fair Isle assemblages fit best into the Givetian and Frasnian groups.

A compilation of these occurrences has been presented by Andreeva (in Pokrovskaya 1966) and, as indicated, uses Chibrikova's (1962) and Naumova's (1953) work. The significant occurrence of *Archaeozonotriletes* (= *Geminospora*) with subordinate *Hymenozonotriletes* is used as a marker for the Givetian stage. The spores recovered by Chibrikova (1962) from the Vorobyevkian of Western Bashkiria contain several species which are similar to the Fair Isle assemblages, with examples such as *Archaeozonotriletes comptus* var. *xpletivus*, *A. meoncanthus*, *A. a. visendus*, and *A. egregius*.

	Sample No.	Zonate	Pseudo-saccate	<i>Geminospora</i> spp. and <i>Aneurospora</i>	<i>Hysterosporites</i>	<i>Aneurospora</i>	Others
Bu Ness Group	Fair 24	6	14	39	2	20	19
	Fair 28	4	39	3	0.5	30	23.5
	Fair 33	2	19	15	3	53	8
Observatory Group	Fair 36	8	47	11	2	13	19
	Fair 67	5	37	2	27	27	2
Ward Hill Group	Fair 66	6	33	36	—	21	1
	Fair 64	19	35	2	5	38	1

TABLE 2. Relative proportions of major miospore types from Fair Isle. The figures are percentages of numbers of each group from 150 total counts.

Ecological considerations

An ecological control on the distribution of some Devonian miospores has been speculated by several authors (e.g. Streeel 1967; Richardson 1965, 1967, 1969), and the example cited is usually that of *Geminospora* spp. (*Archaeozonotriletes* of Soviet palynologists). These miospores are thought to be dispersed from plants growing on and around the lower flood plain and marginal marine areas, whilst miospores from the bifurcate and pseudosaccate zonate groups are more continental in aspect and related to upper flood plain and possibly lacustrine deposits. The assemblages from Fair Isle are relevant to this discussion as they often contain abundant *Geminospora* spp. (fluctuating from 39% to 2%, see Table 2), in what appears to be a true internal basin facies. The presence of *Svalbardia scotica* (Chaloner 1972) in the Bu Ness Group is also significant, because other species are known to contain *in situ* spores of *Geminospora* and *Aneurospora* (see Allen 1980), suggesting that their origin is local. The occurrences are also not restricted in the Fair Isle succession (see text-fig. 6), being found in the minor argillite horizons (?lacustrine deposits) of the Ward Hill Group (alluvial fan deposits) as well as the overbank deposits of the Bu Ness Group. This distribution contrasts strongly with that of Richardson (1965, 1967, 1969), who noted an absence of *Geminospora* from the lacustrine and fluvial deposits from the Orcadian basin lying to the south. A possible explanation is that the time difference between the Orcadian and Fair Isle deposits is sufficient to allow the migration of an 'Archaeozonotriletes' microflora from the Russian Platform, where it occurs in lower Givetian deposits (Raskatova 1974) contemporaneous with the Orcadian Basin. A less appealing hypothesis is that the Fair Isle lacustrine and fluvial deposits were sustained by permanent water flow, giving more equable conditions than those in the Orcadian Basin, and similar to conditions seen on delta tops or marine margins, where *Geminospora* is known to thrive (see Becker *et al.* 1974). These authors describe in detail the distribution of *Aneurospora greggsii*, and suggest it is not restricted by ecological factors in their environment studied, which unfortunately do not include lacustrine or alluvial fan facies. It

seems that this conflict between an edaphic or stratigraphic control will not be resolved without further detailed palaeoecological studies of this type.

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CONODONTS, GONIATITES AND THE BIOSTRATIGRAPHY OF THE EARLIER CARBONIFEROUS FROM THE CANTABRIAN MOUNTAINS, SPAIN

by A. C. HIGGINS and C. H. T. WAGNER-GENTIS

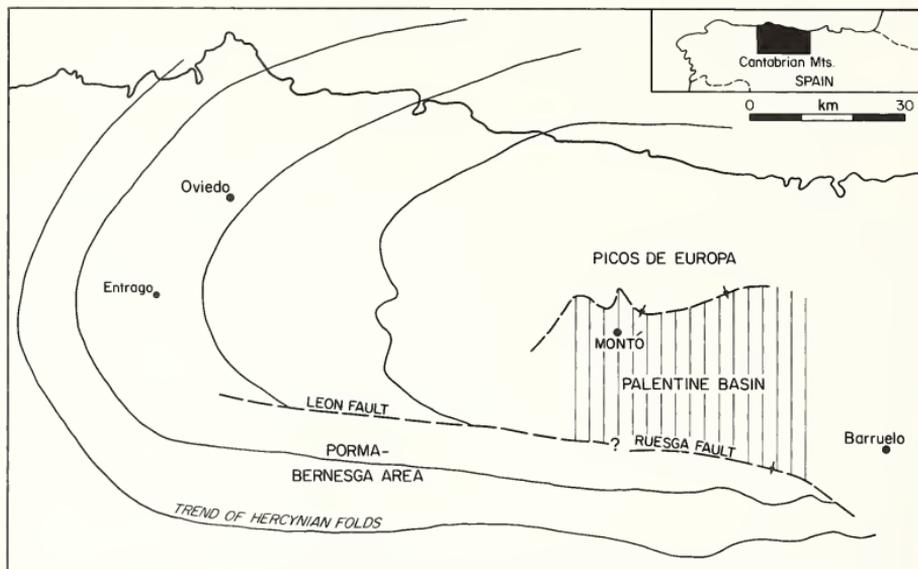
ABSTRACT. Six conodont zones, including one new one, the *Paragnathodus multinodosus* Zone, are represented in the Lower Carboniferous of the Cantabrian Mountains. The absence of conodont zones known to occur in north-west Europe points to four major stratigraphic gaps in the Spanish sequence, three in the Tournaisian and one in the Viséan. High conodont abundances, indicating a low rate of sedimentation in the Tournaisian rocks, and the numerous gaps in the stratigraphic record point to a slow initial Carboniferous transgression. The patchy distribution of earliest Tournaisian sediments contrasts with the widespread distribution of the latest (*anchoralis* Zone) Tournaisian sediments when the transgression reached its culmination. Lower conodont abundances and thicker successions coincide with a more complete Viséan/early Namurian sequence in which only one major break is detectable. A goniatite fauna from the lower Viséan is described including one new genus, *Pseudogirtyoceras* and two new species *P. villabellacoi* and *Winchelloceras palentinus*. This fauna confirms the early Viséan age of the *typicus* Zone. One new species of conodont, *Scaliognathus angustilateralis* sp. nov., is also named.

THE Dinantian and early Namurian sedimentary sequence in the Cantabrian Mountains of north-west Spain consists of less than 50 m of condensed deposits formed on the Cantabrian Block. This was a stable platform uplifted during the late Famennian and the recipient of renewed sedimentation from latest Famennian onwards. The age and nature of these sediments is not always the same all over the area and this is true particularly of the deposits formed during the latest Famennian and Tournaisian. Several formations are involved (compare Wagner, Winkler Prins, and Riding 1971). The earliest deposits belong to the Ermita Formation (Grès de l'Ermitage of Comte 1959) which was laid down after the Famennian uplift and which appears to have a diachronous base, older at the flanks of the uplift and younger in its central part. A calcareous sandstone lithology is the most common for the Ermita Formation but limestone has been recorded in the top part. Samples in the highest Ermita Formation yielded conodonts attributed to the *costatus* Zone (Higgins, Wagner-Gentis, and Wagner 1964), but a few localities have now shown the presence of a *Protognathodus* fauna of earliest Carboniferous age. The Ermita Formation thus appears to span the latest Famennian and the earliest Tournaisian.

In the south-eastern part of the Cantabrian Mountains, corresponding to the northern part of the province of Palencia, there is an area which shows many resemblances to the western Pyrenees and which is characterized by a nodular limestone, the Vidrieros Formation of Van Veen (1965), spanning the Famennian-Tournaisian boundary (Van Adrichem Boogaert 1967). This region does not show the effects of Famennian uplift and contains a different development of Devonian strata, i.e. the Palentine facies of Brouwer (1964). It occupies an area between two major faults, viz. the Ruesga Fault in the south and the southern boundary fault of the Picos de Europa to the north. Appreciable tectonic shortening is a feature of both faults and the abrupt contacts between areas of different facies development is apparently due to extreme telescoping as a result of the tightening of the arcuate fold belt in north-west Spain (R. H. Wagner, pers. comm.).

The Ruesga Fault is apparently continued westwards by the León Fault of Marcos (1967)

(originally described as the León Line by De Sitter 1962). Although this important fracture zone has been widely credited as a syn-sedimentary control, it seems to be due to post-sedimentary tectonics with a telescoping effect which gradually diminishes westwards (R. H. Wagner, pers. comm.). The sediments investigated for the present paper were all laid down south of the León-Ruesga tectonic fault line (text-fig. 1) even though some of the localities are presently north of this fault.



TEXT-FIG. 1. Structural palaeogeographic areas, Palaeozoic, Cantabrian Mountains.

In this area the Ermita Formation is generally present. It is followed by either the Vegamián Formation of black shales or the Baleas Formation of crinoidal limestone. These two formations (Wagner *et al.* 1971) seem to be mutually exclusive. Since they both seem to correspond to the same time interval within the Tournaisian (*cooperi-communis* Zone of the present paper) it may be that the Baleas Limestone was formed on ridges in the basin which received the Vegamián Shales (compare Higgins *et al.* 1964). The Baleas Formation, described by Wagner *et al.* (1971) is only a few metres thick. The Vegamián Formation (Comte 1959; Wagner *et al.* 1971) is generally less than 10 m thick. It is characterized by phosphatic and chert nodules and black shales which are often cherty. Its macrofauna includes the goniatite *Muensteroceras arkansanum* Gordon, as recorded by Wagner-Gentis (in Wagner *et al.* 1971). This species was described originally from the late Kinderhookian of Arkansas, U.S.A.

The most widespread formation in the Carboniferous of north-west Spain is the succeeding Genicera Formation of Wagner *et al.* (1971) which is the 'Marbre Griotte' of Barrois (1882) (also called Villabellaco Formation—Wagner and Wagner-Gentis 1963—and Alba Formation—Van Ginkel 1965). It is characterized by nodular and wavy-bedded limestones and up to 25 m thick. The basal unit (Gorgera Member of Wagner *et al.* 1971) is marly and usually a vivid red colour, although a slightly reddish-grey colour has also been found. Over a large area of northern León, including the Genicera type section, an interval of red shales and cherts (Lavandera Member) separates the basal,

marly unit of nodular limestones from the main part of generally wavy-bedded to nodular limestones (Canalón Member of Wagner *et al.* 1971). The chert unit is absent in the southernmost exposures of northern León and in the Revilla Nappe structure of northern Palencia. Conodont work reported in the present paper shows that the chert unit corresponds to a sizable time gap which is equally apparent where the cherts are absent. The basal unit, which is only a few metres thick, has yielded goniatites of the late *Pericychus* (II β/γ) Zone corresponding to late Tournaisian. Its conodont fauna corresponds to the *anchoralis* Zone. The Gorgera Member may be occasionally absent and although the rare occurrences where this seems to be the case ought to be checked for thrusting (shearing in the

Age	SSW of Genicera (León)		Olleros de Alba (León)
	Formation	Member	Formation
Namurian A/B	Barcaliente		Barcaliente
			Olleros
Visean	Genicera	Canalón	Olaja Beds
		Lavandera	Genicera
		Gorgera	
Tournaisian	Vegamián		Vegamián
Famennian	Ermita		Ermita

TABLE I. Formations in the Porma-Bernesga area, based on Wagner *et al.* (1971).

flanks of isoclinal synclines is of common occurrence in the Cantabrian Mountains), it appears likely that the base of the Genicera Formation may not always be of exactly the same age.

The top of the formation reaches into the lower Namurian (E₂b Zone) and is undoubtedly diachronous. Wagner *et al.* (1971) described the Olaja Beds, a condensed mudstone sequence of only a few metres, as the lateral equivalent of the highest part of the Canalón Member. The lower Namurian Olaja Beds occur only in the southernmost exposures of the Cantabrian Mountains in northern León, where they form the base of a thick terrigenous sequence with turbidites (Olleros Formation of Wagner *et al.* 1971). In the more northerly exposures, the more complete Canalón Member is followed with gradual transition by the Barcaliente Limestone Formation. The latter was formed on a carbonate platform (the same Cantabrian Block as accumulated the Genicera Limestone and Chert Formation) which was sufficiently shallow to give rise to evaporitic sediments. The presence of a turbidite basin to the south indicates the diminished area of the Cantabrian Block in mid-Namurian times, whilst the terrigenous facies of the Olaja Beds provides an early indication of the northwards withdrawal of the southern margin of the block in early Namurian times.



TEXT-FIG. 2. Location of the sampled sections in the southern part of the Cantabrian Mountains.

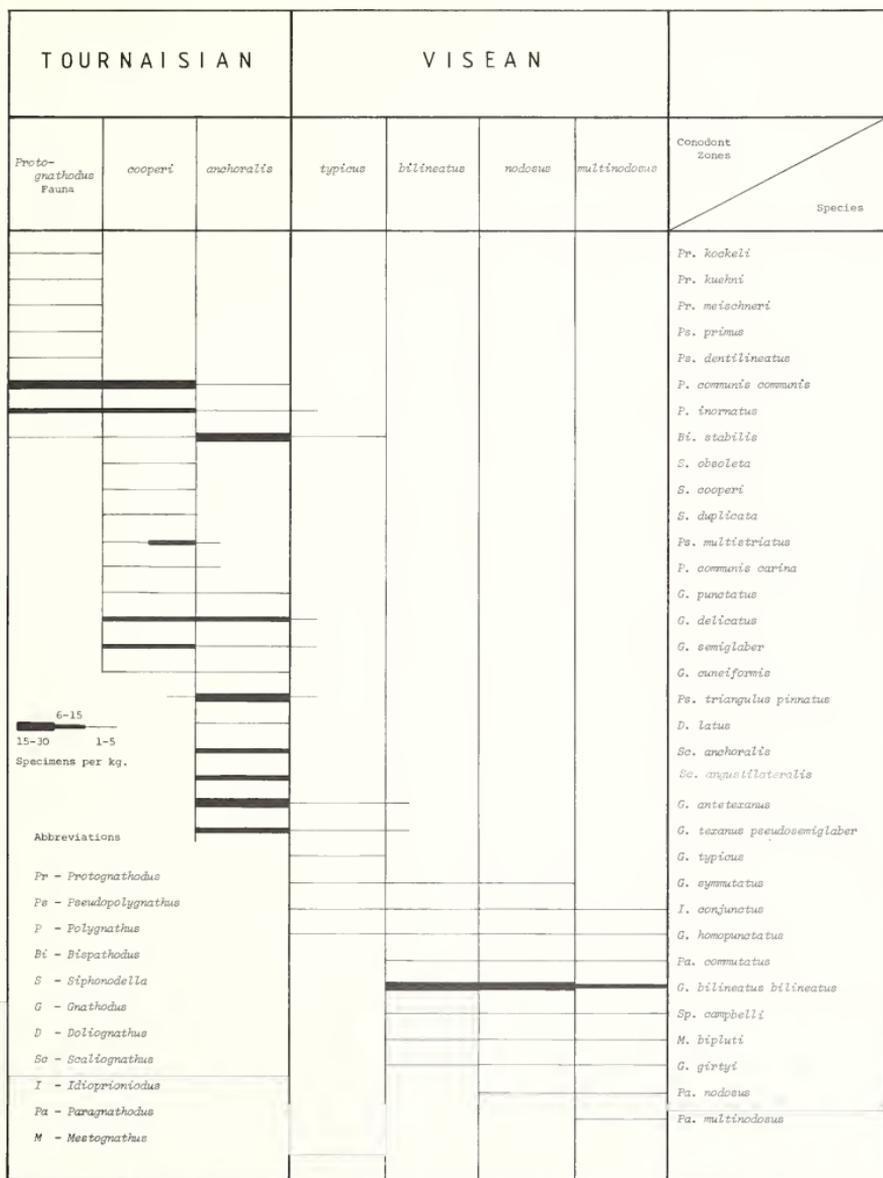
CONODONT ZONES AND LOWER VISEAN GONIAITITE OCCURRENCE

Six conodont zones and a *Protognathodus* fauna are represented in the sequence but the boundaries of the fauna and the lower three zones are non-sequences and the sequence is probably incomplete. Five of these concurrent range zones were defined by Higgins (1974) but are here modified and one zone is new.

Protognathodus fauna. The base of the Ermita Formation is a transgressive horizon of late Devonian age, belonging to the *costatus* Zone of Ziegler (1962). In only two of the sections, the Aviados and the Villabellaco sections in the Porma-Bernesga area, does the base of the Carboniferous rest on pre-*costatus* rocks. On the other hand, only at Santiago de las Villas and Olleros de Alba is there a transition between the Devonian and Carboniferous where a thin limestone at the top of the Ermita Formation yields a conodont fauna belonging to the *Protognathodus* fauna. This fauna includes *Polygnathodus communis communis* Branson and Mehl, *Polygnathus inornatus* sensu Branson and Mehl, *Protognathodus kockeli* (Bischoff), *Protognathodus meischeri* Ziegler, *Protognathodus kuehni* Ziegler and Leuteritz, and one specimen doubtfully referred to *Pseudopolygnathus dentilineatus*. This fauna was referred to the *kockeli-dentilineatus* Zone by Higgins *et al.* (1964) as was a similar fauna described by Adrichem Boogaert (1967) from the Triollo area. The presence of *Protognathodus kuehni* suggests that this fauna belongs to the younger *Protognathodus* fauna of Ziegler (1969). The presence of a newly discovered siphonodellid in this fauna also clearly indicates closer affinity with the Upper rather than the Lower *Protognathodus* fauna. This siphonodellid was referred by Higgins (1974) to *Siphonodella sulcata* (Huddle) but it is poorly preserved and of very doubtful determination. The assignment of these samples to the Upper *Protognathodus* fauna places them in the Carboniferous rather than at the top of the Devonian (Sandberg, Ziegler, Leuteritz, and Brill 1978).

Siphonodella cooperi-polygnathus communis Zone. This zone, defined by Higgins (1974), is widespread in the Porma-Bernesga area where it occurs in the Bales and Vegámian Formations. Key species in the rich and abundant faunas include *Siphonodella obsoleta* Hass, *S. duplicata* Branson and Mehl morphotype 2, and *S. cooperi* Hass morphotype 2 of Sandberg *et al.* (1978). These range from the Upper *Duplicata* Zone to the Upper *Crenulata* Zone according to Sandberg *et al.* (1978). However, *Gnathodus delicatus* Branson and Mehl, *G. punctatus* (Cooper), and *G. semiglaber* Bischoff, which are also present in the zone, overlap the range of species of *Siphonodella* in the Belgian Tournaisian (Groossens 1977b) in late Tn₂. Also present in the zone is *Polygnathus communis carina* Hass which first appears in Tn₃ in the Belgian sequence. A late Tn₂/early Tn₃ age indicates the span of the *cooperi-communis* Zone. This age probably indicates at least partial equivalence to the German *crenulata* Zone (see text-fig. 7).

Anchoralis Zone. The *anchoralis* Zone is easily recognized and is a widespread zone in the Cantabrian Mountains. *Scaliognathus anchoralis* Branson and Mehl, *Doliognathus latus* Branson and Mehl, *Pseudopolygnathus triangulus pinnatus*, *Gnathodus texamus* (Roundy) *pseudosemiglaber* Thompson, and *G. delicatus* are



TEXT-FIG. 3. Ranges of the stratigraphically important conodont species in the Cantabrian Mountains.

species	sample	total per kilo																
		<i>P. communis</i>	<i>P. pinna</i>	<i>P. stabilis</i>	<i>G. abissino</i>	<i>G. semipalmeri</i>	<i>P. marginatus</i>	<i>D. tatus</i>	<i>S. macronotus</i>	<i>S. bischoffi</i>	<i>G. anetianus</i>	<i>G. reianus</i>	<i>G. homopunctatus</i>	<i>G. communis</i>	<i>G. baueri</i>	<i>G. perrilli</i>	<i>P. nodosus</i>	<i>A. multinodatus</i>
	1937B											2	3	14				18
	194		1															5
	194				5						4							2
	1953		1	4	1	2					1	1	3	5				18
	135R																	30
	1351																	45
	352D											5	30	10				45
	N				20	2						2	1	2				5
	M											15	3					40
	L				14							7	4					25
	K				25	4						10	2					41
	H																	1
	I																	2
	G																	2
	W																	2
	H				4	40	4					12						60
	G				45							2						47
	F				6	10	5					3	20					43
	E				2	10	6											24
	O				2	40	2											44
	C																	40
	B				2	20	2					2						40
	A				1	20	10											36
	4				6	10	20					2						36
	3077	12			1	8	3	15										39
	1069T																	1
	S																	1
	R																	2
	Q																	4
	O																	4
	P																	26
	O																	40
	N																	1
	M																	6
	L																	7
	K																	4
	J																	2
	I																	6
	H																	5
	G																	10
	F	4																14
	E																	5
	D																	2
	C																	7
	B																	21
	A																	17
	1072N																	10
	M																	1
	L																	2
	K																	11
	J																	103
	I																	5
	H																	1
	G																	6
	F																	10
	E																	1
	D																	4
	C																	13
	B																	6
	1342	5																13
	1658																	19
	1666																	20
	1668																	4
	1338																	1

species	sample	total per kilo																		
		<i>P. nodosus</i>	<i>P. communis</i>	<i>P. pinna</i>	<i>P. stabilis</i>	<i>G. abissino</i>	<i>G. semipalmeri</i>	<i>P. marginatus</i>	<i>D. tatus</i>	<i>S. macronotus</i>	<i>S. bischoffi</i>	<i>G. anetianus</i>	<i>G. reianus</i>	<i>G. homopunctatus</i>	<i>G. communis</i>	<i>G. baueri</i>	<i>G. perrilli</i>	<i>P. nodosus</i>	<i>A. multinodatus</i>	
	1670																			1
	169																			1
	168																			2
	1617																			4
	166																			4
	165																			1
	1614																			1
	1613																			1
	162																			2
	160																			4
	1394																			1
	1391																			46
	139																			63
	130	3	8	1	42	1	3													58
	1649T																			1
	N																			1
	M																			3
	L																			14
	K																			17
	J																			2
	I																			2
	H																			9
	G																			10
	F																			2
	E																			4
	D																			10
	C																			23
	B																			29
	A																			17
	299																			5
	298																			1
	295																			1
	293																			2
	292																			1
	291																			2
	290																			2
	2909																			1
	2908																			3
	2906																			17
	2905																			5
	2904																			9
	2903																			7
	2902																			14
	2901																			36
	2900																			1
	1365																			10
	2899																			2
	134X																			9
	K																			2
	IA																			10
	VII																			3
	VII																			5
	VI																			13
	V																			5
	IV																			25
	III																			30
	II																			12
	I																			4
	Sito Olajad' Vargo 372																			1
	S.E. of Genicera																			6
	V																			1

TABLE 3. Distribution and abundance of conodonts from the Cantabrian Mountains.

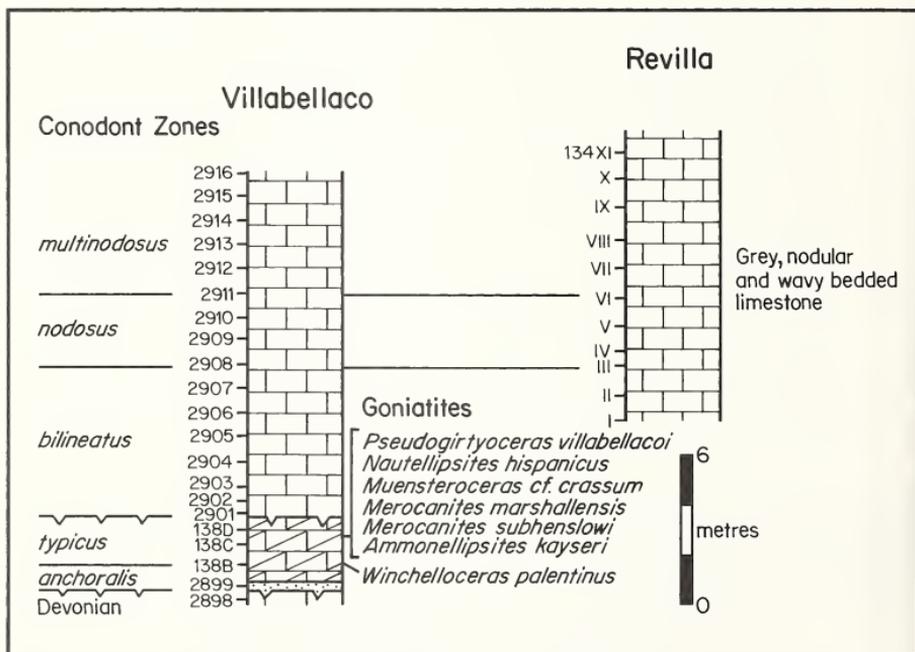
the dominance of species of *Gnathodus* which characterizes much of the Viséan and early Namurian. *G. homopunctatus* Bischoff appears at the base of the zone and this occurrence together with the other species would suggest an equivalence of this zone to the *G. homopunctatus* Subzone of V_{1a} age in Belgium (Grossens 1977b).

138 c, 2-3 m above the base	<i>Merocanites marshallensis</i> (Winchell) <i>Merocanites subhenslowi</i> Wagner-Gentis <i>Ammonellipsites kayseri</i> (Schmidt) <i>Nautellipsites hispanicus</i> (Foord and Crick)
1-1.2 m above the base	<i>Merocanites marshallensis</i> (Winchell) <i>Muensteroceras</i> cf. <i>crassum</i> Foord
138 b, 0.5-0.6 m above the base	<i>Winchelloceras palentinus</i> sp. nov.
136 b, east of locality 138, at the same level as 138 c	<i>Muensteroceras parallellum</i> (Hall)

Merocanites marshallensis and *Winchelloceras* are known from the Marshall Sandstone in Michigan, which is considered to belong to the Osagean (Manger 1979, pp. 214, 215). Popov (1968) recorded *Winchelloceras* from the *Fascipericyclus* 3 Zone (Lower Viséan) of the Tien Shan in Central Asia and (1975) from the c_1v_1 unit in the Urals.

Ammonellipsites kayseri has been described from Liebsstein (Erdbach and Breitscheid section), West Germany in the Pey Zone, in Aragón (Spain). Schmidt (1931) mentioned it with a Lower Viséan fauna and in south-west England it occurs at Tawstock and Coddon Hill (Prentice and Thomas 1960, p. 6).

Muensteroceras parallellum was described from the Rockford Limestone of Indiana. A conodont fauna below the ammonoid layer in the type locality belongs to the Osagean (Rexroad and Scott 1964) and Manger (1979, p. 213) attributes the goniatite bed also to the Osagean. The species is also known from the S_1 unit of the Hassi Sguilma Stage of Pareyn (1961, p. 50 and table IV) which contains a basal Viséan fauna. Librovitch (1927, p. 42) mentioned this species from the Tien Shan, where it occurs with a fauna of the middle and upper 'Pericyclus Stufe' (Schmidt 1925).



TEXT-FIG. 4. Conodont zones and lower Viséan goniatite occurrence in the Villabellaco area, Revilla Nappe.

Muensteroceras cf. *crassum* is known from the Lower Carboniferous Limestone of Ballinacarriga, Co. Limerick, Eire.

Merocanites subhenslowi and *Nautillepsites hispanicus* have previously been described from Olleros de Alba (León) and Villabellaco (Palencia) (Higgins *et al.* 1964; Wagner-Gentis 1960). In both papers it was suggested that they occurred in an equivalent to the lower B-zone, but this is now seen to be incorrect. An earlier horizon is involved. The lower part of the Villabellaco Limestone yielded conodonts of the *typicus* Zone (Higgins, this paper) which corresponds to V_{1a} of the Belgian sequence. An early Visean age is also indicated by the majority of the goniatic species found.

The goniatic fauna from the lower part of the Villabellaco Limestone has *Muensteroceras parallellum* in common with the Rockford Limestone of Indiana, and *Merocanites marshallensis* and *Winchelloceras* (a different but comparable species, *Winchelloceras allei*) with the Marshall Formation of Michigan. The latter has been assigned an early Visean age by Miller and Garner (1955, pp. 118–119) (see also Brenckle, Lane, and Collinson 1974) but a late Tournaisian age by Manger (1979, p. 221, fig. 3). The lower part of the Villabellaco Limestone containing the goniatic species comparable to those of the Marshall Formation, has also yielded conodonts of the *typicus* Zone which belongs to V_{1a} of the Belgian sequence. It thus appears that the Marshall Formation, may be lower Visean rather than upper Tournaisian. On the other hand, *Kazakhstania*, another element of the Marshall Fauna, is regarded as a late Tournaisian index (Librovitch 1940, pp. 324–325; Manger 1971). This goniatic does not occur in the Villabellaco Limestone.

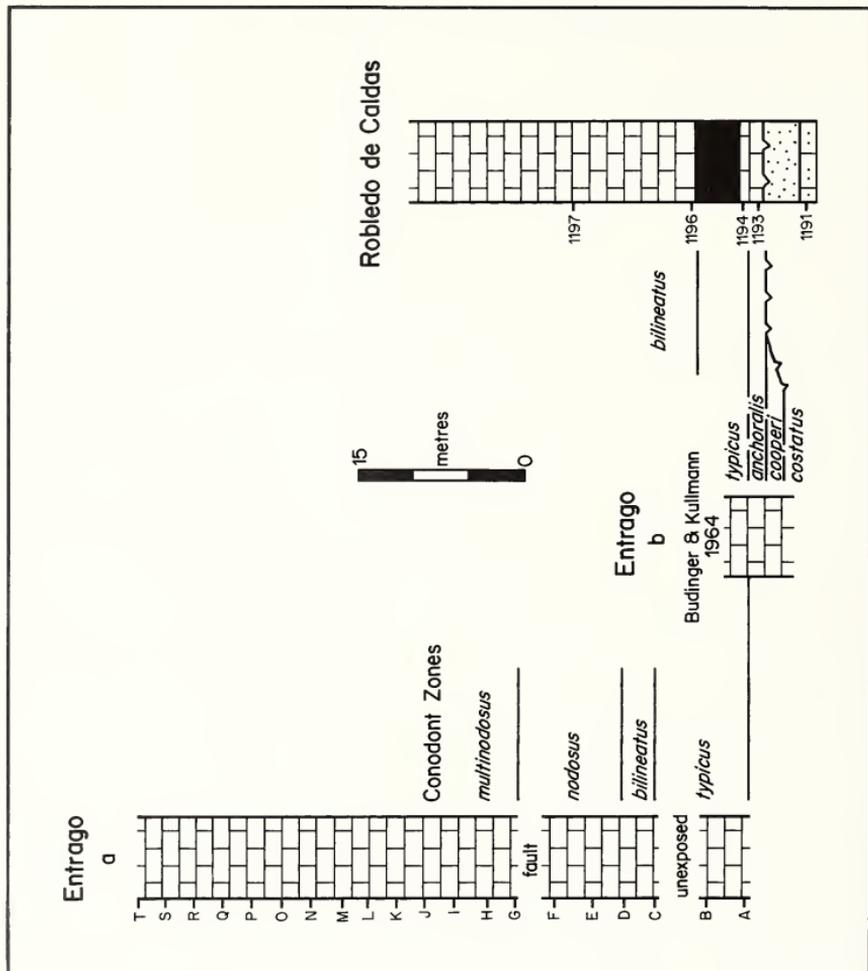
Gnathodus bilineatus Zone. The marked reduction of the *texanus* group and its disappearance a little way into the zone marks the beginning of the *Gnathodus bilineatus* Zone. This change coincides with the appearance of the important *G. bilineatus* (Roundy) and *Paragnathodus commutatus* (Branson and Mehl). This abrupt change is due to the absence of several faunas, notably the late appearance of *P. commutatus* which appears before *G. bilineatus* in northern Europe, and the absence of the *G. texanus* fauna which is important in Missouri (Thompson and Fellows 1970).

Paragnathodus nodosus Zone. The increase in the complexity of *P. commutatus* by the addition of platform nodes marks the appearance of *P. nodosus* (Bischoff). This widespread species appears in the zone of *Neoglyphioceras spirale*, Go β in Germany (Meischner 1970) and in V_{3b} in Belgium (Groessens 1977b). *G. bilineatus* is still a very important zonal constituent.

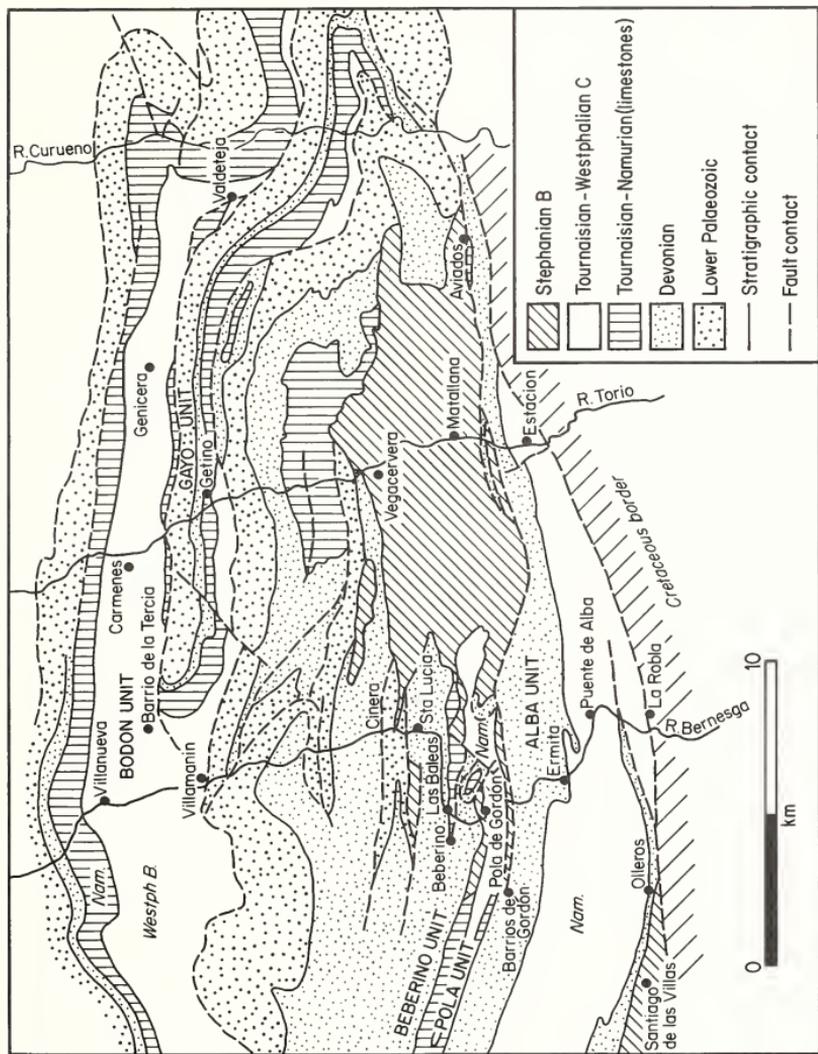
Paragnathodus multinodosus Zone. The increasing complexity of platform ornamentation marks the appearance of *P. multinodosus* (Wirth). Again *G. bilineatus* is an important element of the fauna. Budinger and Kullmann (1964) related the appearance of *P. multinodosus* to the *granosus* Zone (Go γ). The consistent later appearance of *P. multinodosus* relative to *P. nodosus*, often only 1 m higher, is only detected in closely sampled sections. The *P. multinodosus* Zone continues into the overlying Namurian where in the absence of the later form of *G. bilineatus*, *G. bilineatus bollandensis* and the rarity of *G. girtyi* Hass it has not proved possible to subdivide the early Namurian.

Consideration of the Faunas. The faunas are dominated by platformed conodonts with wide basal cavities and flaring platforms typified by species of *Gnathodus* and *Paragnathodus*. In the Visean these are characteristic of deep-water cephalopod limestones in many parts of the world and the deep-water nature of the Visean griotte limestones and the presence of goniatic confirms this as a general observation. Nevertheless, both in the Tournaisian and the Visean there are peculiarities in the faunas which are worthy of note.

The Tournaisian faunas are of two types: one, occurring in the crystalline limestone of the Baleas Formation and the basal unit of the Genicera Formation, is dominated by gnathodids whereas the other, occurring in the fine grained limestone of the Ermita Formation and in the conglomerates and shales of the Vegamián Formation, is dominated by siphonodellids and polygnathids. Meischner (1970) suggested that the gnathodid faunas of the German *anchoralis* Zone were characteristic of schwellen environments whereas the polygnathids dominate in the basin environments. Matthews, Sadler, and Sellwood (1972) suggested that the contrast is between faunas with large basal cavities and flaring platforms, the gnathodids, and those with small basal cavities, the polygnathids. The distribution of the Baleas Formation in the Porma-Bernesga region is in the form of an east-west trending area within the Vegamián shale outcrop and it was suggested by Higgins *et al.* (1964) that it was formed on a ridge, in a deeper-water sea. The conodont faunas would confirm this view, because the Vegamián faunas, although few, are dominated by polygnathid conodonts. Whether the



TEXT-FIG. 5. Conodont zones in the sections at Entrago and Robledo de Caldas.



TEXT-FIG. 6. Generalized geological map of part of northern León after Wagner *et al.* (1971) with structural units after de Sitter (1962).

crystalline limestone faunas of the Baleas were formed in the same depth of water as the griotte limestone is unknown but it seems likely in view of the similarity of conodont type.

The other anomaly occurs in the Visean where the rarity of *G. girtyi* contrasts with its abundance in the basin limestones and shales of northern Europe. This species is occasionally found in the *G. bilineatus* Zone but principally occurs in the *P. nodosus* Zone. In the Pyrenees (Marks and Wensink 1970) it appears to occur only in the *P. nodosus* Zone. There is no record of *G. girtyi* in the Namurian of Spain. Similarly, the absence of *G. bilineatus bollandensis*, the high abundance of *Spathognathodus campbelli* Rexroad, and the almost total restriction of *P. multinodosus* to the Cantabrian Mountains and the Pyrenees, point to the partial geographic isolation of this area during the early Namurian (E_1, E_2).

IMPLICATIONS OF THE CONODONT DATINGS FOR THE HISTORY OF THE AREA

Comparison of the conodont sequence with more complete ones in Belgium, Germany, and Great Britain indicates the presence of considerable breaks in the Lower Carboniferous succession in the Cantabrian Mountains. However, there is little evidence of extensive erosion and the lack of faunal reworking and the high faunal abundance implies slow but continuous deposition separated by periods of non-deposition. The sequence of events is as follows:

		Average number of specimens/Kg	
NAMURIAN (E_1, E_2)			
—	<i>multinodosus</i> Zone	} — 39 27	
	<i>nodosus</i> Zone		
	<i>bilineatus</i> Zone		
		Continuous deposition	
VISEAN			
	<i>typicus</i> Zone	Widespread non-deposition	
		Widespread deposition	19
—		Local non-deposition	
	<i>anchoralis</i> Zone	Major transgression	97
		Widespread non-deposition, some erosion. Continuation of swell topography during early part of the zone	
TOURNAISIAN	<i>cooperi-communis</i> Zone	Development of swells	89
		Widespread non-deposition	
	Upper <i>Protognathodus</i> f.	Patchy distribution	
—		Erosion surface in most areas	
DEVONIAN	<i>costatus</i> Zone	Widespread transgression	

Late Devonian history. Adrichem Boogaert (1967) clearly demonstrated the transgressive nature of the late Devonian rocks which, in the form of the Ermita Formation, commonly rest unconformably on the underlying rocks.

Tournaisian history. There are undoubtedly sections in the Cantabrian Mountains which show a transition from the Devonian into the Lower Carboniferous. The sections at Santiago de las Villas and Olleros de Alba in the Porma-Bernesga area yield the earliest Carboniferous, Upper *Protognathodus*, fauna in a sequence which is uninterrupted from the Devonian. Unfortunately, the latest Devonian rocks do not yield conodont faunas. A transition probably also exists in the Vidrieros Formation in the northern part of the Palentine Basin (Adrichem Boogaert 1967) where the *costatus* Zone is followed by the *Protognathodus* fauna, but a full sequence of zones has not yet been demonstrated. Similarly, there may well be a transition in the Cándamo Formation in Loreda, but again a full sequence of zones has not been proved (Del Rio and Menéndez Alvarez 1978). These are

CANTABRIAN MOUNTAINS	BELGIUM (after Groessens 1975, Higgins & Bouckaert 1968)		GERMANY (after Meischner 1970, Conil & Paproth 1968)	SIPHONODELLA ZONATION (after Sandberg et al. 1978)	
<i>Pa. multinodosus</i>	E ₂	<i>G. bilineatus bollandensis</i>	E ₂	<i>G. bilineatus schmidti</i>	
	E ₁	//	E ₁	<i>Pa. nodosus</i>	
	V _{3c}	<i>Pa. nodosus</i>	Go _γ		
<i>Pa. nodosus</i>	V _{3by}		Go _β		
<i>G. bilineatus bilineatus</i>	V _{3ba}	<i>G. bilineatus bilineatus</i>	Go _α	<i>G. bilineatus bilineatus</i>	
//	V _{2-V3a}	Few conodonts		-----	
<i>G. typicus</i>	V _{1b}	<i>M. beckhami</i>		<i>anchoralis-bilineatus</i>	
	V _{1a}		<i>Pa. commutatus</i>	interregnum.	
<i>S. anchoralis</i>	Tn ₃	<i>S. anchoralis</i>		<i>S. anchoralis</i>	
			<i>G. homopunctatus</i>		Pe
			<i>E. burlingtansensis</i>		
<i>S. cooperi-P. communis</i>	Tn ₃	<i>P. communis carina</i>	<i>D. latus</i>	?	
			<i>Do. bouckaerti</i>	<i>S. crenulata</i>	
			<i>Sp. bultyncki</i>		
<i>U. Protognathodus fauna</i>	Tn _{1b} -Tn ₂	<i>Siphonodella</i>		<i>Si. triangulus triangulus</i>	
			<i>Do. hossi</i>	<i>Si. triangulus inaequalis</i>	
				<i>kookeli-dentilineatus</i>	
				<i>U. Protognathodus fauna</i>	
<i>costatus</i>	Tn _{1a}	<i>Protognathodus fauna</i>		<i>L. Protognathodus fauna</i> <i>M. & U. costatus</i>	
				<i>isosticha-U. crenulata</i> <i>L. crenulata</i>	
			Ws	<i>sandbergi</i>	
			Ga	<i>U. duplicata</i> <i>L. duplicata</i>	
				<i>sulcata</i>	
				<i>praesulcata</i>	

TEXT-FIG. 7. Correlation of the conodont sequence in the Cantabrian Mountains with those of Belgium and Germany. The suggested faunal and stratigraphic breaks in the Spanish sequence are indicated by diagonal lines.

the exceptions, however, for the Devonian–Carboniferous boundary is usually an erosion surface representing a regression of early Carboniferous age. In the Porma–Bernesga area the gap at the base of the Carboniferous increases in size in a northerly direction from Santiago de las Villas to Viadangos de Arbas where the Visean rests directly on the late Devonian (see text-fig. 8). This trend is also seen in the pre-Ermita unconformity in this area (Adrichem Boogaert 1967) where it was interpreted as part of a general trend of increasing hiatus in a northerly and easterly direction towards the ‘Asturian Geanticline’ which occupies the central part of the Cantabrians. The same trend towards this platform area is evident in the Lower Carboniferous, but is one of increasing disconformity rather than unconformity and is an expression of the Bretonic Movements.

These early Tournaisian (Tn_{1b}) deposits represent the termination of the late Devonian transgression and were followed by a long period of regression. Evidence of the upper part of the *sulcata* Zone and the following zones up to the upper part of the *sandbergi* Zone of Sandberg *et al.* (1978) is lacking. Comparison with Belgium (Groessens 1977b) reveals the absence of all but the highest part of the *Siphonodella* Zone or lower part of the *Polygnathus communis carina* Zone which implies a gap ranging from Tn_{1b} to Tn_{3a} . This regression is represented in all sections of the Porma–Bernesga area by an erosion surface. The subsequent transgression resulted in a different pattern of sedimentation due in part to the emergence of positive areas in a generally subsiding basin. Dominating the facies pattern is the Vegamián Formation, a thin sequence of black, often cherty, shales with thin conglomeratic and phosphatic nodule horizons. In the Porma–Bernesga area a conglomeratic sandstone at the base of the Vegamián Formation at Santiago de las Villas and Genicera yields a fauna of polygnathids, siphonodellids, and pseudopolygnathids belonging to the *cooperi-communis* Zone. The upper limit of the Formation is more difficult to define. The highest beds of the Genicera section yield *Pseudopolygnathus triangulus pimata* Voges, which ranges through Tn_3 in Belgium and in other sections it is overlain by beds of *anchoralis* (Tn_{3c}) age. A pre-*anchoralis* age for the major part of the Vegamián seems likely, although an early *anchoralis* age for the highest part cannot be ruled out. To the east and north-east of the Porma–Bernesga area, the base of the Vegamián appears to be of *cooperi-communis* age (Adrichem Boogaert 1967) where the faunas were referred to the lower *anchoralis* zone. The upper surface appears to be diachronous since Budinger and Kullmann (1964) recovered late Visean (GoIII a/ β) goniatites from the highest part of the Formation, although Wagner *et al.* (1971) question the attribution of these faunas to the Vegamián Formation.

In the Porma–Bernesga area, along a zone extending from Aviados to Pola de Gordón, the Vegamián black shales are absent and their place is taken by the crystalline limestones of the Baleas Formation. This thin unit, 12 m thick, is rich in conodonts with an average of eighty-nine conodonts per kilogram, indicating slow sedimentation. The faunas are of the swell type and indicate the presence of a swell extending east–west through the Porma–Bernesga area, which is here named the Pola de Gordón Swell. In the area to the east, north of Sabero, a similar crystalline limestone again replaces the Vegamián Shales and is also of *cooperi-communis* age (Adrichem Boogaert 1967). It may represent the easterly continuation of the Pola de Gordón Swell. At Entrago, Budinger and Kullmann (1964) recorded from the lower part of the sequence a crystalline limestone of ‘Baleas’ type also yielding a mid-late Tournaisian conodont fauna. As in the area to the south, the Vegamián is absent and it seems probable that this marks the position of another swell. These swells are close to, and parallel with, the early Carboniferous coastline (see Adrichem Boogaert 1967) and represent crinoidal banks forming on ridges close to the shore-line.

The *anchoralis* Zone, although extremely thin (c. 2 m) is the most widespread horizon in the Tournaisian of the Cantabrian Mountains and represents a considerable extension of the sea. In the majority of sections the base of the zone is an erosion surface, but one section, at Genicera, exhibits a transition from the Vegamián Formation into the overlying Genicera Formation. The earliest deposits of the zone included the top 1 m of the Baleas Formation in the Pola de Gordón area where erosion surfaces at the base and top separate the unit from *cooperi-communis* Zone below and the later part of the *anchoralis* Zone above. The most widespread part of the zone occurs at the base of the Genicera Formation where it occupies the basal metre of the red and grey nodular limestones

(griotte). The fauna commonly occurs in a fine grained non-nodular limestone and is of the 'swell' type being composed of gnathodids together with some locally abundant polygnathids and pseudopolygnathids. However, there are no swells identifiable in this zone, merely a general shallowing over the whole region except in the extreme east where the Vegamián Formation persists. In the south-east, the Revilla Nappe, the Vegamián Formation is absent and the oldest Carboniferous is a thin sandy limestone of *anchoralis* age representing the southerly extension of the Lower Carboniferous sea.

Visean history. As already stated, it is believed that the *anchoralis* Zone is incomplete, only the lower part being present. There is, however, no obvious physical expression of this break in the rock successions except the occasional absence of the *anchoralis* faunas as at Viadangos de Arbas and possibly at Gildar-Montó where Budinger and Kullmann (1964) date the base of the Carboniferous as late Visean.

The Visean begins with the *typicus* Zone, less than 5 m thick, and with a much-reduced conodont abundance of nineteen specimens per kilogram compared to ninety-seven per kilogram in the *anchoralis* Zone, indicating more rapid deposition. At the top of the zone the nodular limestones give way to horizons and nodules of radiolarian cherts in red shales, which are extensively developed in the Porma-Bernesga-Esla area.

Immediately above the chert the fauna changes markedly with the incoming of *Gnathodus bilineatus* and the change reflects the absence of at least one fauna. In comparison with Belgium and Ireland *Paragnathodus commutatus* appears later in Spain, both in the Cantabrian Mountains and in the Pyrenees (Marks and Wensink 1970), by at least one zone. Also absent is the *G. bulbosus* fauna of mid-Osage age (Thompson and Fellows 1970). It is possible that these zones are represented by the chert horizon but in chert-free sections the faunal break is still present. This non-sequence is clearly of more than local significance.

Above the chert the sequence appears to be unbroken, although still condensed, and both the goniatite and the conodont records are complete.

SYSTEMATIC PALAEOLOGY

(A. C. Higgins)

CONODONTS

Where specimens can be related to natural assemblages they are referred to multi-element species such as *Gnathodus bilineatus* and *Idioprioniodus conjunctus*. Where this is not possible specimens are referred to disjunct species. The non-platform elements in the Spanish sections are too disproportionately represented, either due to breakage or selective sorting, to allow the construction of multi-element species by means of similarity of ratios and ranges.

Type and figured specimens are housed in the micropalaeontology collection, Department of Geology, University of Sheffield.

Multi-element species

Genus GNATHODUS Pander, 1856

Type species. *Gnathodus mosquensis* Pander 1856.

Gnathodus bilineatus bilineatus (Roundy) 1926

1926 *Polygnathus bilineata* Roundy, p. 13, pl. 3, fig. 10a-c.

1964 *Gnathodus bilineatus* (Roundy), Schmidt and Müller 1964, p. 114, figs. 7, 8.

P element

Plate 34, figs. 1, 3

For a recent synonymy see Higgins 1975, p. 28.

Remarks. In the *Gnathodus bilineatus* Zone two morphotypes of this species occur. One is the typical form of *G. bilineatus* with an inner platform consisting of a transversely ribbed ridge extending to the posterior end of the platform whereas the other has a short inner platform which does not extend to the posterior end. The latter morphotype was referred to *G. delicatus* by Adrichem Boogaert (1967) and to *G. bilineatus* subsp. nov. by Higgins (1974). Although it bears some similarities to *G. delicatus* it would considerably extend the range of that species, and its occurrence is separated from that species by a stratigraphic gap. It is probably better regarded as a variant of *G. bilineatus* rather than a relative of *G. delicatus*.

O Element

Plate 34, fig. 19

1932 *Bryantodus delicatus* Stauffer and Plummer, p. 29, pl. 2, fig. 27.

1941 *Ozarkodina delicatula* (Stauffer and Plummer), Ellison, p. 120, pl. 20, figs. 40-42, 47.

For a recent synonymy see Higgins 1975, p. 69.

Remarks. The denticles of the O element and the other non-platform elements of *Gnathodus bilineatus* are ornamented with marked striations similar to those of the Oz element of *Idiognathodus delicatus* illustrated by von Bitter (1972). They consist of striations, 1 to 2 microns thick, rounded and sometimes continuous but sinuous and in other instances thickening and thinning down the length of the denticle. This pattern has been described by Norby (1975).

N Element

Plate 34, fig. 25

1933 *Synprioniodina* sp. Gunnell, p. 296, pl. 31, fig. 6.

1941 *Synprioniodina microdenta* Ellison, pp. 108-111, 119, pl. 120, figs. 43-46.

For a recent synonymy see Higgins 1975, pp. 38, 39.

A_{1a+b} Elements

Plate 34, figs. 20, 22

1957 *Hindeodella ibergensis* Bischoff, p. 28, pl. 8, figs. 33, 37, 39.

For a recent synonymy see Higgins 1975, pp. 38, 39.

Remarks. Baesemann (1973) provided a complete description of these two elements. The A_{1a} element, typically with forwardly inclined denticles on the anterior process is illustrated extensively by Higgins (1975, p. 39, fig. 8a, c, d, f). The A_{1b} element, with strongly inwardly flexed denticles on the anterior process is illustrated by Higgins (1975, p. 39, fig. 8b, e).

A_{1c} Element

1959 *Hindeodina uncata* Hass, p. 383, pl. 47, fig. 6.

A recent synonymy is given in Higgins (1975, p. 44).

Remarks. Although this element was not included by Baesemann (1973) or von Bitter (1972) in *Idiognathodus delicatus* it is commonly present in Lower and Upper Carboniferous faunas in association with gnathodid and idiognathodid elements and it was recorded from such assemblages by Schmidt and Müller (1964, p. 117, fig. 9 (6)).

A₂ Element

Plate 34, fig. 24

1957 *Angulodus wabrathi* Bischoff, p. 17, pl. 5, figs. 44, 45.1975 *Hindeodella simplex* (Higgins and Bouckaert), Higgins 1975, pl. 5, figs. 10, 12, 13.

A recent synonymy is given in Higgins 1975, pl. 42.

Remarks. A complete description is given in Higgins and Bouckaert (1968, pp. 28, 29) and Baesemann (1973, p. 704).

A₃ Element

Plate 34, fig. 26

1965 *Hibbardella acuta* Murray and Chronic, p. 598, pl. 73, figs. 3-5.

A recent synonymy is given in Higgins 1975, p. 34.

EXPLANATION OF PLATE 34

All specimens $\times 40$ *Gnathodus bilineatus bilineatus* (Roundy)

Figs. 1, 3. P Element, Villabellaco Section, sample 2902, oral views of 2902 (1 and 2).

Fig. 19. O Element, Olleros de Alba Section, sample OLI, inner lateral views of OLI (1).

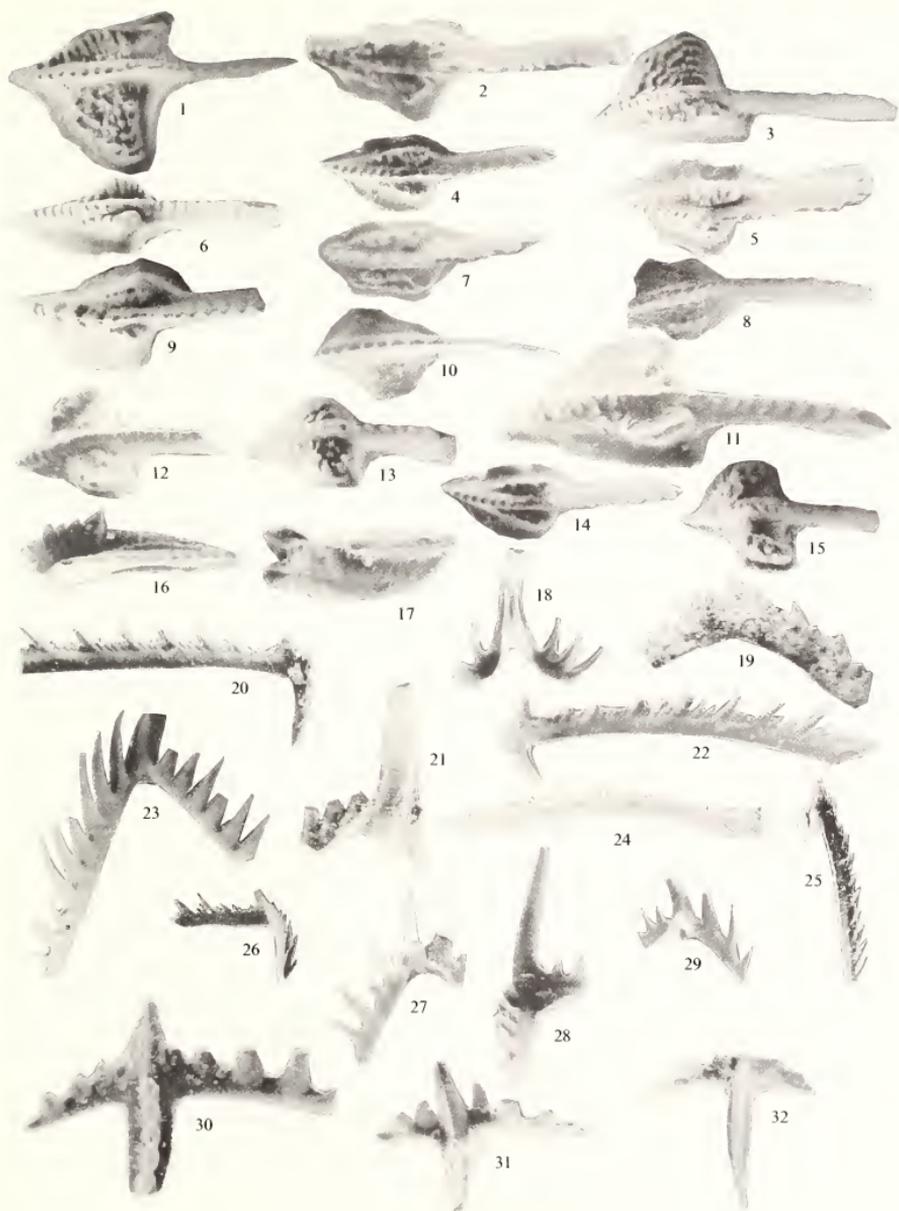
Fig. 20. A_{1b} Element, Entrago Section, sample 1149C, inner lateral view of 1149C (1).Fig. 22. A_{1a} Element, Entrago Section, sample 1149K, inner lateral view of 1149K (1).Fig. 24. A₂ Element, Matallana Section, sample 1060A, inner lateral view of 1060A (1).

Fig. 25. N Element, Entrago Section, sample 1149C, inner lateral view of 1149C (2).

Fig. 26. A₃ Element, Entrago Section, sample 1149K, inner lateral view of 1149K (2).Fig. 2. *Gnathodus delicatus* Branson and Mehl, Pola de Gordón Section, sample 3085, oral view of 3085 (1).Figs. 4, 14. *Gnathodus cuneiformis* Mehl and Thomas. 4, Baleas Quarry, Sample 1264, oral view of 1264 (18).

14, Olleros de Alba Section, sample OLV, oral view of OLV (1).

Fig. 5. *Gnathodus typicus* Cooper. Olleros de Alba Section, sample OLIV, oral view of OLIV (1).Fig. 6. *Gnathodus semiglaber* Bischoff. Baleas Quarry, sample 1264, oral view of 1264 (19).Fig. 7. *Gnathodus homopunctatus* Bischoff. Revilla Section, sample 134V, oral view of 134V (1).Fig. 8. *Protognathodus collinsoni* Ziegler. Santiago de las Villas Section, sample 1310, oral view of 1310 (1).Fig. 9. *Gnathodus girtyi girtyi* Hass. Revilla Section, sample 134IX, oral view of 134IX (1).Fig. 10. *Protognathodus meischneri* Ziegler 1969. Santiago de las Villas Section, sample 1310, oral view of 1310.Fig. 11. *Gnathodus texanus pseudosemiglaber* Thompson and Fellows 1970, Matallana Section, sample 1060A, oral view of 1060A (2).Figs. 12, 13, 15. *Paragnathodus multinodosus* (Wirth). Revilla Section, sample 134IX, oral view of 134IX (2-4).Figs. 16, 17. *Mestognathus beckmanni* Bischoff. Villabellaco Section, sample 2910, oral and aboral views of 2910 (1).*Idioprioniodus conjunctus* (Gunnell)Fig. 18. B_{3a} Element, Entrago Section, sample 1149K, posterior view of 1149K (3).Fig. 21. N₁ Element, Olleros de Alba Section, sample OLI, outer lateral view of OLI (2).Fig. 23. B_{1b} Element, Entrago Section, sample 1149C, inner lateral view of 1149C (3).Fig. 27. N₂ Element, Matallana Section, sample 1060A, outer lateral view of 1060A (3).Fig. 28. B_{1a} Element, Matallana Section, sample 1060A, inner lateral view of 1060A (4).Fig. 29. B_{3b} Element, Matallana Section, sample 1060A, outer lateral view of 1060A (5).Fig. 30. *Scaliognathus* sp. nov. Olleros de Alba section, sample 1340, oral view of specimen 1340 (1), $\times 60$.Fig. 31. *Scaliognathus* sp. nov. Olleros de Alba section, sample OLI, oral view of specimen OLI (5), $\times 60$.Fig. 32. *Scaliognathus* sp. nov. Olleros de Alba section, sample OLI, oral view of specimen OLI (4), $\times 60$.



HIGGINS and WAGNER-GENTIS, Earlier Carboniferous conodonts

Genus IDIOPRIONIODUS Gunnell 1933

- 1933 *Idioproniodus* Gunnell, p. 265.
 1952 *Duboisella* Rhodes, p. 895.
 1972 *Neoproniodus* Rhodes and Müller, von Bitter, p. 68.
 1973 *Idioproniodus* Gunnell, Baesemann, p. 703.
 1974 *Idioproniodus* Gunnell, Merrill and Merrill, pp. 119-130.

Type species. Idioproniodus typus Gunnell, 1933.

Idioproniodus conjunctus (Gunnell) 1931

- 1931 *Prioniodus conjunctus* Gunnell, p. 247, pl. 29, fig. 7.
 1974 *Idioproniodus conjunctus* (Gunnell), Merrill and Merrill, p. 120.

Remarks. Merrill and Merrill (1974) proposed this species for pre-Missourian representatives of *Idioproniodus* which would be assigned to *Idioproniodus typus* (Gunnell) except for the presence of an N₂ (metalonchodiniid) element.

N₁ Element

Plate 34, fig. 21

- 1931 *Prioniodus conjunctus* Gunnell, p. 247, pl. 29, fig. 7.

A complete synonymy is given in Higgins 1975, p. 66.

N₂ Element

Plate 34, fig. 27

- 1931 *Prioniodus bidentatus* Gunnell, p. 247, pl. 29, fig. 6.
 1941 *Metalonchodina bidentata* (Gunnell), Branson and Mehl, p. 106, pl. 19, fig. 34.

A complete synonymy is given in Higgins 1975, p. 63.

B_{1a} Element

Plate 34, fig. 28

- 1933 *Idioproniodus typus* Gunnell, p. 265, pl. 31, fig. 47.
 1941 *Ligonodina tya* (Gunnell), Ellison, p. 114, pl. 20, figs. 8-11.
 1953 *Ligonodina roundyi* Hass, p. 82, pl. 15, figs. 5-9.
 1972 *Neoproniodus conjunctus* (Gunnell), Von Bitter, p. 69, pl. 12, fig. 3, Hi element.
 1973 *Idioproniodus lexingtonensis* (Gunnell), Baesemann, p. 703, pl. 3, fig. 1.

Remarks. Higgins (1975) regarded *Ligonodina roundyi* and *L. tya* as separate species because the former species has discrete anterior process denticles. However, both species have the same range and there are transitional specimens throughout this range.

B_{1b} Element

Plate 34, fig. 23

- 1931 *Prioniodus clarki* Gunnell, p. 247, pl. 29, fig. 8.
 1941 *Lonchodina clarki* (Gunnell), Ellison, p. 116, pl. 20, figs. 21, 27, 30, 31.
 1957 *Lonchodina* cf. *projecta* Ulrich and Bassler, Bischoff, p. 34, pl. 1, fig. 20.
 1961 *Lonchodina* cf. *projecta* Ulrich and Bassler, Higgins, pl. 11, fig. 10.
 1968 *Lonchodina bischoffi* Higgins and Bouckaert, p. 43.
 1972 *Neoproniodus conjunctus* (Gunnell), Von Bitter, p. 69, pl. 12, fig. 4a-c, Pl. element.

- 1973 *Idiopriionodus lexingtonensis* (Gunnell), Baesemann, p. 704, pl. 3, fig. 2, B_{1b} element.
 1975 *Lonchodina bischoffi* Higgins and Bouckaert, Higgins, p. 59, pl. 2, figs. 1-4, 8.

For a complete description see Higgins and Bouckaert (1968), p. 43.

Remarks. None of the illustrated specimens of *Lonchodina clarki* from the Pennsylvanian are as complete as the specimens assigned to *L. bischoffi* which have been described from the Viséan and Namurian. Both the anterior process and the posterior process of the former species are incomplete. None the less, in all other respects the two species are identical and there seems little justification in retaining them as separate species.

B₂ Element

- 1931 *Prioniodus lexingtonensis* Gunnell, p. 246, pl. 29, fig. 4.
 1941 *Ligonodina lexingtonensis* (Gunnell), Ellison, p. 115, pl. 20, figs. 13-15.
 1973 *Idiopriionodus lexingtonensis* (Gunnell), Baesemann, p. 704, pl. 3, figs. 3, 8.

For a more complete synonymy and a description see Higgins (1975), p. 58.

B_{3a} Element

Plate 34, fig. 18

- 1931 *Prioniodus subacodus* Gunnell, p. 246, pl. 29, fig. 5.
 1941 *Hibbardella subacoda* (Gunnell), Ellison, p. 118, pl. 20, figs. 22, 26.
 1953 *Roundya barnettana* Hass, p. 89, pl. 16, figs. 8, 9.
 1958 *Roundya costata* Rexroad, p. 26, pl. 2, figs. 5-8.
 1972 *Neopriionodus conjunctus* (Gunnell), Von Bitter, p. 70, pl. 16, figs. 2a, b, Tr element.
 1973 *Idiopriionodus lexingtonensis* (Gunnell), Baesemann, p. 704, pl. 3, fig. 9, B_{3a} element.

Remarks. Specimens from the Missourian illustrated by Baesemann (1973) and the late Pennsylvanian illustrated by Von Bitter (1972) and referred to *Roundya subacoda* are indistinguishable from early Carboniferous specimens of *R. barnettana*. The distinction between the two species is the massivity of the unit of *R. subacoda* compared to *R. barnettana*. Comparison between them is made difficult by the incomplete nature of the later Pennsylvanian specimens but the distinction would seem to be of superficial importance.

B_{3b} Element

Plate 34, fig. 29

- 1941 *Lonchodina ?ponderosa* Ellison, p. 116, pl. 20, figs. 37-39.
 1958 *Lonchodina paraclaviger* Rexroad, p. 22, pl. 4, figs. 7-10.
 1973 *Idiopriionodus lexingtonensis* (Gunnell), Baesemann, p. 704, pl. 3, figs. 4, 5, B_{3b} element.
 1975 *Lonchodina paraclaviger* Rexroad, Higgins, p. 60, pl. 2, fig. 9.

Remarks. The similarity between *Lonchodina ponderosa* and *L. paraclaviger* is illustrated by Higgins 1975, pl. 2, figs. 9, 11. Both species have processes almost in the same plane, subequal denticles on the anterior process which are approximately equal in size to the cusp, and a similar basal cavity. The subsymmetrical nature of the unit suggests that this is a B₃ element as suggested by Baesemann rather than a B₂ element.

Disjunct elements

Genus DOLIIONATHUS Branson and Mehl, 1941

Type species. *Doliognathus latus* Branson and Mehl, 1941.

Doliognathus latus Branson and Mehl, 1941

For synonymy up to 1967, see Thompson (1967).

- 1970 *Doliognathus latus* Branson and Mehl, Thompson and Fellows, p. 45.
 1971 *Doliognathus latus* Branson and Mehl, Higgins, pl. 2, figs. 1, 3-6, 8.
 1971 *Doliognathus* cf. *latus* Branson and Mehl, Higgins, pl. 2, figs. 2, 7.

Remarks. The considerable variation in this species was illustrated by Voges (1959, p. 274) and Higgins (1971, pl. 2). The typical form, illustrated by fig. 1 of pl. 2 (Higgins 1971) has a transversely ribbed or noded platform, smoothly curved margins, and the outer lateral process is approximately at right angles to the main axis of the unit. The main variant (pl. 2, figs. 2 and 7) has more pronounced platform ribs, strongly irregular platform margins, and the outer lateral process is more strongly curved or directed posteriorly. This latter form was referred to *Doliognathus* cf. *latus* by Higgins (1971).

Genus GNATHODUS Pander, 1956

Type species. *Gnathodus mosquensis* Pander, 1956.

Gnathodus cuneiformis Mehl and Thomas

Plate 34, figs. 4, 14

- 1947 *Gnathodus cuneiformis* Mehl and Thomas, p. 10, pl. 1, fig. 2.
 1971 *Gnathodus* cf. *girtyi* Hass, Higgins, pl. 5, fig. 3.

A more complete synonymy is given in Thompson and Fellows 1970, pp. 45, 46.

Remarks. Thompson and Fellows (1970) pointed out that *Gnathodus cuneiformis* is homeomorphic with *G. girtyi* in the United States where the former species occurs in the Osagean and the latter in the Chesterian Stage. The same pattern can be observed in Spain where *G. cuneiformis* occurs in the *anchoralis* zone of late Tournaisian age and *G. girtyi* occurs in the *bilineatus* Zone of late Viséan age. The range of variation of *G. girtyi* is much greater than that of *G. cuneiformis* but symmetrically platformed specimens of both species are indistinguishable.

Gnathodus delicatus Branson and Mehl

Plate 34, fig. 2

- 1938 *Gnathodus delicatus* Branson and Mehl, p. 145, pl. 34, figs. 25-27.
 1971 *Gnathodus delicatus* Branson and Mehl, Higgins, pl. 5, figs. 5, 7, 8, 11, 13.

Recent synonymies have been given by Butler (1973, p. 497) and Matthews *et al.* (1972, p. 559).

Remarks. Butler (1973) commented that specimens from the upper part of the range of this species show the development of a distinct parapet at the anterior end of the inner side of the platform. This form (pl. 5, figs. 5, 7 of Higgins 1971) also occurs in the Spanish sections where it overlaps the range of *Gnathodus antetexanus*, a species which, as pointed out by Butler, has a similar feature.

Gnathodus girtyi girtyi Hass, 1953

Plate 34, fig. 9

- 1953 *Gnathodus girtyi* Hass, p. 80, pl. 14, figs. 22-24.
 1975 *Gnathodus girtyi girtyi* Hass, Higgins, p. 31, pl. 10, figs. 5, 6.

A more complete synonymy is given in Higgins (1975), p. 31.

Remarks. Only the weakly ornamented subspecies of *Gnathodus girtyi* is represented in the Spanish succession and it is a rare species.

Gnathodus typicus Cooper, 1939

Plate 34, fig. 5

1939 *Gnathodus typicus* Cooper, p. 388, pl. 42, figs. 77, 78.1964 *Gnathodus typicus* Cooper, Rexroad and Scott, p. 31, pl. 2, fig. 3.1970 *Gnathodus typicus* Cooper, Thompson and Fellows, pp. 89, 90, pl. 3, figs. 3, 13.

Remarks. Specimens with a short anteriorly pointing inner platform and a weakly ornamented outer, wide, and rounded platform are referred to this species. Expansion of the carina would allow it to be placed in *Gnathodus semiglaber* with which species it has much in common.

Genus PARAGNATHODUS Higgins, 1975

Type species. *Spathognathodus commutatus* Branson and Mehl, 1941.

Remarks. *Paragnathodus commutatus* and *P. nodosus* (Bischoff) 1957, have recently been described by Higgins 1975, pp. 70–72. The composition of the multi-element genus is unknown but it is likely to correspond to the natural assemblage *Lochreia* of Scott 1942.

Paragnathodus multinodosus (Wirth), 1967

Plate 34, figs. 12, 13, 15; text-fig. 10b

1962 *Gnathodus commutatus* var. *multinodosus* Higgins, pp. 8, 9, pl. 2, figs. 13–18.1967 *Gnathodus commutatus multinodosus* n.ssp. Wirth, p. 208, pl. 19, figs. 19, 20.1974 *Gnathodus commutatus multinodosus* Higgins, Austin and Husri, pl. 2, fig. 13.

Discussion. Variation in this species is mainly seen in the shape of the cup and its ornamentation. The cup shape can vary from being subsymmetrical to asymmetrical where the inner side is strongly folded both anteriorly and posteriorly and does not gradually taper to the posterior. The nodes typically evenly cover the platform surface where they are situated on a slightly raised shelf. Pl. 34, fig. 12, illustrates a specimen in which the nodes are raised on two anteriorly directed ridges identical to those found in *Paragnathodus nodosus* and it may be a variant of this species. Scanning photographs reveal the presence of micronodes on the major nodes of *P. multinodosus* (Pl. 35, fig. 2).

Remarks. The distribution of this species is very restricted. Apart from its widespread presence in the Cantabrian Mountains it occurs in the Pyrenees (Wirth 1967; Marks and Wensink 1970; Perret 1974) and possibly in Ireland (Austin and Husri 1974) but is unknown elsewhere despite the large numbers of faunas of this age which have been described. The Irish occurrence is abnormal because it apparently occurs before *P. nodosus*, whereas in Spain it appears slightly later.

Genus SCALIOGNATHUS Branson and Mehl, 1941

Type species. *Scaliognathus anchoralis* Branson and Mehl, 1941.

Discussion. Despite the widespread nature and stratigraphical importance of this distinctive anchor-shaped genus it remains monospecific. The Spanish successions, being condensed and broken by non-sequences, do not give a clear pattern of evolution of the genus. Nevertheless, the material is well preserved and abundant, and it is possible to identify the main variations in the genus. Three main forms are recognized:

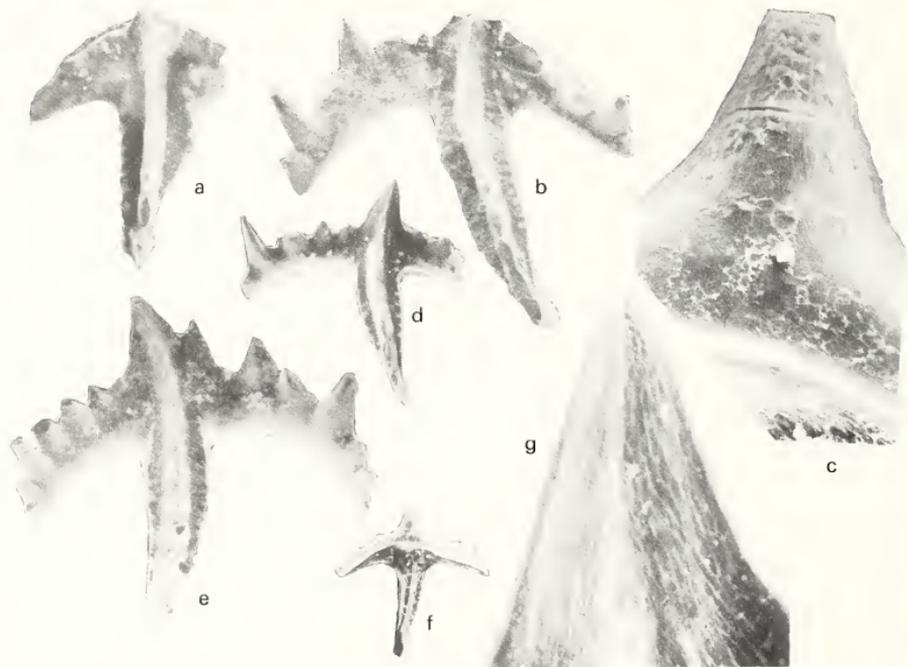
1. Forms with plate-like lateral and anterior processes. These are referred to *Scaliognathus anchoralis*.
2. Forms with a plate-like anterior process, but blade-like subequal lateral processes which are curved anteriorly. These are referred to *S. angustilateralis* sp. nov.
3. Forms with straight unequal lateral limbs which project at right angles to the anterior process. The posterior limbs are blade-like. These are referred to *Scaliognathus* sp. nov.

Groessens (1977a) suggested an origin for *Scaliognathus* from *Dollymae bouckaerti* (Groessens) in which the first scaliognathid was a slender, highly arched form with poor plate development. This form would resemble form 2 above.

Scaliognathus anchoralis Branson and Mehl, 1941

Text-fig. 9a, b, d, g

- 1941 *Scaliognathus anchoralis* Branson and Mehl, p. 102, pl. 19, figs. 29-32.
 1964 *Scaliognathus anchoralis* Branson and Mehl, Higgins *et al.* pl. iv, fig. 17.
 1967 *Scaliognathus anchoralis* Branson and Mehl, Adrichem Boogaert, p. 50, pl. 5, figs. 2-4, 8, 9.
 1969a *Scaliognathus anchoralis* Branson and Mehl, Matthews, pp. 272, 273, pl. 49, figs. 2, 4, 8, and 9 only.
 1969b *Scaliognathus anchoralis* Branson and Mehl, Matthews, pl. 51, figs. 1, 2.
 1971 *Scaliognathus anchoralis* Branson and Mehl, Groessens, pl. 1, fig. 10 only.
 1971 *Scaliognathus anchoralis* Branson and Mehl, Higgins, pl. 3, figs. 3, 5-7, 9; pl. 4, fig. 2.
 1974 *Scaliognathus anchoralis* Branson and Mehl, Matthews and Thomas, pl. 50, figs. 8, 9.
 1974 *Scaliognathus anchoralis* Branson and Mehl, Jenkins, pl. 119, figs. 6-9.



TEXT-FIG. 9. *a*, *Scaliognathus anchoralis* Branson and Mehl. Olleross de Alba section, sample 1340, oral view of specimen 1340 (2), $\times 60$. *b*, *Scaliognathus anchoralis* Branson and Mehl. Baleas Quarry, sample 1264, oral view of specimen 1264 (23), $\times 60$. *c*, *f*, *Scaliognathus angustilateralis* sp. nov. Baleas Quarry, sample 1264; fig. *c* aboral view of cusp, $\times 1080$; fig. *f* aboral view of specimen 1264 (20), $\times 60$. *d*, *g*, *Scaliognathus anchoralis* Branson and Mehl. Olleross de Alba section, sample OLI; fig. 5 oral view of specimen OLI (3), $\times 60$; fig. *g* detail of main denticle, $\times 360$. *e*, *Scaliognathus angustilateralis* sp. nov. Baleas Quarry, sample 1264, oral view of holotype, specimen 1264 (22), $\times 60$.

Diagnosis. Paired conodonts with an anchor-like shape consisting of three processes. The anterior process is wide, tapering to its anterior extremity, the two posterior lateral processes are also wide and plate-like with a row of posteriorly inclined denticles on a flat and horizontal upper surface, which is in the same plane as the surface of the lateral process.

Description. The anterior limb is broad at the posterior tapering anteriorly with a convex outer and a convex, straight or slightly concave, inner margin. There is a prominent median carina consisting of large discrete denticles at the anterior becoming fused into a low ridge towards the posterior. At the posterior the carina is continued beyond the extremity of the platform as a horn-like denticle which is commonly large and may have a triangular cross-section where the carinal ridge continues up its oral face, but there is no sign of this in the holotype which has a small posterior denticle. There is commonly a sulcus on either side of the carina and bordering the sulci is a row of nodes which may develop into transverse ridges. The lateral extension of the anterior limb is marked, giving rise to a plate-like structure with sharp margins and a flat to concave upper surface.

The lateral processes are as long or slightly shorter than the anterior limb either in length, denticulation, or curvatures. They are projected or curved anteriorly at approximately 70° to the anterior limb and, if curved, curvature is stronger on the outer limb. They are as wide or wider than the anterior limb in the median area of the unit but taper to a point. The oral surface is flat and in the same plane as the oral surface of the anterior limb with which it is continuous. There is commonly a row of low nodes along its anterior margin. Near, or at the posterior margin, is a row of posteriorly inclined denticles which may be subequal in size or increase slightly in height towards the extremity of the limbs. The holotype and paratype have a prominent shelf, with a row of the transverse ridges posterior to the denticle row, but this is atypical for the species in general and more commonly the shelf, although often present, is insignificant. The denticles may be discrete, but are more commonly in contact in the lower third of their length.

The aboral surface of both the anterior and the lateral limbs is convex and smooth except for prominent split keels which are grooved along their length. The keels meet at the centre of the lateral limbs and a triangular open pit which is open in small specimens but becomes more closed in adult specimens. The anterior face of the lateral process is almost at right angles to the oral face, whereas the posterior face is at an angle of approximately 45 degrees.

Discussion. The holotype of Branson and Mehl (1941, pl. 19, figs. 30, 32) has very broad plate-like lateral processes and a denticular row which originates near the midline of these processes. The specimen figured by Jenkins (1974, pl. 119, fig. 6) is close to the holotype but few others, mainly from Europe, are exactly of this type. The description and diagnosis given above retains the plate-like nature of the processes but the typical specimen has a denticular row originating from the posterior edge of the processes which typifies the majority of figured specimens. This redefinition of the species would include form 1 and possibly form 2 of Matthews (1969a).

Range. *Scaliognathus anchoralis* Zone.

No. of specimens fifty.

Scaliognathus angustilateralis sp. nov.

Text-fig. 9c, e, f

- 1967 *Scaliognathus anchoralis* Branson and Mehl, Adrichem Boogaert, p. 185, pl. 3, fig. 11.
 1969 *Scaliognathus anchoralis* Branson and Mehl, Matthews, pp. 272, 273, pl. 49, figs. 1, 6 only.
 1971 *Scaliognathus anchoralis* Branson and Mehl, Groessens, pl. 1, fig. 9 only.
 1971 *Scaliognathus anchoralis* Branson and Mehl, Higgins, pl. 3, figs. 1, 2, 4, 8, 10 only.
 1973 *Scaliognathus anchoralis* Branson and Mehl, Butler, p. 510, pl. 58, figs. 6 and 7 only.

Derivation of name. Refers to the narrowness of the lateral process.

Holotype. Text-fig. 9d, from the Baleas Formation, Baleas Quarry, Pola de Gordón. Slide 1264(22).

Diagnosis. A species of *Scaliognathus* with narrow lateral processes which are posteriorly inclined, curved anteriorly, and in the same plane as the row of denticles which are developed on its surface.

Description. The anterior limb is slender, plate-like, with a convex outer and convex to concave inner margin which are approximately parallel in the posterior half but taper sharply in the anterior half usually terminating before the end of the process. The oral surface of the limb is bisected by a median carina consisting of partially fused, large denticles in the anterior half which becomes a fused, low, nodular ridge in the posterior half extending up the oral face of the horn-like terminal denticle. The margins of the limb are slightly crenulate because of the development of a row of nodes and transverse ridges on each side. These are separated from the carina by a shallow sulcus.

The lateral limbs are subequal and are curved anteriorly, often strongly, and in extreme variants the anterior half of the outer limb may be parallel to the anterior limb. There is no development of a plate on the limbs and they consist of narrow, strongly posteriorly inclined and often curved, blade-like processes. There may be a row of small nodes along the anterior margin or the oral face may be smooth. The denticles originate from the posterior margin and are in the same plane as the processes. They are long, discrete for more than half their length, and laterally compressed.

The aboral side is convex and has a raised split keel which meets in a triangular pit.

The oral surface of the platform adjacent to the main denticle and the carina is covered by an irregular to hexagonal pattern of furrows. These cross and interrupt a pattern of branching fine striae. The oral surface of the main denticle also has a pattern of coarse striations but raised rather than sunken and always semiregular. These run approximately parallel to the margin of the denticle and meet at the ridge which bisects it. There are no fine striae on the oral surface. The aboral surface has an irregular pattern of coarse striations, again ridges, overlying a finer one, but in this instance the finer one may branch off the coarser ones. These patterns are also found in *Scaliognathus anchoralis* and *Scaliognathus* sp. nov.

Range. Lower part of the *anchoralis* Zone.

No. of specimens sixty.

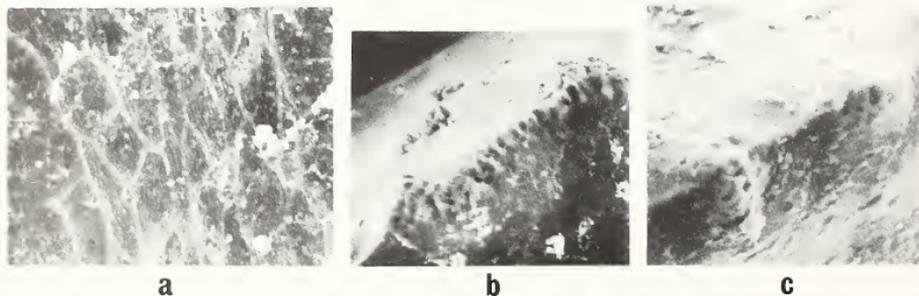
Scaliognathus sp. nov.

Plate 34, figs. 30-32; text-fig. 10a

1969 *Scaliognathus anchoralis* Branson and Mehl, Matthews, pp. 272, 273, pl. 49, figs. 5 and 7 only.

Description. Anterior limb is slender and strongly arched with convex margins to a weakly developed plate. The oral surface of the plate is unornamented and smooth except for the median row of discrete pointed denticles which are inclined posteriorly.

The lateral limbs are unequal, the outer being up to twice the length of the inner. Both limbs are slender, being only slightly thickened adjacent to the junction with the anterior limb. They are steeply inclined, almost vertical, with a slight inclination towards the posterior. Their oral edge is ornamented with discrete, long denticles which are laterally flattened, with up to five on the outer and two or three on the inner side. The denticles are in the same plane as the limbs. The largest denticle is at the end of the carina and is triangular being bisected by a low ridge.



TEXT-FIG. 10. *a*, *Scaliognathus* sp. nov. Detail of platform area adjacent to main denticle of specimen 1340 (1), $\times 1080$. *b*, *Paragnathodus multirnodosus* (Wirth). Detail of carinal node of specimen 1341X, $\times 550$. *c*, *Protognathodus meischeri* Ziegler 1969. Detail of carinal node of specimen 1310 (2), $\times 550$.

The aboral side of the anterior limb is convex but that of the lateral limb is sharp edged except adjacent to their junction with the anterior limb. All the limbs have split keels which meet in a triangular cavity beneath the base of the triangular denticle.

Range. Upper part of the *anchoralis* Zone.

GONIATITES

(C. H. T. Wagner-Gentis)

Family PROLECANITIDAE Hyatt, 1884
Genus MEROCANITES Schindewolf, 1922

Type species. *Ellipsolithes compressus* Sowerby, 1813.

Merocanites marshallensis (Winchell)

Plate 35, figs. 1, 2, 6; text-fig. 11a, b

1862 *Goniatites Marshallensis* Winchell, pp. 362, 363.

1955 *Merocanites marshallensis* Winchell, Miller and Garner, pp. 154-157, pl. VII, figs. 5-9, text-figs. 13C and 16.

Material. Two specimens and a large number of whorl-sections from localities 138, 138D, 1548, from the Villabellaco Limestone in Palencia.

Description. The shell is a serpenticone with a rectangular cross-section of the whorl. The venter and ventro-lateral edge are both rounded, the umbilical wall is flat and perpendicular to the lateral side (see text-fig. 11b). Neither ornament nor constrictions have been observed. The suture consists of an inflated ventral lobe of which the siphonal point can be rather long. The ventro-lateral saddle is rounded, constricted, and low. The first lateral lobe is pointed, constricted, and not as deep as the ventral lobe, but it is wider than the ventral or second lateral lobe. The following lateral saddle is rounded, constricted, and higher than the ventro-lateral saddle. The second lateral lobe is pointed, constricted, and longer than the first lateral lobe. The last lateral saddle is rounded, constricted, and smaller than the preceding saddles. The third lateral lobe is pointed, considerably smaller than the previous lateral lobes, and slightly asymmetrical. The suture crosses the umbilical wall in a straight line, sloping downwards. It forms a lobe on the dorsal side, which is followed by a narrow, rounded saddle. The median, dorsal lobe is narrow, long, and rounded (see text-fig. 11a).

The dimensions of one of the shells (loc. 138D) are: diameter 38 mm; width 10 mm; umbilicus 14 mm; height of whorl 15 mm; opening 13 mm.

Remarks. *Merocanites marshallensis europaeus* Kullmann, 1963, pp. 276-278, from the Esla area and Puente de Alba, province of León, is quite different from *M. marshallensis* (Winchell), in that its whorl cross-section is too circular, its ventral lobe, although inflated, is considerably slimmer, and its third lateral lobe is too developed.

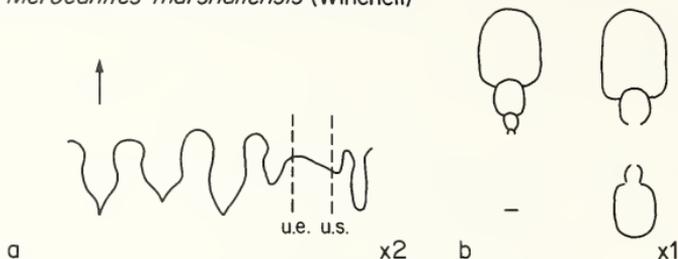
Comparisons. The specimens described here differ from *M. applanatus bicarinatus* Pareyn in that the first lateral lobe is wider; the whorls are slightly more indented and, above all, no remnants are found of any ventro-lateral ridges. One specimen from Olleros de Alba (León), which is identical to *bicarinatus*, shows very clearly the differences mentioned above.

Occurrence. *M. marshallensis* (Winchell) is known from the Marshall Sandstone in Michigan, U.S.A., where it occurs together with *Winchelloceras allei*, *Muensteroceras oweni*, *Kazaklistania karagandaensis*, *Gattendorfa stunni*, and *Imitoceras romingeri* which indicate a basal Osagean age (Furnish and Manger 1973, p. 3). In the Villabellaco Limestone (Palencia), it occurs together with *Merocanites subhenslowi*, *Nautellipsites hispanicus*, *Ammonellipsites kayseri*, and *Pseudogirtyoceras villabellaco* at 1.5 to 2.5 m above the base of the limestone, which indicate a lowest Viséan age.

Family MUENSTERO CERATIDAE Librovitch, 1957

Genus MUENSTERO CERAS Hyatt, 1883

Type species. *Goniatites oweni* var. *parallela* Hall, 1860.

Merocanites marshallensis (Winchell)

TEXT-FIG. 11. *a*, Suture of specimen BM(NH) C.82316. *b*, Cross-section of same specimen.

Muensteroceras parallellum (Hall)

Plate 35, figs. 4, 5; text-fig. 12

- 1860 *Goniatites oweni* var. *parallela* Hall, p. 100, figs. 13–14.
 1903 *Muensteroceras parallellum* Hall, J. P. Smith, pp. 121, 122, pl. XVI, fig. 3; pl. XIX, figs. 1, 2.
 1927 *Muensteroceras* aff. *parallellum* Hall, Librovitch, pp. 32, 33, pl. V, figs. 8, 9; pl. VI, fig. 1.
 1951 *Munsteroceras parallellum* Hall, Miller and Collinson, p. 471, fig. 7.
 1961 *Munsteroceras parallellum* Hall, Pareyn, pp. 96, 97, pl. VII, figs. 1–3.

Material. One solid specimen from locality 136B from the Villabellaco Limestone (Palencia).

Description. The shell is a very flat, involute platycone, with rounded venter and flat sides. At a diameter of 60 mm the width measures 15 mm. The umbilicus is poorly preserved, but is probably one-sixth of the diameter. The previous whorl, however, at a diameter of 22 mm has a width of 10 mm, which is twice as wide as the last whorl. It also has more rounded lateral sides than those of the last whorl. Neither constrictions nor ornament are preserved. The sutures consist of ventral lobes with parallel sides which touch each other, and thus form two parallel lines on the venter. The ventro-lateral saddles are fairly narrow and rounded; the lateral lobes are V-shaped and their points reach lower than the ventral lobes; they do not, however, touch the preceding ventro-lateral saddles. The lateral lobes are wide and rounded. There is a small, narrow, pointed umbilical lobe on the umbilical edge. The dimensions of the shells are: diameter 60 mm; width 15 mm; umbilicus 10–12 mm; height of whorl 25 mm.

Comparisons. *Muensteroceras parallellum* is very similar to *M. rotella* de Koninck but the latter appears to differ by having the ventral lobes encasing each other, whereas in *M. parallellum* they only touch each other.

EXPLANATION OF PLATE 35

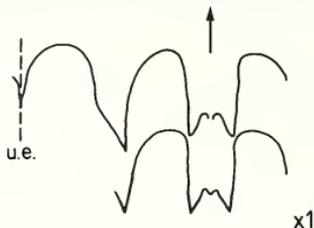
- Fig. 1. *Merocanites marshallensis* (Winchell). BM(NH) C.82315. Lateral view, showing the rather wide ventro-lateral lobe, $\times 3$.
 Fig. 2. *Merocanites marshallensis* (Winchell). BM(NH) C.82316. Lateral view, showing shape of shell, $\times 3$.
 Fig. 3. *Muensteroceras* cf. *crassum* (Foord). BM(NH) C.82318. Ventro-lateral view, showing sutures, $\times 3$.
 Fig. 4. *Muensteroceras parallellum* (Hall). BM(NH) C.82317. Showing lateral and part of ventral sutures, $\times 1$.
 Fig. 5. *Muensteroceras parallellum* (Hall). Same specimen as fig. 4. Lateral view, showing the different shapes of the last and penultimate whorl, $\times 1$.
 Fig. 6. *Merocanites marshallensis* (Winchell). BM(NH) C.82315. Ventral view, showing inflated ventral lobe, $\times 1$.



HIGGINS and WAGNER-GENTIS, Earlier Carboniferous goniatites

Occurrence. Villabellaco Limestone, locality 136b, at approximately the same horizon as 138c, but further east in the outcrop. *M. parallelum* was found originally in the Rockford Limestone of Indiana, U.S.A. It is also known from Hassi Sguilma in Algeria, in the S_1 unit of Pareyn 1961, and from the Tien Shan in Central Asia (Librovitch 1927).

Muensteroceras parallelum (Hall)



TEXT-FIG. 12. Suture of specimen BM(NH) C.82317.

Muensteroceras cf. *crassum* Foord

Plate 35, fig. 3; text-fig. 13

- 1903 *Glyphioceras* (*Muensteroceras*) *crassum* Foord. pp. 193–194, pl. XLIII, fig. 10a-c.
 1927 *Muensteroceras crassum* Foord; Librovitch, pp. 34–35, pl. VI, fig. 6a-c.
 1941 *Muensteroceras crassum* Foord; Delépine, p. 58, pl. II, figs. 4–6.
 1961 *Muensteroceras crassum* Foord; Pareyn, pp. 100–101, pl. VIII, figs. 11–16.
 1964 *Muensteroceras* cf. *crassum* Foord; Wagner-Gentis in Higgins *et al.*

Material. One solid specimen from the Villabellaco Limestone, found between localities 138b and c.

Description. The shell is an involute ellipsocone. Width about half the diameter. The whorls have a rounded venter and rounded sides, with the greatest width near the umbilicus. The umbilicus is approximately one-quarter of the diameter. Umbilical edges are rounded and the umbilical wall is almost perpendicular and sloping towards the centre of the umbilicus (see text-fig. 13b).

No ornament has been preserved. There is a faint, shallow impression of a constriction which crosses three-quarters of the sides more or less in a straight line, and then forms a rounded sinus across the venter.

The suture line consists of a fairly narrow, parallel-sided ventral lobe with a low median saddle. The ventrolateral saddles are rounded and narrow; the lateral lobes are pointed and as deep as the ventral lobe. The ventral side of the lateral lobe is straight, whereas the umbilical side is curved. The second lateral saddle is low, wide, and rounded. The umbilical lobe is small and pointed, and situated just past the umbilical edge, on the umbilical wall (see text-fig. 13a). The suture lines do not encase each other.

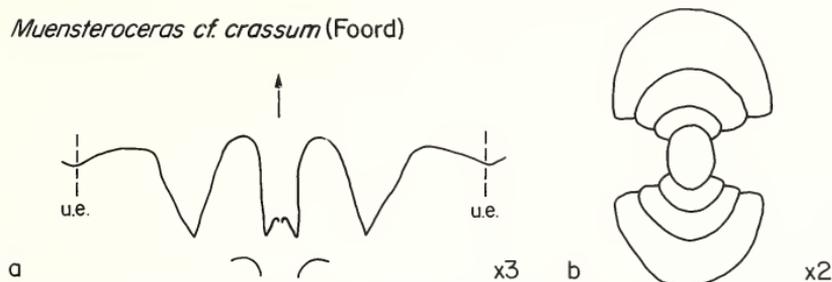
Dimensions. Diameter 23 mm; width 12 mm; umbilicus 6 mm; height of whorl 9 mm.

Comparisons. The specimen compares with *Muensteroceras subglobosum* Librovitch, 1927, pp. 35–36, text-fig. 17; pl. VI, fig. 7; pl. VII, figs. 1, 2, in having a similar suture line, but differs in having a larger umbilicus.

Occurrence. Villabellaco Limestone (Palencia) between the localities 138b and c. It has also been described from Olleros de Alba (León). *M. crassum* was first recorded from the Lower Carboniferous Limestone of Ballinacarriga, Co. Limerick, Eire. It is also known from Hassi Sguilma, in Algeria, in the S_1 unit of Pareyn (1961), and from the Tien Shan in Central Asia (Librovitch 1927).

Family PERICYCLIDAE HYATT, 1900
 Genus AMMONELLIPSITES Parkinson, 1822

Type species. *Ellipsolithes funatus* Sowerby, 1814.

Muensteroceras cf. crassum (Foord)TEXT-FIG. 13. *a*, Suture of specimen BM(NH) C. 82318. *b*, Cross-section of same specimen.*Ammonellipsites kayseri* (Schmidt)Plate 36, figs. 2, 3, 5-7; text-fig. 14*a, b*1889 *Pericyclus virgatus* Holzapfel, p. 34, Taf. III, figs. 8, 9.1925 *Pericyclus kayseri* Schmidt, pp. 554, 555, Taf. 20, fig. 10.

Material. Ten specimens from the Villabellaco Limestone (Palencia) and one specimen from Olleros de Alba (León). All show sutures and a number show the ornament fairly clearly or at least traces of the ornament. A plaster cast of Holzapfel's specimen (1889, III, figs. 8, 9) has been used in the description.

Description. The shell is discoidal, involute with a small umbilicus. The venter and the sides are rounded. The early whorls are wider than high, but gradually become higher than wide. The greatest width is half-way down the lateral side of the whorl. The umbilicus, about one-fifth of the diameter, has rounded shoulders and rounded sides, which are perpendicular to the lateral sides (see text-fig. 14*b*).

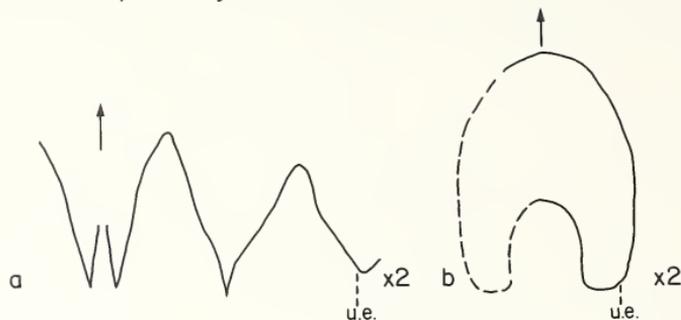
The ornamentation consists of fairly fine undivided ribs, which lean slightly forward over the sides, and form a very shallow sinus over the venter. The ribs are sharp edged and on the venter the distance between the ribs is more than the width of the rib itself. A specimen with a diameter of about 20 mm has six ribs per 5 mm, on the venter. No constrictions are observed.

The suture consists of a medium saddle, which reaches to one-third of the ventro-lateral saddles. These are slightly spatulate with rounded points and have a tendency to diverge. The rounded points are due to the easy erosion of the sharp point. The lateral lobe is spatulate and pointed. The second lateral saddle is spatulate with a rather blunted point and reaches four-fifths of the height of the first lateral saddle. The umbilical lobe is situated on the umbilical wall and is pointed and wide.

B.M. (N.H.) numbers	Villabellaco Limestone			Plastercast of holotype Holzapfel's specimen
	C82324	C82321	C82322	
Diameter	20 mm	19 mm	—	38.5 mm
Width	10 mm	11 mm	17 mm	19 mm
Umbilicus	—	4 mm	—	8 mm
Height of whorl	8 mm	8 mm	20 mm	17 mm
Height of opening	—	6 mm	12 mm	12 mm

Comparison. The specimens look very similar to *Pericyclus virgatus* de Koninck, and Holzapfel identified his specimens from Liebstein with this species. Unfortunately, *Pericyclus virgatus* does not show any sutures and it is therefore impossible to decide whether *kayseri* is the same as *virgatus*.

Occurrence. In the Erdbach and Breitscheid cephalopod limestone at Liebstein, Germany (Holzapfel 1889, pp. 34 and 35; Schmidt 1925, p. 494), which according to Schmidt (1925) belongs to the I_7 zone of the Viséan, which

Ammonellipsites kayseri (Schmidt)

TEXT-FIG. 14. *a*, Suture of specimen BM(NH) C.82322. *b*, Cross-section of specimen BM(NH) C.82322.

is also known as the *Pey* of the Erdbachium, the very base of the Visean. From Spain, Schmidt (1931, p. 1035) recorded it together with *P. kochi*, *Imiteroceras* sp., *Merocanites applanatus*, *Muensteroceras* aff. *inconstans*, *M. cf. spheroidale*, in Palencia at 1.3 to 2.8 m above the base of the Villabellaco Limestone, and in León at Olleros de Alba. In Great Britain it is mentioned by Prentice and Thomas (1960, p. 6) from Tawstock and Codden Hill where it occurs with *Prolecanites* aff. *similis*.

Family GIRTYOCERATIDAE Wedekind, 1918

Genus WINCHELLOCERAS Ruzhencev, 1965

Type species. Beyrichoceras allei Miller and Garner, 1955.

Winchelloceras palentinus sp. nov.

Plate 36, fig. 1; text-fig. 15a-c

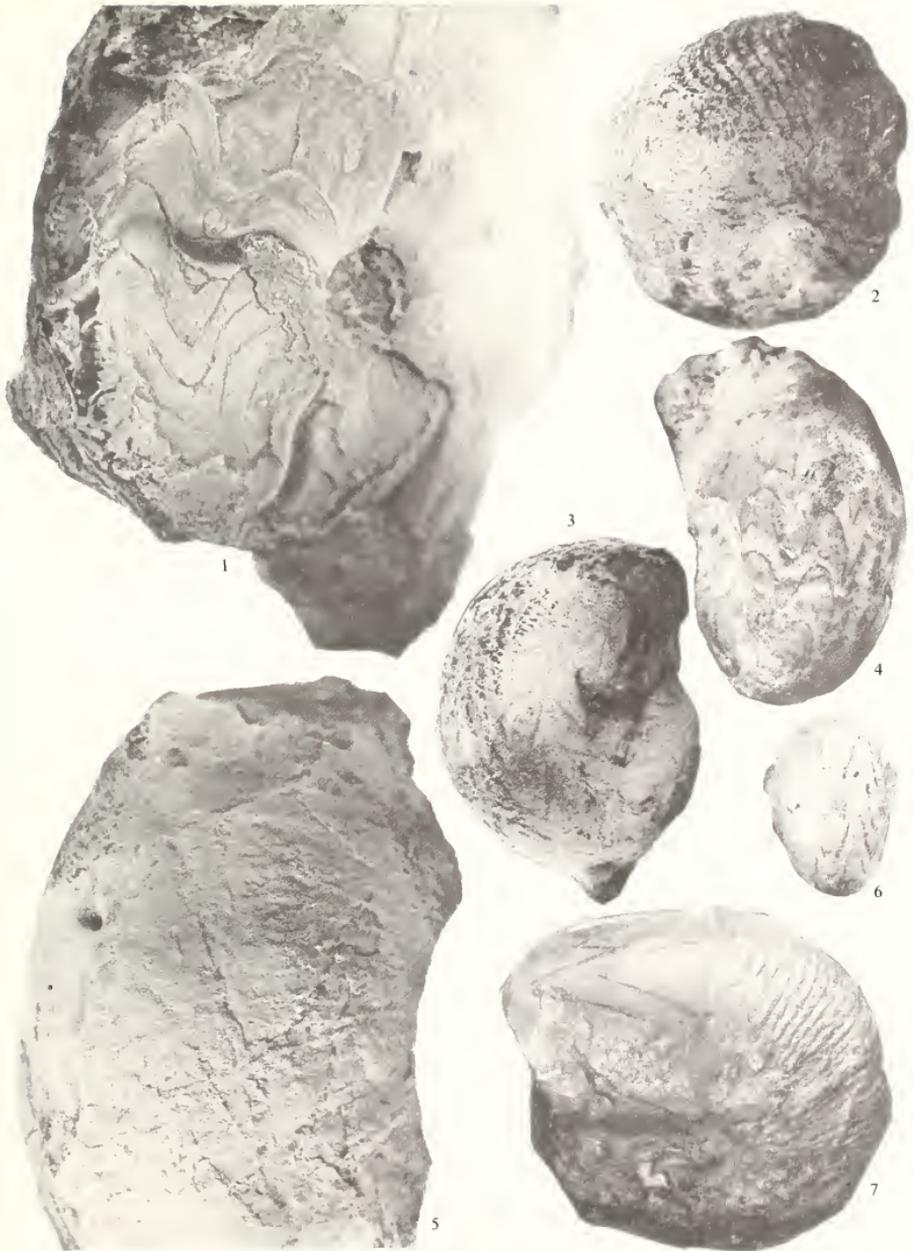
Type material. One solid specimen preserved in a marly limestone, showing part of the living chamber, sutures, and constrictions.

Repository of holotype. British Museum (Nat. Hist.), No. C82317.

Diagnosis. Shell involute, platyconiform with an umbilicus less than one-sixth of the diameter. Constrictions strongly marked, with a deep, narrowly rounded sinus on the venter, ventro-lateral

EXPLANATION OF PLATE 36

- Fig. 1. *Winchelloceras palentinus* sp. nov. BM(NH) C.82319. Ventro-lateral view, showing sutures and constriction, $\times 3$.
 Fig. 2. *Ammonellipsites kayseri* (Schmidt). BM(NH) C.82324. Ventro-lateral view, showing ornament, $\times 3$.
 Fig. 3. *Ammonellipsites kayseri* (Schmidt). BM(NH) C.82320. Ventro-lateral view, showing ornament and suture, $\times 3$.
 Fig. 4. *Pseudogirtyoceras villabellaco* sp. nov. BM(NH) C.82323. Ventro-lateral view, showing sutures and keeled venter, $\times 3$.
 Fig. 5. *Ammonellipsites kayseri* (Schmidt). BM(NH) C.82322. Lateral view, showing traces of ornament and sutures, $\times 3$.
 Fig. 6. *Ammonellipsites kayseri* (Schmidt). BM(NH) C.82321. Ventral view showing sutures, $\times 2$.
 Fig. 7. *Ammonellipsites kayseri* (Schmidt). Plastercast of holotype. Lateral view, $\times 1.5$.

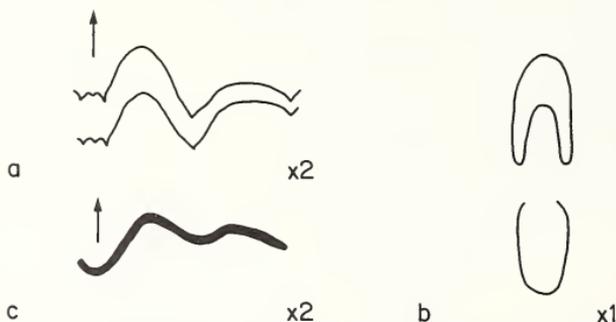


HIGGINS and WAGNER-GENTIS, Earlier Carboniferous goniatites

salient, shallow sinus, and low salient on the lateral sides. Suture with a ventral lobe, of which the spikes are pointed outwards and the cheeks strongly diverging apically. At a diameter of 38 mm the median saddle is still at the very bottom of the ventral lobe. Ventro-lateral saddle rounded, lateral lobe pointed, second lateral saddle wide and rounded. A small V-shaped umbilical lobe is positioned on the umbilical wall.

Description. The shell is a nearly flat, involute platycone. The fairly flat, only slightly rounded, venter is perpendicular to the almost flat lateral sides. The ventro-lateral edge is rounded and there is a suggestion of a groove just below the edge. From there, the lateral side gently curves to become flat near the umbilical region, where the shell has its greatest width. The umbilicus is small, and stepped with rounded edges and narrow walls, which are perpendicular to the sides (see text-fig. 15b).

Winchelloceras palentinus nov. sp.



TEXT-FIG. 15. *a*, Suture of specimen BM(NH) C.82319. *b*, Cross-section, same specimen. *c*, Constriction, same specimen.

No ornament is preserved. The shell shows four deep, narrow constrictions per whorl. They form a deep, narrowly rounded sinus over the venter and a ventro-lateral salient, which may create the impression of a ventro-lateral groove. On the lateral side the constrictions form a shallow sinus and low salient. They then fade out into the umbilicus (see text-fig. 15c).

The sutures have a ventral lobe with an extremely low median saddle, flanked by spikes that are pointing outwards. The cheeks of the ventral lobe are sinuous, first bending outwards and then straightening, in a manner which is opposite to the sinuous cheeks of the ventral lobe in the beyrichoceratids. The ventro-lateral saddles are rounded. The pointed lateral lobes are wide and slightly inflated and the second lateral saddles are wide and rounded, ending in a small V-shaped lobe on the umbilical wall (see text-fig. 15a). There are twelve sutures visible on the last whorl, half of the whorl forming the living chamber.

The dimensions of the shell are: diameter 38 mm; width 10 mm; umbilicus 6 mm; height of whorl 19 mm; height of opening 7 mm.

Comparisons. Differs from *Winchelloceras allei* in having a lower median saddle, a flatter venter, and generally a slimmer outline.

Occurrence. Found in the basal 50 cm of the Villabellaco Limestone (Palencia) section. The genus is known from the U.S.A., where it occurs in the Coldwater shale/Marshall sandstone of Michigan, which is of basal Osagean age (Furnish and Manger 1973). It is also recorded from Tien Shan (Popov 1968) and the Urals (Popov 1975) in rocks of C_1V_1 age.

PSEUDOGIRTYOCERAS gen. nov.

Type species. *Pseudogirtyoceras villabellacoi* sp. nov.

Diagnosis. *Pseudogirtyoceras* closely fits the description of *Girtyoceras*, but is distinguished by having a narrow ventral lobe.

Repository of type species. British Museum (Nat. Hist.), No. C82323.

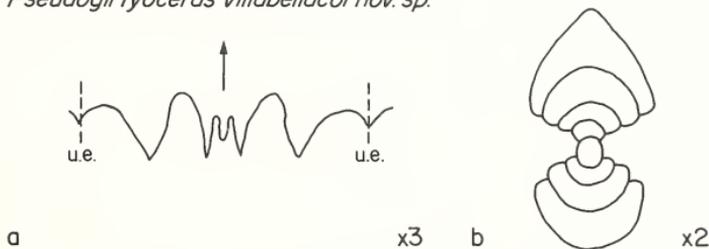
Pseudogirtyoceras villabellaco sp. nov.

Plate 36, fig. 4; text-fig. 16a, b

Description. The shell is an involute oxycone at a diameter of 20 mm. At a diameter of approximately 15 mm the venter is still rounded but at 20 mm it starts to form a keel. The greatest width (10 mm) is at the umbilicus from where the sides curve gently to the keel. The umbilicus is two-sevenths of the diameter, its walls being nearly perpendicular to the sides with which it makes a rounded edge (see text-fig. 16b). Two constrictions are visible, and these form a wide, shallow sinus on the lateral sides and a sinus on the ventral side. No ornament is preserved.

The suture consists of an extremely narrow ventral lobe, with its cheeks diverging apically. The two secondary lobes on both sides of the median saddle are narrow and pointed. The median saddle reaches over half the height of the ventral lobe. The siphonal notch consists of a deep loop. The first lateral saddles are rounded and directed towards the umbilicus. The first lateral lobes are V-shaped and pointed, whereby the ventral cheek is convex and the umbilical cheek is concave. The second lateral saddle is wide and rounded and at the umbilical edge there is a small, pointed umbilical lobe (see text-fig. 16a).

Pseudogirtyoceras villabellaco nov. sp.



TEXT-FIG. 16. *a*, Suture of specimen BM(NH) C.82323. *b*, Cross-section of same specimen.

Comparison. This specimen is similar to *Girtyoceras* form H of Moore (1946, p. 403) but differs in having a much narrower ventral lobe.

Occurrence. It occurs in the Villabellaco Limestone (Palencia) at locality 138D, 3 m above the base, together with *Nautellipsites hispanicus*, *Ammonellipsites kayseri*, *Merocanites marshallensis*, and *M. subhenslowi*.

Merocanites subhenslowi Wagner-Gentis

See Higgins *et al.* 1964, pp. 238–245, pl. III, figs. 11–13; pl. IV, fig. 14; text-figs. A–C, for the description of this species.

Nautellipsites hispanicus (Foord and Crick)

See Wagner-Gentis 1960, pp. 43–51, figs. 1–3, for the description of this species.

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LIASSIC PLESIOSAUR EMBRYOS REINTERPRETED AS SHRIMP BURROWS

by RICHARD A. THULBORN

ABSTRACT. A peculiar nodule from the Upper Liassic (Toarcian) shales of Whitby, Yorkshire, is interpreted as an infilled burrow system which was probably excavated by a shrimp-like crustacean (possibly *Glyphea* sp.). This interpretation is supported by comparisons with fossil crustacean burrows in the ichnogenus *Thalassinoides*. The nodule had formerly been regarded as a cluster of fossil embryos from the aquatic reptile *Plesiosaurus*.

IN September 1887 H. G. Seeley delivered four reports on fossil reptiles to the British Association meeting at Manchester. Three of those reports dealt with anatomy and systematics, but the fourth concerned the more unusual subject of fossil embryos. Seeley described and exhibited a peculiar nodule showing supposed embryos of a Jurassic plesiosaur—an aquatic reptile of the suborder Plesiosauria (order Sauropterygia). His account of the embryos was summarized the following year (Seeley 1888), though a full description did not appear until 1896.

Seeley's plesiosaur embryos have attracted little attention: they have never been figured, and it is difficult to find more than passing mention of them in the literature of vertebrate palaeontology. They were briefly noticed by Woodward (1898, p. 161), Williston (1914, p. 94), and de Saint-Seine (1955, p. 422), but seem never to have been re-examined in detail. Abel's classic work *Vorzeitliche Lebensspuren* (1935) devoted much attention to embryos and neonates of ichthyosaurs (reptile order Ichthyosauria), but made no mention at all of plesiosaur embryos. There has often been speculation about the mode of reproduction in plesiosaurs (see, for example, Robinson 1975), but the embryos described by Seeley seem to have been overlooked.

This paper provides the first illustrations of the supposed plesiosaur embryos, and offers a reinterpretation of these curious fossils.

MATERIAL

The material described by Seeley was acquired in 1909 by the British Museum (Natural History), where it is now catalogued as R 3585. It comprises: an irregular nodule of pyritic mudstone and shale, approximately 11 × 8 × 8 cm (text-fig. 1); a small fragment, broken from the main nodule; five slides, each with a thin section; a slide with twenty-three stained serial sections from the neck region of a modern lizard embryo. The small fragment was detached in Seeley's search for internal structure, and it provided material for the thin sections; the serial sections of the lizard embryo had been obtained for comparative purposes (Seeley 1896, p. 21).

The nodule almost certainly came from coastal exposures of the Upper Lias (Whitbian sub-stage of the Toarcian) near Whitby, Yorkshire. Seeley received the nodule in 1887 from J. F. Walker (then curator of the Yorkshire Natural History Society), who had obtained it from a dealer in Whitby. The Whitby fossil-dealers were not averse to importing their wares from the Lower Liassic of Lyme Regis, Dorset, but probably did so only in the case of exceptionally fine and valuable specimens (notably fossil fishes; see Blake 1876, pp. 257–259). The Liassic shales near Whitby are rife with oddly shaped concretions and nodules (Hallam 1962; Howarth 1962), and it seems unlikely that a dealer would have imported an example from Dorset when so many were to hand locally.

The Whitby Lias is about 76 m thick, and may be summarized as follows (incorporating data from Hallam 1962; Howarth 1962, 1973; Hemingway 1974):

FORMATION	THICKNESS (m)	AMMONITE ZONE	STAGE
Dogger	(sandstones and ironstones)	unconformity	BAJOCIAN
Cement Shales	5.5	<i>Hildoceras bifrons</i>	} TOARCIAN
Main Alum Shales	22.0		
Hard Shales	4.5		
Bituminous Shales	23.5	<i>Harpoceras falciferum</i>	
Jet Rock Shales	8.5		
Grey Shales	13.5	<i>Dactyloceras tenuicostatum</i>	

The succession consists of shales, with minor argillaceous limestones and rare seams of siderite mudstone. Nodules and concretions are extremely abundant; some are scattered at random through the shales, while others occur in constant bands which serve as useful marker horizons (see Howarth 1962). Concretions in these marker horizons often have highly distinctive shapes, and have been named accordingly—'cannon balls', 'cheese doggers', 'curling stones', 'pseudovertebrae', and so on. Unfortunately the nodule described by Seeley cannot be referred with certainty to any of these marker horizons. Seeley's specimen has a matrix of soft, grey, flaky, and non-bituminous shale, and is unlikely, for that reason, to have been obtained from the zone of *Harpoceras falciferum*—where the shales are usually brown in colour and often have a characteristic 'oily' smell. Nor is it very likely that Seeley's specimen came from the Hard Shales or the Main Alum Shales: in many places these shales weather to a brown or reddish colour, and they sometimes produce efflorescent alum. The specimen probably originated from the Grey Shales or the Cement Shales.

DESCRIPTION

The supposed plesiosaur embryos are rounded masses of grey-brown mudstone protruding from a core of flaky grey shale (text-fig. 1). The shale is very soft, and contains tiny blebs and veins of white calcite, together with occasional flecks of black plant material. The bodies of the embryos are slightly harder than the shale matrix, extremely fine-grained, and rich in finely divided pyrite. Seeley originally believed the embryos to be phosphatic (1888), but later determined that they were in fact pyritic (1896). The embryos, and some areas of intervening shale, have a greasy lustre which has probably been enhanced, if not produced, by repeated handling of the specimen.

Seeley identified and numbered four principal embryos, with 'indications of three or four others' (1896, p. 20). His numbering is still visible on the specimen, in faded red ink, and will be followed here (see text-fig. 2). For the sake of brevity I will also adhere to Seeley's descriptive terminology (e.g. the 'head' of embryo 1, the 'limbs' of embryo 3, and so on); and to assist my discussion the specimen will be oriented as a spheroid with the 'head' of embryo 1 directed to the 'North Pole'.

Seeley's description (1896) is both detailed and accurate and need not be repeated here. However, the specimen has certain features that were not mentioned by Seeley. First, it is badly damaged in the region of the 'North Pole', where it seems that several large flakes have been removed by hammer blows (text-figs. 1A, 2A). The fragment detached to provide thin sections was clearly the last piece to be removed, for it can still be fitted on to the main nodule, where it forms part of an older fracture-scar. In some places the specimen appears to have been subjected to rather rough mechanical preparation; there are, for example, very deep needle-marks along the right side of the 'neck' of embryo 1.

The embryos are clustered in a partly overlapping arrangement; the 'neck' of embryo 3, for example, is largely concealed by the 'body' of embryo 1. Elsewhere one embryo may be joined to another without the slightest trace of a dividing line (see text-fig. 1B). The arrangement of the supposed embryos is not entirely random: they extend in a radiating pattern, along meridians, when viewed from the 'South Pole' (text-fig. 2B).

Seeley could find no definite trace of organic structure in the specimen, and his identification of 'embryonic plesiosaurs' rested almost entirely on the criterion of shape. He considered that embryo 1 showed 'the head, neck, body, tail and limbs of such a shape as a plesiosaur would show', and pointed out that the other embryos were basically similar in form; differences in shape between one embryo and another were taken to reflect 'various stages of development' (Seeley 1896, p. 23). Nevertheless, Seeley did attempt to identify anatomical

features such as bones and teeth within the embryos—though he did so with extreme circumspection. These possible organic structures merit close inspection.

Placenta. A 'smooth film of hard clay' over parts of the specimen was considered by Seeley to have 'much the aspect of a defining membrane of a placenta-like character' (1896, p. 20). This apparently refers to the greasy lustre on the embryos and on some intervening areas of shale. The lustre is almost certainly artificial, for it is easily reproduced by gently rubbing a finger-tip over a fresh patch of the shale.

Median dorsal ridge. 'Each of the four principal specimens is characterized by a median longitudinal ridge or blunt angle which extends down . . . what I regard as the dorsal surface; corresponding in position to the neural spines of the vertebrae' (Seeley 1896, p. 21). The ridge is visible in unweathered and undamaged portions of the embryos, though it is sometimes very faint. Nowhere is there any trace of organic structure in, or beneath, the ridge; and there is no evidence to confirm that the ridge is 'dorsal' in position.

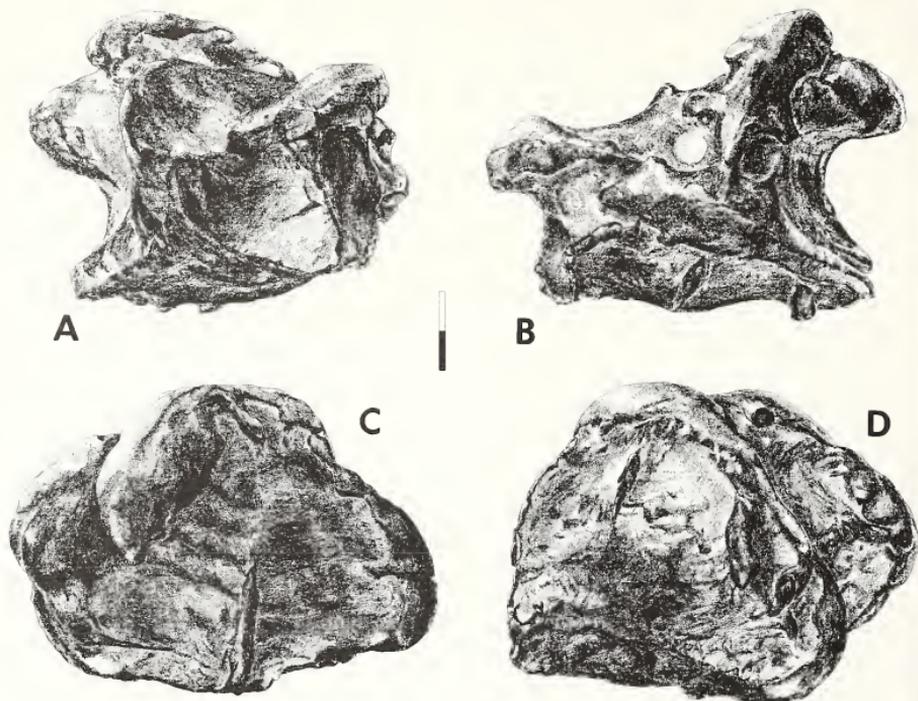
Sclerotic ring. On the right side of the 'head' in embryo 1 is a shallow oval pit which was tentatively identified by Seeley as the orbit. This pit originally contained 'a scale with a radiated structure, which had the appearance of being a sclerotic circle of bones about the eye', but this was subsequently lost from the specimen (Seeley 1896, pp. 22, 24). The supposed orbit is now floored by a paper-thin layer of finely crystalline pyrite, which is overlain near the anterior margin by a patch of shale containing flecks of white calcite. The floor of the orbit appears to be featureless—though Seeley maintained that there was possibly 'some evidence of a radiating structure' (1896, p. 25). The 'radiated scale' described by Seeley is unlikely to have been a sclerotic ring, because it was originally applied to the concave floor of the 'orbit': sclerotic plates are usually embedded in the lateral half of the eyeball, and therefore tend to be arched outwards from the orbit (Walls 1942). If the 'radiated scale' were a series of sclerotic plates it would be necessary to suppose that the entire eyeball had been squashed flat in the embryo; and if the eyeball had been squashed or ruptured it would be reasonable to expect evidence of similar distortion in other regions of the soft-bodied embryos. In any case, it seems improbable that delicate and superficial ossifications would have been preserved, while deeper and presumably more robust bones were obliterated. I suspect that the 'radiated scale' was no more than a thin vein of calcite, resembling similar veins in other parts of the nodule.

Scapula. The 'left forelimb' of embryo 2 is truncated by a fracture, behind which 'the dorsal aspect of the limb appears to include a surface bone in the position of the ascending process of the plesiosaurian scapula' (Seeley 1896, p. 23). I can find no trace of bone in this area; there is a slight surface irregularity postero-dorsal to the 'limb', but this is not particularly reminiscent of the outline of a scapula. Moreover, the ascending ramus of the plesiosaurian scapula is situated in front of the glenoid cavity, and not behind it.

Muscle segments. According to Seeley, 'there appear to be some faint indications of transverse segmentation like that of muscles, in the region of the neck in the specimen No. 1, and in the dorsal region in specimen No. 2' (1896, p. 23). There seems to be no trace whatsoever of segmental structure in embryo 2. Much of the 'neck' of embryo 1 has an irregular, flaky, and pitted surface. In its posterior third the right side of the neck carries a series of deep needle-marks which extend into the adjoining shale; it is improbable that these would be taken as evidence of segmentation, even at a casual glance. Above this line of needle-marks is a smooth area which proves, on close inspection ($\times 50$), to carry an ornament of extremely fine, straight, and parallel scratches. These microscopic scratches were most probably produced with a mild abrasive: they are so regular in depth, spacing, and orientation (antero-dorsal to postero-ventral) that they cannot have been produced individually, and they are so unvaryingly straight and parallel that they do not seem to be a natural feature. Over all, there is no clear evidence of segmentation in any of the embryos.

Mandible and teeth. 'It is possible . . . that the lower jaw may be indicated in the film of clay, which is imperfectly preserved beneath the head [of embryo 1], and that some small badly preserved white spots arranged in linear succession are indications of teeth' (Seeley 1896, p. 24). The 'head' of embryo 1 meets the shale matrix without any indication of a separate mandible. Alongside the right surface of the 'head' is a string of tiny white spots, each about 0.15 mm in diameter; these are blebs of calcite similar to those scattered throughout the specimen, and their roughly linear arrangement seems to be fortuitous.

Skull roofing bones, external nostrils, and parietal foramen. All these features were tentatively identified by Seeley on the 'head' of embryo 1. The surface of the 'head' is marked with a random assortment of pits, furrows, and scratches, all of which seem to be preservational and weathering effects comparable to those in other parts of the embryos. None of the grooves or scratches can justifiably be regarded as a mid-line suture between skull roofing bones, and none of the pits can be matched up into a pair that could convincingly represent the external nostrils.

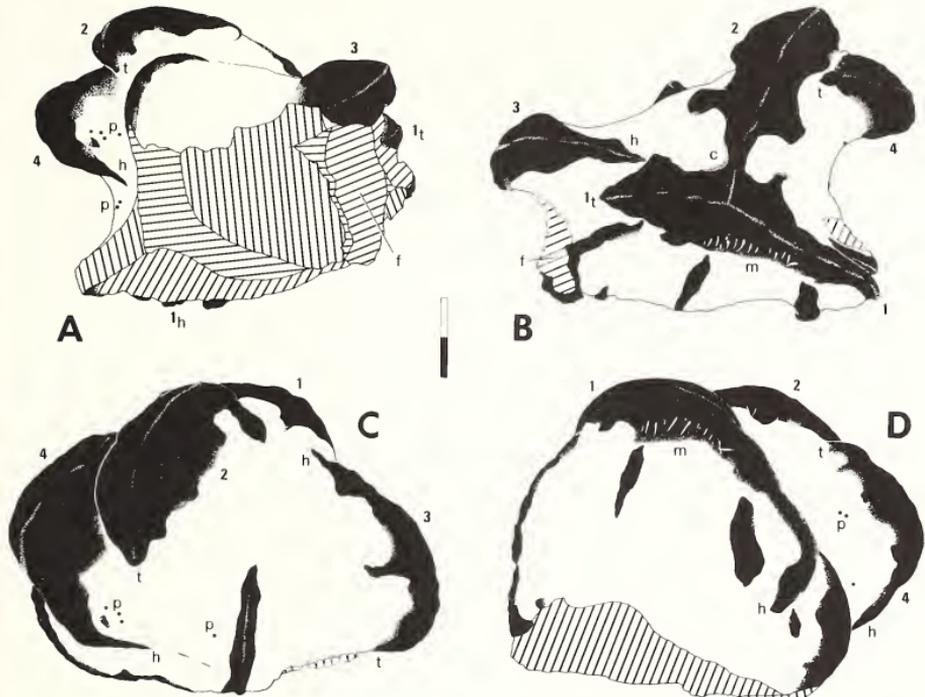


TEXT-FIG. 1. Four views of nodule from the Upper Liassic of Whitby, Yorkshire, showing supposed plesiosaur embryos. BM(NH) R.3585; scale indicates 2 cm.

Other anatomical features of the embryos (heads, necks, bodies, tails, and limbs) were identified by Seeley purely on the basis of their shape and their position. In summary, there seems to be no evidence of organic structure in any of the supposed embryos.

DISCUSSION

There are several reasons why the specimen is unlikely to be a cluster of plesiosaur embryos. First, it lacks any definite organic structure. Some of the anatomical features identified by Seeley (1896) are no more than surface irregularities, scratches, pits, and similar weathering effects (e.g. 'scapula', 'nostrils', and 'skull bones'); other such features are patches of calcite (e.g. 'teeth') or artifacts (e.g. 'placenta'). Second, the supposed embryos show differences in shape and proportions. Seeley accounted for this variation by suggesting that the embryos were in different stages of development, but this is not a particularly convincing explanation. Where embryos, neonates, or juveniles of reptiles are preserved as natural groups of fossils the siblings are invariably in the same state of development—as, for example, in ichthyosaurs (Hauff 1921; Hoffmann 1958; Urlrichs, Wild, and Ziegler 1979), in nothosaurs (Halstead 1969), and in ornithopod dinosaurs (Horner and Makela 1979). Next, and most important, it is highly improbable that soft-bodied embryos could have been preserved 'in the round' in a shale matrix. Sediment compaction usually ensures that soft organisms are preserved in a partly or completely flattened state, yet the supposed plesiosaur embryos form a



TEXT-FIG. 2. Diagrammatic interpretation of text-fig. 1. Shale matrix unshaded, and supposed plesiosaur embryos (here regarded as sediment-filled crustacean burrows) indicated by solid shading. Fracture surfaces indicated by oblique shading. Supposed embryos (= burrows) are numbered following Seeley (1896), and each has its 'dorsal ridge' (= groove in burrow floor) shown schematically. Abbreviations: c—cut surface; f—area from which a fragment was detached to provide thin sections for Seeley (1896); h—'head' of supposed embryo (= part of shaft leading to burrow chamber); m—needle-marks (shown schematically) along the side of supposed embryo 1 (= burrow 1); p—spots indicating location of possible faecal pellets; t—'tail' of supposed embryo (= burrow termination). Scale indicates 2 cm.

spheroidal mass which is not obviously flattened or distorted. If this specimen were a group of embryos it would be necessary to suppose that it had been enclosed in a syngenetic or diagenetic concretion (following terminology of Pantin 1958), or that the embryos had been mineralized before compaction of the surrounding sediment. The specimen was clearly not enclosed in a concretion, for the supposed embryos are separated and overlain by soft shale; and it seems unlikely that embryos could have been mineralized *in utero* or in an unconsolidated shale matrix. In rare circumstances human embryos are known to undergo spontaneous abortion and calcification—to become 'stone babies' or 'lithopedia' (Halstead and Middleton 1972)—but there are no reports of comparable abnormalities among fossil vertebrates. It seems a very remote possibility that the supposed plesiosaur embryos could be reptilian equivalents of 'lithopedia'.

What, then, is the most probable identity of the specimen? It is quite unlike a concretion, or even an aggregate of small concretions. Some parts of the supposed embryos bear a resemblance to coprolites, but the specimen as a whole seems too complicated in structure to be a mass of coprolites

or of intestinal fillings. Each of the supposed embryos is a multi-lobed object (with several lobes representing the 'tail' and the 'limbs'), whereas individual coprolites are normally sausage-shaped, spiral, fusiform, or pellet-like objects which are not developed into lobes (see Amstutz 1958, and many references therein). Nor does the specimen resemble any known endocranial cast of a vertebrate (Edinger 1929; Jerison 1973).

From a review of literature dealing with trace fossils and problematica I strongly suspect that the supposed plesiosaur embryos are actually the sediment-filled burrows of a crustacean—most probably a shrimp resembling those of the decapod superfamily Thalassinoida. The thalassinoid shrimp *Callianassa* excavates distinctive burrow systems in modern marine sediments (see Braithwaite and Talbot 1972), and comparable burrows have been reported as far back as the Triassic (Fiege 1944; Ireland, Pollard, Steel, and Thompson 1977) and even the Upper Carboniferous (Warne and Olson 1971; Chamberlain and Clark 1973). Fossil thalassinoid burrows are often referred to the ichnogenus *Thalassinoides* (reviewed by Bromley and Frey 1974); they vary considerably in size and architecture, according to the specific identity of the burrower (e.g. see Braithwaite and Talbot 1972) and to the nature of the sediments (e.g. see Bromley 1967). Nevertheless, it is possible to give a brief generalized description (based on Weimer and Hoyt 1964; Glaessner 1969; and sources mentioned above). A thalassinoid burrow system comprises one or more chambers (or tunnels) opening to the sea floor by a steeply inclined shaft which is wide enough to permit free passage of the burrower. A second shaft, which is often narrower and distinctly tapered, extends to the surface from another part of the chamber system. The shrimp occupies one of the chambers and creates a current by movements of its swimmerets; water enters the wider shaft and is expelled through the narrower shaft, often serving to flush out faecal pellets. The chamber occupied by the shrimp is big enough for the animal to turn round completely in somersault fashion. The various chambers are connected by constricted passages, and the shrimp may excavate several short galleries from the sides of a chamber. In some cases the chambers occur at random, while in others they may form a spiral or radial pattern. In soft sediments the shafts may be deep, and there may be many chambers excavated at several horizons; in more resistant sediments the burrow system may comprise little more than ramifying tunnels confined to a preferred horizon. When such burrow systems are encountered as fossils they are commonly filled with minerals or sediments which differ from the surrounding rock.

The supposed plesiosaur embryos are readily interpreted as thalassinoid burrow fillings (see text-fig. 2). Their ovoid 'bodies' seem to represent a series of chambers arranged in a roughly radial pattern, while their 'necks' may be identified as steeply inclined shafts connecting chambers at different levels or leading towards the former sea floor. Some of the 'necks' have a distinctly tapered tip and may be regarded as excurrent shafts. There is no trace of a broader incurrent shaft, but this would most likely have been situated in the region of the badly damaged 'North Pole'. The 'tails' are probably burrow-ends, which are 'usually somewhat conical, coming to a blunt point' in thalassinoid burrows from the English Chalk (Bromley 1967, p. 162). The 'limbs' of the supposed embryos may be identified as short galleries developed from the walls of the main chambers.

Nearly all major features of the supposed embryos can be matched in thalassinoid burrows of one sort or another. And several other facts would seem to confirm that Seeley's specimen is a thalassinoid burrow system. The shale matrix of the specimen contains a few tiny spheroidal objects (about 0.5 mm in diameter) which may possibly be faecal pellets flushed out from the interior of the burrow; several of these occur in the shale around embryo 4. Next, the invertebrate fauna of the Whitby Lias includes a variety of small decapod crustaceans, and some of these (*Glyphea* spp. and *Eryma* sp.) are similar in size and configuration to modern burrowing shrimps. Blake listed seven species of crustaceans from the Whitby Lias, and mentioned that 'numerous crustacean claws occur in many zones' (1876, p. 429). *Glyphea* and *Eryma* are not close relatives of the living thalassinoid shrimps, but 'it must be remembered that similar burrows indicate possibly similar body shape and behaviour, not systematic identity of the burrower' (Glaessner 1969, p. 430). Bromley and Frey (1974) listed many crustaceans known to construct burrows of *Thalassinoides* type, and among these were Jurassic shrimps of the superfamily Glypheoidea (Sellwood 1971; Bromley and Asgaard 1972).

It is possible, then, that one or more of the crustaceans reported from the Whitby Lias (most probably *Glyphea* spp.) may have constructed thalassinoid burrows. Remains of crustaceans are rarely found inside thalassinoid burrows, probably because the animals left their burrows to moult (see Glaessner 1969, p. 434). Finally, burrows are abundant at some horizons in the Whitby Lias. The distribution of these burrows was studied by Morris (1979), who did not specify the occurrence of *Thalassinoides* but mentioned that the trace fossil assemblages were dominated by *Chondrites*. In other sedimentary settings *Chondrites* may be associated with another trace fossil, *Gyrolithes*, which is sometimes linked with *Thalassinoides* to form a single burrow system (Bromley and Frey 1974). This very indirect evidence may hint at the existence of thalassinoid burrows in the Upper Lias at Whitby; such an occurrence would not be surprising, since *Thalassinoides* is widespread in the British Lower Lias (Sellwood 1970; Sellwood, Durkin, and Kennedy 1970). It is worth noting that Morris found *Chondrites* restricted to a 'normal' shale facies—'a homogeneous bioturbated sediment often containing sideritic nodules or horizons' (1979, p. 117). Morris studied only the lower part of the Toarcian succession at Whitby (as high as the Hard Shales), so that his 'normal' shales are in fact represented by the Grey Shales. It has already been deduced, on other grounds, that the supposed plesiosaur embryos came from the Grey Shales or from the Cement Shales (which were not considered by Morris). In other words, it seems probable that Seeley's specimen came from a 'normal' shale horizon in which burrows are abundant.

In summary, the nodule interpreted by Seeley (1896) as a group of plesiosaur embryos bears a strong resemblance to a system of thalassinoid burrow fillings. Crustaceans known from the Whitby Lias may well have included forms capable of excavating such burrows; and burrows (though not specifically identified as thalassinoid) are abundant in the 'normal' shale facies from which the nodule is likely to have come. The specimen has only one structural feature that I have been unable to match in any other thalassinoid burrow: this is the distinct 'dorsal ridge' noted by Seeley. If the specimen is interpreted as a burrow system this 'dorsal ridge' will actually represent a longitudinal groove in the floor of each burrow chamber. It is reasonable to suppose that this groove was produced by the appendages or the telson of the crustacean inhabitant.

Thalassinoid burrow fillings have commonly been mistaken for quite different objects; Bromley reported (1967, p. 158) that thalassinoid burrows of Upper Cretaceous age have been interpreted as benthonic algae, plant roots, sponges, solution channels, concretions, and trace fossils of unidentified marine organisms. Seeley's misinterpretation is all the more understandable when one considers that his specimen had been 'improved' by artificial means. Parts of the supposed embryos seem to have been smoothed off and polished with a mild abrasive, leaving a microscopic pattern of unnaturally straight and parallel scratches. And in places it appears that the main burrow chambers (or embryo 'bodies') have been trimmed to a more suggestive shape by removal of some side-galleries (which would otherwise have remained as rather puzzling supernumerary 'limbs'). Such trimming is apparent along the right side of embryo 1, where there is a series of deep needle-marks. These marks extend from the fossil *into* the shale matrix, whereas needle-marks produced in normal preparation would extend in the opposite direction. Either this work with a needle was intended to remove portions of the fossil, or it was an unbelievably clumsy attempt at preparing the specimen. Next, the suitably constricted appearance of the 'neck' in embryo 2 (text-fig. 2B) is due partly to the fact that it has been cut down with a knife-blade or similar instrument. The cut surface is easily visible; it is flat and sharp-edged, in contrast to the irregular and broadly rounded surfaces elsewhere. Finally there is evidence of a much coarser, but none the less effective, 'improvement': several hammer blows in the region of the 'North Pole' removed any trace that might have existed of an incumbent shaft leading to the burrow system. It is not altogether surprising to discover these alterations to Seeley's specimen, for many such 'improved' or 'repaired' fossils are known to have come from the dealers at Whitby (see, for example, Blake 1876, p. 428; Dance 1976, p. 103).

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LIMPET GRAZING ON CRETACEOUS ALGAL-BORED AMMONITES

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ABSTRACT. Phosphatized internal moulds of *Anahoplites* sp. and *Euhoplites* sp. reveal sets of six-toothed radula marks closely comparable to those scratched on to Recent molluscs by *Acmaea* (*Tectura*) *virginea* in water depths of up to 25 m on the muddy inshore shelf of western Scotland. Both the Recent and Cretaceous acmaeid marks truncate algal borings. Depth of the Gault sea during the Spathi subzone (M. Albian) was probably between 8 and 30 m, i.e. within the euphotic zone. Subsequent to lithification and phosphatization the moulds were bored by phoronids and scraped by regular echinoids.

FARROW and Clokie (1979) have recently drawn attention to the close association between the Recent limpet *Acmaea* (*Tectura*) *virginea* (Müller 1776) and the shell-boring alga 'conchocelis' on which it feeds. 'Conchocelis' is the resting phase of red seaweeds of the family Bangiaceae: use of the term is as in Farrow and Clokie (1979). In this paper we describe a similar association from the Lower Cretaceous which gives an indication of the depth of deposition of part of the Gault Clay and additionally demonstrates the persistence of acmaeid radula design. The fossil material consists of both shells and ammonite steinkerns bearing grazing traces: nearly all come from the Spathi Subzone of the Middle Albian, only one specimen from Dunton Green being of uncertain horizon. The grazing traces were collected from Copt Point, Folkestone, and are found on ten out of fifty-eight phosphatic internal moulds of hoplitid ammonites.

We outline the evidence for our interpretation of these traces, and document their occurrence alongside the only known species of Acmaeidae from the British Gault.

CHARACTERISTICS OF THE ASSOCIATED FAUNA

The form of the grazing traces from the Gault with their six parallel incised grooves preserved as negatives has led us to conclude that they probably belonged to an acmaeid. Patelliform shells are uncommon in the north-west European Albian, and particularly so in the Gault facies. There is one exception, however, *Patella tenuistriata* Michelin, 1838. This species is recorded from Folkestone by Price (1879) from his beds 2 II, 2 V, 2 VI, 2 VII, and 7 VIII, that is, scattered through the Middle Albian. We have examined nine specimens from the Gault at Folkestone with no further locality information. Of these, two are preserved on ammonite or nautiloid shells. Their protoconchs appear to have been lost during life and no epifauna or epiphyte is apparent. Further specimens of particular interest are two specimens from the Hampden Park borehole, Sussex, from the Spathi Subzone, the same subzone as our grazing trails. Another specimen, from an uncertain horizon of the Gault at Dunton Green, Kent (IGS Z5013), has a well-preserved muscle scar which confirms their identification as Acmaeidae. The only other limpet-like forms from the British Gault are attributed to the Calyptraeacea. Since these are suspension feeders, they are unlikely to have produced the incised traces we describe.

The clays of the Spathi Subzone occur widely across south-east England and have an extremely restricted benthonic fauna preserved. We are indebted to Adrian Morter of the I.G.S. for information concerning the faunas of this horizon, put together from information from several boreholes in East Anglia. Morter's Bed 3 contains common *Birostrina concentrica* and '*Ostrea*' cf. *incurva*, and less commonly the brachiopod *Moutoniathyris*, the gastropods *Anticonulus* and *Rissoina*, the bivalves *Entolium*, *Inoceramus*, *Pycnodonte*, *Ludbrookia*, *Neithea*, *Pectinucula*, and the echinoid *Hemiaster*.

Morter's Bed 2, a grey clay bioturbated with *Chondrites* and other traces, contains the bivalves *Birostrina*, *Inoceramus*, *Mesosacella*, *Pectinucula*, *Pseudolimea*, *Pycnodonte*, *Rastellum*, the brachiopods *Kingena*, *Moutonithyris*, and *Tamarella*, and the solitary coral *Cyclocyathus*. These faunas are typical of the Spathi Subzone benthos. One or two additions are known from Folkestone, including *Oistotrigonia fittoni* (Deshayes), which seems to be restricted to the clay facies.

We suggest that the fauna was limited by the fine-grained sediments. These were, however, not always oxygen-deficient, as nuculoid infaunal deposit feeders form a significant part of the fauna. Shells of nektonic cephalopods are present in sufficient numbers to have provided a substrate for epifaunal grazers and this would have been the case for the acmaeids. The trochaceans and rissoaceans may also have browsed on shell fragments, or storm-derived algae or sponges.

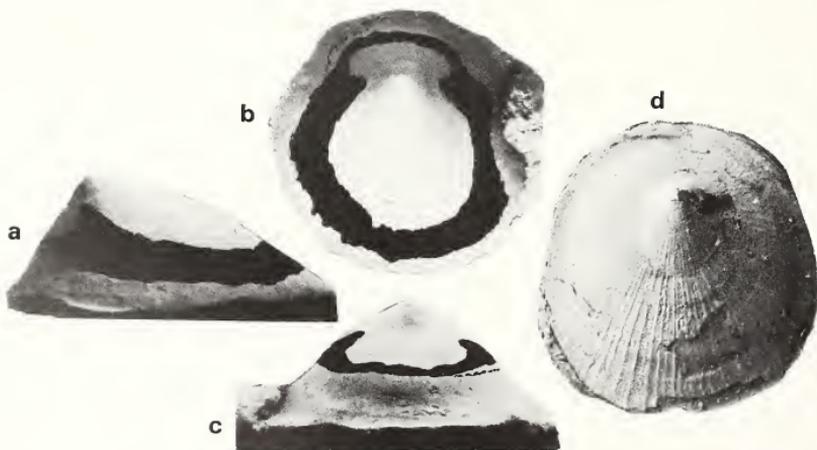
We feel that the coincidence of the occurrence of *Acmaea*-like grazing traces and the records of the only known species of Acmaeidae from the British Middle Albian is sufficient to justify our interpretation as one being the product of the other.

SYSTEMATIC DESCRIPTION

Acmaea tenuistriata (Michelin, 1838)

Material. Shells: nine specimens from the Gault of Folkestone (M.-U. Albian) BM(NH) GG.19971-19978; two specimens from the Spathi Subzone, M. Albian, Hampden Park borehole, Sussex, IGS, BDL 6727 and 6731; one specimen from an unspecified nodule bed in the Gault, Dunton Green, Kent, IGS Z5013.

Description. Broad, oval, bilaterally symmetrical, limpet-like shells with the apex approximately half-way between the mid-point and the anterior margin. The height is approximately one-third of the length. The largest specimen is about 15 mm in length. There is a radiating ornament of fine ribs with wide inter-spaces. No protoconchs are preserved. The shell structure is partly preserved in two specimens, BM(NH) GG.19977-19978 (text-fig. 1*d*), and consists of concentrically arranged cross lamellae which appear like vertical prisms in radial section. The shell is preserved entirely in a pinkish form, typical of Gault shells originally formed entirely of aragonite. The body and foot attachment scar is well preserved in IGS Z5013 and is illustrated in text-fig. 1*a-c*. It consists of a broad horseshoe-shaped area of scar joined at its anterior by a thinner line.



TEXT-FIG. 1. *Acmaea tenuistriata* (Michelin). *a-c* steinkern with muscle attachment scar inked in: IGS Z5013, unspecified nodule bed, Gault, Dunton Green, $\times 4$. (*a*) view of left side, (*b*) dorsal, (*c*) view of anterior. (*d*) specimen with part of the shell preserved: BM(NH) GG.19977, Middle-Upper Albian, Copt Point, Folkestone, $\times 3$, dorsal view.

Discussion. The shape of this shell and the form of its muscle scar are characteristic of the Family Acmaeidae. The general shape of this species, with its apex placed anterior to the mid-point, and its fine radial striae, are reminiscent of the subgenus *Acmaea* (*Tectura*) Gray, type species *A. virginea* (Müller), quoted as *Patella parva* da Costa (jun. sub. syn.) rather than *Acmaea* s.s., type species *A. mitra* (von Eschscholtz), a Californian species with a taller shell and central apex. However, without a thorough revision of the fossil members of the family we feel unable to place this species in a particular subgenus.

Grazing traces

Seven specimens are in the BM(NH); four collected by EBA and GEF, GG 19979–19982, and three collected by H. Lister, GG 19983–19985. The grazing traces are preserved as exquisitely detailed protruberances on the surfaces of the phosphatic moulds (Pl. 37, figs. 2–4). Individual markings, up to 200 μm wide by 400 μm long when fully developed, consist of six relatively broad ridges separated by narrow furrows. Overlapping of adjacent marks, however, rarely permits the full complement of ridges to be appreciated, and sets of sub-parallel ridges are the norm, their orientation being more consistent on some specimens (Pl. 37, fig. 4) than on others (Pl. 37, fig. 3). Successive truncation of sets of ridges suggests at least three phases of trace activity, the lowest being poorly preserved and having a smoothed appearance.

Borings

Three types seem to be present. The first consists of a widespread fine granulation on the surface of moulds where radula traces occur, in the form of small upstanding mounds of circular cross-section (Pl. 37, fig. 4). These represent the infilling of borings into the original ammonite shell. Having an approximate diameter of 6 μm they are probably algal in origin.

The second and third types represent unfilled borings into the lithified phosphatic moulds. The former are oval in cross-section, 500 μm in diameter, and penetrate deeply into the moulds: the latter are tunnels very close to the surface of the moulds which clearly truncate grazing traces in places (Pl. 37, fig. 3). The tunnels measure about 100 μm in depth and between 180 and 300 μm in maximum diameter, and are visible for a few millimetres before disappearing, only to reappear. These are probably the work of phoronids (Bromley 1970).

COMPARISON WITH RECENT TRACES

The Gault traces are similar to Recent *A. (Tectura) virginea* radula marks incised into mollusc shells (Pl. 37, fig. 1) but are preserved in a negative form. The comparison extends from over-all similarity of shape to details of six broadly incised elements, demonstrating a closer affinity in radula design between the presumed Gault acmaeid and the Recent *A. (T.) virginea* than between living *A. virginea* and *A. tessulata* (Müller 1776), whose radula is of four-pronged construction.

However, the Gault grazing traces are wider and less consistent in orientation than are those of the Recent *A. (T.) virginea*. This size difference is a reflection of the sizes of the causative limpets. For example, the longest Gault acmaeid measures 15 mm whereas the Recent British *A. (T.) virginea* is scarcely more than 7 mm long. Variation in the size of Recent *Acmaea* dictates the width of the grazing traces produced, 'scoops' ranging from 80 to 100 μm wide.

DEPTH OF DEPOSITION OF THE GAULT CLAY

The similarity between the fossil and Recent grazing traces is the more remarkable on account of the further association between the grazing marks and the fine granulation seen on the Gault specimens—the negative of the algal borings seen pitting the Recent examples. It is this association that sheds light on the depositional environment of the Gault during the Spathi Subzone, and in order to assess the probable depth of water it is necessary to consider something of the ecology of living *Acmaea*.

The genus *Acmaea* occurs widely in intertidal and shallow water-shelf habitats and there is much evidence for an algal grazing habit. Craig (1968) has described *A. pelta* living on micro- and macroalgae. Black (1976) described *A. incessa* living exclusively on the kelp *Egregia*, and many intertidal species graze upon epilithic algae (Kozloff 1973; Carefoot 1976). Fretter and Graham (1976) recorded *A. virginea* on algal-coated shell debris off the British coast. While these observations suggest that the depth was within the photic zone, it is possible to make a more refined estimate by looking in more detail at a single area.

Living Acmaea virginea on the Scottish continental shelf

Farrow and Clokie (1979, Table 1) working in the Firth of Clyde, found *A. virginea* down to only 18 m, coincident with the local limit of the euphotic zone as measured biologically by the last record of 'conchocelis' (Clokie, Boney, and Farrow 1979). This correlation is well established regionally, *Acmaea* extending into deeper water where substrates are coarser, environmental energy higher, and water clearer, as off the Orkney Islands where the euphotic limit is 38 m (Farrow, Allen, Akpan, and Brown 1981). A muddier, Firth-of-Clyde or Firth-of-Lorne-type environment is more appropriate as a Gault analogy, although the present latitude of 56° N is further north than that of Folkestone in the Alban, which was more like 33° N (Smith, Briden, and Drewry 1973, fig. 7, map 2).

Evidence on *A. virginea* distribution in one area of the Firth of Clyde is summarized on text-fig. 2. It is clear that the limpet extends down to within a few metres of the euphotic limit. Since, however, *Acmaea* grazing is intensive only where algal infestation is heavy we may conclude that deposition of the Gault Clay during this part of the Spathi Subzone was well within the euphotic zone. Depth was unlikely to have been greater than 30 m and could even have been as shallow as 8 m.

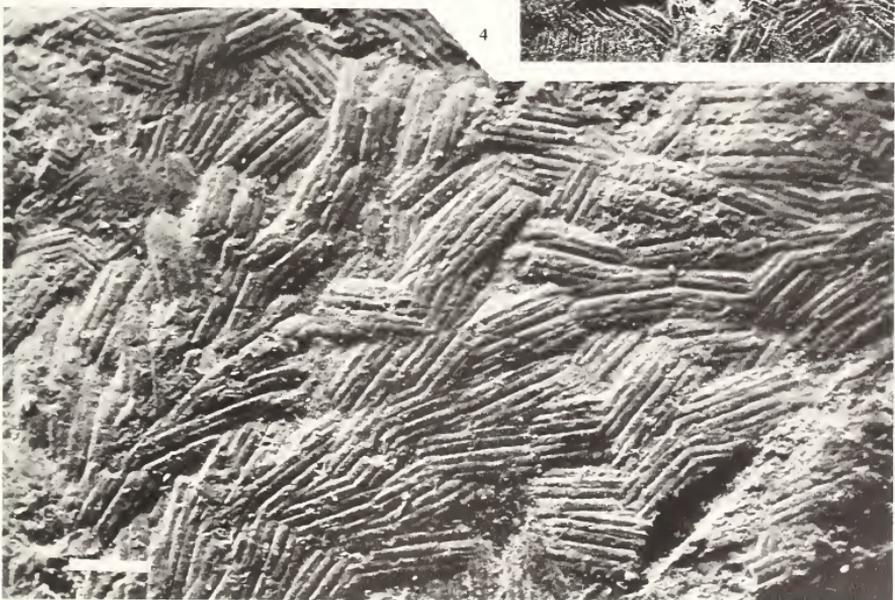
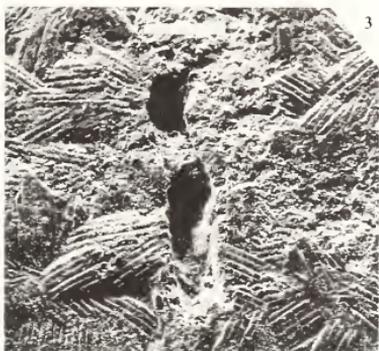
TAPHONOMY

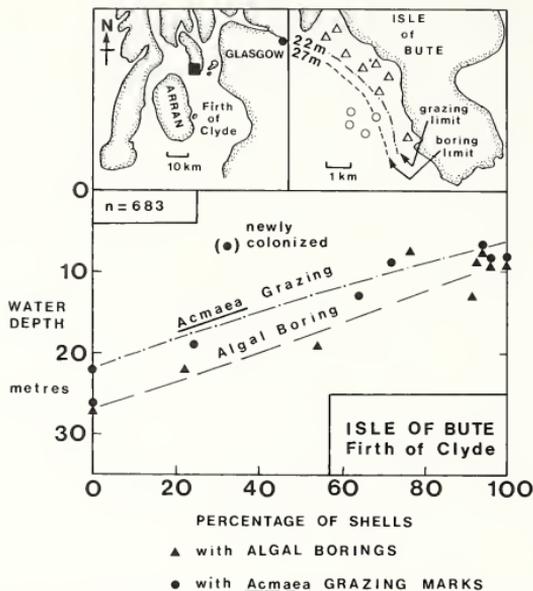
The evidence is clear that these Gault ammonites were infested with shell-boring algae to such an extent that the full thickness of shell must have been riddled with them, for the limpet grazing marks were made on the inside of the body chambers: any on the outside would have had negligible fossilization potential. It remains to be established, however, whether the algae infested dead shells drifting near the ocean surface, maybe for several years (House 1973, p. 309; though cf. Reyment 1958), or whether they bored into the shells when the latter were on the sea bed. Since the environmental interpretation for this part of the Gault hinges on this point, further consideration is necessary. There is some supporting circumstantial evidence.

First, there is the occurrence of probable regular echinoid scratches both on the phosphate moulds and on associated shell debris: this scratching is commonest today within the euphotic zone. However, the occurrence of these traces on the ammonite moulds post-dates not only the grazing marks but also lithification of the moulds, and could be ruled misleading. Second, it is to be doubted whether the 'conchocelis' phase of members of the family Bangiaceae (coastal red algae) would be sufficiently dispersed to infest a multiplicity of widely scattered floating cephalopods. It seems easier

EXPLANATION OF PLATE 37

- Fig. 1. Grazing traces of Recent *Acmaea* (*Tectura*) *virginea* on algal bored *Dosinia* shell: 9 m: Isle of Bute, Firth of Clyde, Scotland. For locality see text-fig. 2.
- Fig. 2. Grazing traces of Lower Cretaceous acmaeid on surface of hoplitid ammonite skeinkern: note the grazing front (cf. fig. 1): BM(NH) GG.19983: Spathi Subzone, Middle Albian, Copt Point, Folkestone.
- Fig. 3. Phoronid boring cutting through acmaeid grazing traces on surface of hoplitid ammonite steinkern: BM(NH) GG.19980: Spathi Subzone, Middle Albian, Copt Point, Folkestone.
- Fig. 4. Grazing traces of Lower Cretaceous acmaeid on surface of hoplitid ammonite steinkern: note their relatively consistent orientation (cf. fig. 3): BM(NH) GG.19979: Spathi Subzone, Middle Albian, Copt Point, Folkestone.





TEXT-FIG. 2. Depth of occurrence of Recent shells showing algal borings and *Acmaea* grazing marks: Firth of Clyde, Scotland. Note that the limit of grazing is slightly shallower than the limit of algal boring by 'conchocelis' (taken as a biological indication of the limits of the euphotic zone).

to envisage punctured shells being concentrated on the sea bed by winnowing and wave action, thus providing a typical habitat for the acmaeids, which are unknown pseudo-planktonically.

The following taphonomic sequence is therefore suggested:

1. Damaged ammonite shells sink on to muddy sea floor and are colonized by boring algae on their inner and outer surfaces (damage is supported by incomplete preservation: Reymont 1958; Seilacher 1971).
2. *Acmaeid* limpets colonize the dead shells, 'feeding' on the endolithic algae in 'sweeping' fashion where infestation is high, but with more clearly defined 'scoops' where infestation is lower.
3. Draught filling of very fine mud replicates the body chamber before the limpet grazing has reached such an advanced stage that the weakened shell falls apart: many ammonites may have been grazed to destruction in the absence of an intervening smothering of mud. (Attempts artificially to replicate modern grazing traces with Epotex resin have been markedly less successful than Nature's amazingly high-fidelity moulds in the Gault!)
4. Burial, lithification, and phosphatization (with dissolution of aragonite?).
5. Re-exhumation by winnowing of mud: concentration of nodules without transportation.
6. Boring by polychaetes? and phoronids: biting by regular echinoids.

CONCLUSIONS: BORING ALGAE AND MOLLUSCAN GRAZING TRACES IN THE FOSSIL RECORD

The long geological record of both the boring algae (e.g. *Palaeoconchocelis starmachii* from the Silurian of Poland, Campbell 1980) and the patellaceans (Trias-Rec.) suggests that earlier radula marks may soon come to light. Boekschoten (1967) and Voigt (1977) have recorded a range of

molluscan traces as far back as the upper Jurassic, with chiton marks more frequently encountered than those of limpets. Taylor (1981, pl. 2/3) has figured what are clearly acmaeid radula marks on an *Isognomon* from the Portlandian, *kerberus* Zone. Again they seem to be associated with an algal-bored shell.

The implications of the kind of approach reported in this paper are twofold. First, it shows that when reasonably stringent sampling programmes are put into effect on present-day continental shelves it is possible to refine the determination of palaeoecological parameters, in this instance water depth. As this parameter is a difficult one to assess in clay sequences, this is a step forward, and the result for the Spathi Subzone of the Gault of 8–30 m may come as something of a surprise. The second implication lies in the evidence which is afforded for a remarkable lack of change in radula design or pattern of feeding in the acmaeids since the Lower Cretaceous.

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A REVIEW OF RECENT AND QUATERNARY ORGANIC-WALLED DINOFLAGELLATE CYSTS OF THE GENUS *PROTOPERIDINIUM*

by REX HARLAND

ABSTRACT. A review is given of Recent and Quaternary organic-walled dinoflagellate cysts belonging to the genus *Protoperidinium* Bergh emend. Balech 1974. There is a similarity between the taxonomies based upon thecal and cyst morphologies, the major difference being one of hierarchy. A scheme is presented which attempts to amalgamate the two taxonomic systems, and which shows the range of cyst morphology attributable to a single living genus, the general non-conservative nature of certain cyst morphologies, and the use of common cyst forms amongst different dinoflagellates. Two new names, *Fuscusasphaeridium* and *Asymmetropedinium*, are introduced, and *Quinquecupis* Harland is emended and diagnosed in Latin.

RECENTLY a number of important reviews have appeared describing the taxonomy of peridiniacean dinoflagellates and their cysts. These include Lentini and Williams (1975) and Stover and Evitt (1978), both of which were mainly concerned with dinoflagellate cysts, their morphology, and particularly their archeopyle shape and structure. Unfortunately little or no attention was paid to the taxonomy of extant dinoflagellates and their cysts, or to the recently fossilized cysts found in Quaternary sediments. Similarly, in the field of phylogeny a major revision of a part of the genus *Peridinium* Ehrenberg 1832 was published by Balech (1974), but with little reference to dinoflagellate cysts. This paper attempts to look at the classification of living peridiniacean dinoflagellates, particularly those associated with the genus *Peridinium*, in relation to Recent and Quaternary dinoflagellate cysts.

TAXONOMY OF THE GENUS *PERIDINIUM*

The genus *Peridinium* was erected in 1832 by Ehrenberg with *Peridinium cinctum* (O. F. Müller) as the type species. In the early part of the twentieth century, with the advent of major oceanographical expeditions and the increasing number of species attributed to the genus (now well over 200) a number of schemes to subdivide the genus were published. Jörgensen (1913) comprehensively reclassified the genus, and used the number of plates that border the first apical as the principal character in the formation of subgenera, and the pattern of the dorsal plates on the epitheca, in particular the relationship with the precingular plate series, for the division of the subgenera into sections.

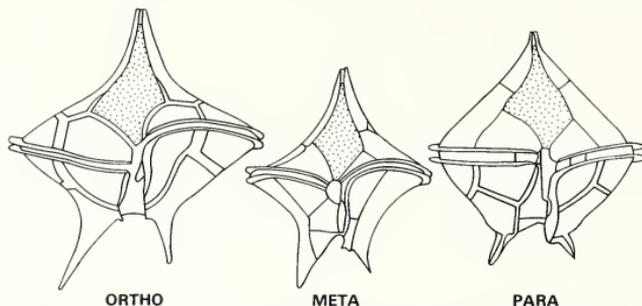
In the first instance the genus was divided into two subgenera: *Orthoperidinium* [1' contacts four plates 1'', 2', 4', and 7''] and *Metaperidinium* [1' contacts five plates 2', 1'', 2'', 4', and 7'']. The third condition *Paraperidinium* [1' contacts six plates 2', 1'', 2'', 4', 6'', and 7''] was not given subgeneric status because of the considerable variation in the length of the sutures between the plates. The subgenus *Orthoperidinium* was then divided into the following three sections:

<i>Tabulata</i>	2a plate contacts 3'' and 4'' or 4'' and 5'' plates
<i>Conica</i>	2a plate contacts 3'', 4'', and 5''
<i>Oceanica</i>	2a plate contacts 4'' only,

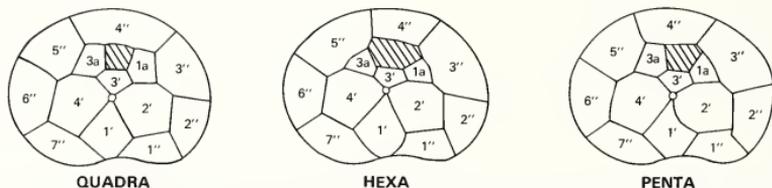
Similarly the subgenus *Metaperidinium*:

<i>Pyriformia</i>	2a plate contacts 3'' and 4'' or 4'' and 5''
<i>Paraperidinium</i>	see discussion above
<i>Humilia</i>	2a plate contacts 4'' only; with solid antapical horns
<i>Divergens</i>	as above with hollow antapical horns.

This system was revised by Paulsen (1931) to take into account a greater number of characters, and he used the terms 'ortho'-contacts 1'', 2', 3', 4', and 7'', 'meta'-contacts 1'', $\pm 2''$, 2', 3', 4', $\pm 6''$, and 7'', and 'para'-contacts 1'', 2'', 2', 3', 4', 6'', and 7'' to characterize the first apical plate (see text-fig. 1); and 'quadra'-contacts 4'' only, 'hexa'-contacts 3'', 4'', and 5'' and 'penta'-contacts 3'' and 4'' to characterize the dorsal epithecal configuration, especially the contacts at the posterior border (see text-fig. 2). Paulsen included in his treatment of *Peridinium*, forms with two intercalary plates as



TEXT-FIG. 1. Species of *Protoperidinium* illustrating the three different types of first apical plates (after Graham 1942). The first apical plate is stippled. The ortho species also shows growth bands.



TEXT-FIG. 2. Examples of the three different styles of dorsal epithecal tabulation (after Graham 1942). The second dorsal intercalary plate is hachured.

opposed to the normal three referring them to the subgenus *Archaeoperidinium* (=genus *Archaeoperidinium* of Jörgensen (1913)). These taxonomic schemes all rely upon the 'stability' of plate patterns in the region of the first apical and dorsal epithecal plates and in general on the possession of three dorsal intercalary plates. Graham (1942) noted, however, that the number of plates in the cingulum could be important in the taxonomy of *Peridinium* species and that their study had been neglected despite the fact that the dissection of the plates was not difficult.

Balech (1974), in his major revision of a part of the genus *Peridinium*, used the nature of the cingular plates to differentiate between freshwater *Peridinium sensu stricto* with five cingular plates, and marine *Peridinium* species with four cingular plates. The generic name *Protoperidinium* Bergh was used to accommodate these marine species. *Protoperidinium* was then subdivided into three subgenera based upon the number of precingular and intercalary plates. Further subdivisions were recognized using the criteria first employed by Jörgensen (1913) and Paulsen (1931).

Although the basis of this taxonomic subdivision is the number, shape, and size of the plates together with the tabulation pattern, I have never seen a reasoned account explaining why the number of cingular plates and the number of intercalary plates should be given hierarchical priority over the configuration of the first apical plate, or why the configuration of the first apical plate should be given

priority over the mutual relationship of the second intercalary plate and its neighbours. Indeed, evidence from the cyst morphology suggests that the shape and relative position of the second intercalary plate is possibly *more* significant, because it is through this site that excystment occurs. Recent work by Gocht and Netzel (1974, 1976) on the overlap system in peridiniacean and gonyaulacacean dinoflagellates (Dürr and Netzel 1974) has suggested that this second intercalary site is the keystone for both overlap or imbrication (Dörhöfer and Davies 1980), and in archeopyle formation, and that it must be genetically determined. This is in contrast to the first apical plate which does not appear to play such a major role in thecal or cyst function.

It is, however, Balech's (1974) scheme that is used herein as a basis for discussing the contribution of cyst morphology. We are obliged to use thecal morphology as the starting-point since the information is potentially complete and only a small proportion of the dinoflagellates produce fossilizable cysts as a part of their life-cycle (Dale 1976). Cysts of the genus *Protoperidinium* are known to have a varied morphology ranging from simple spheres to quite complex cysts with processes and horns. Often the common unifying feature is the style of archeopyle formation, which always involves the use of an intercalary paraplate with or without its adjacent paraplates. Only in rare cases is it possible to distinguish a clear paratabulation. In this study emphasis is necessarily placed upon gross morphology and archeopyle formation in investigating the relationships of the various *Protoperidinium* cysts to their respective thecal stages.

SYSTEMATIC DESCRIPTIONS

In each of the subsequent discussions of genera, subgenera, sections, and species, the relevant cyst morphologies will be particularly noted, with further comment reserved for later sections. Cysts known to the author are described in some detail, otherwise the reader is referred to the best published description. The accompanying thecal tabulation diagrams have been standardized, do not necessarily correspond to details of the particular taxa in nature, and should therefore be treated as diagrammatic.

All the cysts illustrated here are registered in the MPK series and are housed in the Palynological Collections of the Institute of Geological Sciences (IGS), Leeds.

The taxonomic changes that have resulted from this review, including the erection of two new taxa and the change in status of several others, are all handled within the Appendix. The taxonomic system used herein is, however, summarized in Table 1.

Division PYRRHOPHYTA Pascher 1914
 Class DINOPHYCEAE Fritsch 1929
 Order PERIDINIALES Haeckel 1894
 Family PERIDINIACEAE Ehrenberg 1832
 Genus PROTOPERIDINIUM Bergh *emend* Balech 1974

Type species. *Protoperidinium pellucidum* Bergh 1881; S.D. by Loeblich, Jr. and Loeblich, III, 1966.

Remarks. This genus accommodates, for the most part, the marine species formerly belonging to the genus *Peridinium* Ehrenberg. They have four cingular plates in contrast to the five in *Peridinium sensu stricto*. An exception is *P. faeroense* Paulsen which has five cingular plates (Dale 1978). The type species possesses a para first apical plate arrangement and a hexa dorsal epithecal configuration (text-fig. 3). Cysts capable of fossilization have not been recorded for the type species.

Subgenus *Minusculum* (Lebour) Balech 1974

Type species. *Protoperidinium (Minusculum) bipes* (Paulsen) Balech 1974; O.D.

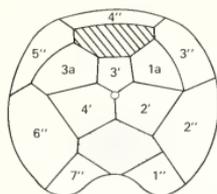
Remarks. This subgenus is characterized by six precingular plates and three intercalary plates. The unique 'boomerang' shape of plate 6'' (Balech 1974) is also a significant feature (text-fig. 4). No fossilizable cysts have been observed from species attributable to this subgenus.

TABLE 1. Taxonomy of *Protoperidinium* species that produce fossilizable cysts

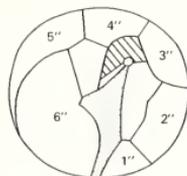
GENUS	SUBGENUS		SECTION	SPECIES	
<i>Protoperidinium</i>	<i>Minusculum</i>		—	—	
	<i>Archaeperidinium</i>		<i>Archaeperidinium</i> stat. nov.	<i>minutum</i>	
			<i>Stelladinium</i> stat. nov.	<i>compressum</i>	
			<i>Fuscusphaeridium</i> nomen nov.	<i>avellana</i> <i>denticulatum</i> <i>excentricum</i>	
	<i>Protoperidinium</i>	Para	Quadra	—	—
			Penta	—	—
			Hexa	<i>Protoperidinium</i> stat. nov.	<i>latissimum</i>
		Meta	Quadra	—	—
			Penta	—	—
			Hexa	—	—
		Ortho	Quadra	<i>Votadinium</i> stat. nov.	<i>claudicans</i> <i>oblongum</i>
			Penta	<i>Asymmetropedinium</i> nomen nov.	<i>punctulatum</i>
			Hexa	<i>Brigantedinium</i> stat. nov.	<i>conicoides</i>
				<i>Selenopemphix</i> stat. nov.	<i>conicum</i> <i>nudum</i> <i>subinerme</i>
				<i>Quinquecuspis</i> stat. nov.	<i>leonis</i>
				<i>Trinovantedinium</i> stat. nov.	<i>pentagonum</i>

TABLE 1. Taxonomy of *Protoperidinium* species that produce fossilizable cysts

GENUS	SUBGENUS	SECTION	SPECIES	
<i>Protoperidinium</i>	<i>Minusculum</i>	—	—	
		<i>Archaeperidinium</i> stat. nov.	<i>minutum</i>	
		<i>Stelladinium</i> stat. nov.	<i>compressum</i>	
	<i>Archaeperidinium</i>		<i>Fuscusphaeridium</i> nomen nov.	<i>avellana</i> <i>denticulatum</i> <i>excentricum</i>
			Quadra	—
			Penta	—
			Hexa	<i>latissimum</i>
			Quadra	—
			Penta	—
			Hexa	—
<i>Protoperidinium</i>		<i>Protoperidinium</i> stat. nov.	<i>latissimum</i>	
		—	—	
		—	—	
		—	—	
		Quadra	<i>claudicans</i> <i>oblongum</i>	
		Penta	<i>punctulatum</i>	
<i>Protoperidinium</i>		<i>Asymmetropedinium</i> nomen nov.	<i>conicoides</i>	
		<i>Brigantedinium</i> stat. nov.	<i>conicum</i> <i>nudum</i> <i>subinterme</i>	
		Hexa	<i>leonis</i>	
		<i>Quinquecuspsis</i> stat. nov.	<i>pentagonum</i>	
		<i>Trinovantedinium</i> stat. nov.		



TEXT-FIG. 3 (left). Epithecal tabulation of *Protoperidinium* (*Protoperidinium*) *pellucidum* Bergh ex Loeblich, Jr. and Loeblich, III (after Lebour 1925).



TEXT-FIG. 4 (right). Epithecal tabulation of *Protoperidinium* (*Minusculum*) *bipes* (Paulsen) Balech (after Balech 1974).

Subgenus *Archaeperidinium* (Jørgensen) Balech 1974

Type species. *Protoperidinium* (*Archaeperidinium*) *minutum* (Kofoid) Loeblich, III, 1969; O.D.

Remarks. *Archaeperidinium* has seven precingular plates, an ortho first apical and two intercalary plates, and contains at least five species that are known to produce fossilizable cysts. These are described and discussed herein.

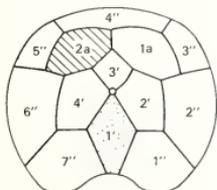
Protoperidinium (*Archaeperidinium*) *minutum* (Kofoid) Loeblich, III 1969

Text-fig. 5

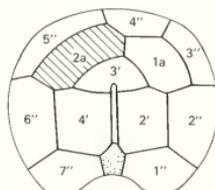
Remarks. The thecal plate configuration of this the type species shows the distinct ortho first apical and two symmetrically placed intercalary plates. The cysts produced by this species are described in Wall and Dale (1968) and illustrated on their pl. 4, fig. 7 but they have not been seen by the present author. The archeopyle, however, is reported to be intercalary (? 1a or 2a) but is rarely seen as an aperture; Wall and Dale's (1968) illustration appears to show an attached operculum. The cyst is otherwise characterized by short, hollow processes with a flat-topped distal extremity that bears spinules around the circumference. The cysts are known from Recent sediments. Incubation experiments (Wall and Dale 1968) have clearly established the link between this theca and cyst.

Protoperidinium (*Archaeperidinium*) *avellana* (Meunier) Balech 1974

Text-fig. 6, 7B; Plate 38, figs. 4-9



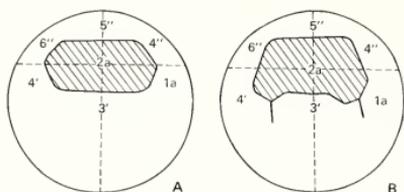
TEXT-FIG. 5 (left). Epithecal tabulation of *Protoperidinium* (*Archaeperidinium*) *minutum* (Kofoid) Loeblich, III (after Wall and Dale 1968).



TEXT-FIG. 6 (right). Epithecal tabulation of *Protoperidinium* (*Archaeperidinium*) *avellana* (Meunier) Balech (after Wall and Dale 1968).

Remarks. The thecal tabulation illustrated shows the salient features but it is interesting to note that there is some asymmetry in the position of the intercalary plates and especially plate 4". The cysts of this species have been described and illustrated by Wall and Dale (1968, pl. 4, fig. 2) and consist of spherical, smooth-walled brown bodies with a single dorsal intercalary archeopyle. The shape of the operculum is seen in Wall and Dale (1968), Reid (1977), Harland (1977) and in the present illustrations. The degree of reflection of the detailed thecal plate shape is often quite remarkable.

There can be some confusion between these cysts and those of *P. (A.) denticulatum* (Gran and Braarud) Balech 1974 although the archeopyles are distinct (text-fig. 7). In palynological preparations many such cysts are often so crumpled that a proper analysis of the archeopyle shape is not always possible. Also, the archeopyle shape can be somewhat modified and need not be a perfect reflection of the thecal plate counterpart. Incubation experiments (Wall and Dale 1968) have established the link between this theca and this cyst.



TEXT-FIG. 7. Apical view of the cysts A—*Protoperidinium (Archaeperidinium) denticulatum* (Gran and Braarud) Balech (after Wall and Dale 1968), and B—*P. (A.) avellana* (Meunier) Balech showing the distinct archeopyle shapes, both symmetrical.

The cyst was originally described as *Chytroeisphaeridia cariacensis* Wall 1965, but may be placed in Reid's (1977) genus *Brigantedinium* recently validated by Harland and Reid (1980) in Harland, Reid, Dobell, and Norris (1980). However, the type species of *Brigantedinium*, *B. simplex*, is the cyst of *P. (Protoperidinium) conicoides* (Paulsen) Balech, a member of a separate subgenus. The placement of *P. (A.) avellana* in *Brigantedinium* may, therefore, be inappropriate and perhaps a separate designation needs consideration (see later discussion).

Cyst description. Simple spheroidal brown cyst made up of autophragm or with two very closely adpressed wall layers. Paratabulation not present although the archeopyle shape does hint at the configuration of the 2a, 4', 3', and 1a contacts (text-fig. 7b). Cyst wall generally smooth but may appear somewhat shagreenate; the possible indications of two indentations on the ? sulcal area may be a reflection of flagellar pores. Archeopyle intercalary formed by the loss of paraplate 2a which is transversely elongate and symmetrical (see text-fig. 7b). Operculum free. Cyst diameters fall generally within the range 50.0-55.0 μm .

EXPLANATION OF PLATE 38

All figures are illustrated at a magnification of $\times 500$ and were photographed in plain transmitted light unless otherwise indicated.

Figs. 1-3. *Protoperidinium (Protoperidinium* sect. *Brigantedinium) conicoides* (Paulsen) Balech, Nomarski interference contrast. 1, dorsal view of MPK 1232 showing simple morphology and standard hexa archeopyle. 2, ventral view of MPK 1232 with the two flagellar indentations. 3, dorsal view with the archeopyle and operculum, specimen MPK 1243.

Figs. 4-9. *Protoperidinium (Archaeperidinium* sect. *Fuscusphaeridium) avellana* (Meunier) Balech, figs. 4 and 5 by Nomarski interference contrast. 4, apical view showing symmetrical archeopyle with operculum in place, specimen MPK 1236. 5, ditto, specimen MPK 1238. 6, oblique view with operculum coming free, specimen MPK 1235. Figs. 7-9, various levels of focus showing operculum free and more crumpled nature of the cyst, specimen MPK 2768.

Figs. 10-12. ?Indet. *Protoperidinium* cyst, various levels of focus to show the general morphology and the zigzag archeopyle split, specimen MPK 2769.



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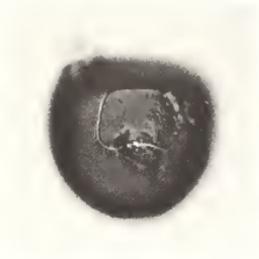
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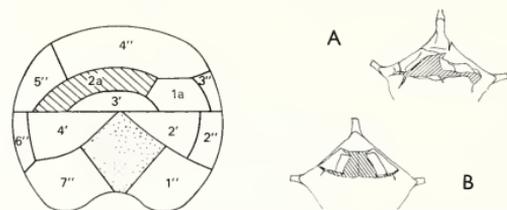


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Protopteridinium (Archaepteridinium) compressum (Abé) Balech 1974

Text-figs. 8, 9; Plate 39, fig. 12

Remarks. The thecal tabulation shows the features of this subgenus, but in particular the asymmetry in the disposition of the intercalary and 4th plates is worth noting. Text-fig. 8 shows the theca as expanded whereas in life the species is compressed dorso-ventrally, hence the name. The cyst of this species is particularly striking in its stellate morphology, and has been described by Wall and Dale (1968), Bradford (1975), Reid (1977), and Harland (1977). The archeopyle is intercalary and formed by the displacement of two paraplates which remain attached laterally (text-fig. 9). They are



TEXT-FIG. 8 (left). Epithelial tabulation of *Protopteridinium (Archaepteridinium) compressum* (Abé) Balech (after Wall and Dale 1968).

TEXT-FIG. 9 (right). Archeopyle formation in *Protopteridinium (Archaepteridinium) compressum* (Abé) Balech, A—Specimen MPK 1256 (see Pl. 39, fig. 12), B—Idealized scheme.

symmetrically placed and fold back to open a large archeopyle. It is thought that both 1a and 2a paraplates are involved. They do not appear to reflect the asymmetry of the theca. These cysts are unique and to date at least two species (herein Pl. 39, fig. 12, and in Wall and Dale 1968, pl. 2, figs. 15–17) are known, only one of which can be definitely assigned to *P. (A.) compressum*. Incubation experiments (Wall and Dale 1968) have established the link between this theca and the illustrated cyst described below.

Cyst description. Stellate, peridinioid cysts, compressed dorso-ventrally made up of autophragm. Wall smooth, and epitract smaller than hypotract. Cyst carries one apical, two antapical, and two lateral horns that are long, solid, and acicular. Thickening of the horn bases is sometimes apparent. Paratabulation not present. Archeopyle intercalary formed by the opening of two intercalary paraplates that remain attached laterally. Cysts range in length, excluding the processes, from 26.0–37.0 μm .

Protopteridinium (Archaepteridinium) denticulatum (Gran and Braarud) Balech 1974

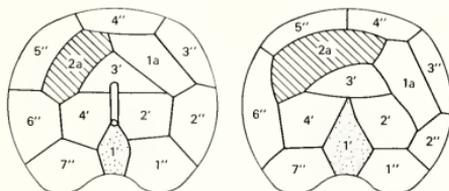
Text-figs. 7A, 10

Remarks. The tabulation of this species shows a remarkable similarity to that of *P. (A.) avellana* especially with respect to the slight asymmetry of the two intercalary plates; best seen in relation to the position of plate 4th. It is, therefore, perhaps not surprising that the cyst illustrated and described by Wall and Dale (1968, pl. 3 fig. 30) is very similar to that produced by *P. (A.) avellana* (see Wall and Dale 1968, p. 277) although the identification is admittedly not positive. Archeopyle formation is by loss of a single transversely elongate intercalary paraplate whose configuration is symmetrical, but unlike that of *P. (A.) avellana* (text-fig. 7). In palynological preparations confusion between the two forms is common. The form illustrated here has a provisional assignment to this species. Incubation experiments by Wall and Dale (1968) failed to positively identify the theca therefore a clearly established link between this theca and cyst is not possible.

Protoperidinium (Archaeperidinium) excentricum (Paulsen) Balech 1974

Text-fig. 11

Remarks. The thecal tabulation of this species is very similar to both those of *P. (A.) avellana* and *P. (A.) denticulatum*. The cysts are brown oval bodies that Wall and Dale (1968, p. 278) describe as being flattened in a polar direction. The archeopyle has not been described. Cysts attributable to this species have not been seen by the present author. Although cysts enclosed by thecae were recorded by Wall and Dale (1968) it is not clear if any thecae were obtained by incubation and positively identified.



TEXT-FIG. 10 (left). Epithcal tabulation of *Proto-peridinium (Archaeperidinium) denticulatum* (Gran and Braarud) Balech (after Wall and Dale 1968).

TEXT-FIG. 11 (right). Epithcal tabulation of *Proto-peridinium (Archaeperidinium) excentricum* (Paulsen) Balech (after Lebour 1925).

Discussion of the subgenus *Archaeperidinium*

Dinoflagellate cysts of the subgenus *Archaeperidinium* fall into three distinct categories. The first is exemplified by the type species, a cyst with short processes and a single intercalary archeopyle; the second a stellate cyst with a two paraplate intercalary archeopyle; and finally the third with brown spherical/spheroidal cysts with single intercalary transversely elongate archeopyle. These differences in gross cyst morphology underline differences in the tabulation pattern; the type species is symmetrical; the second is very markedly asymmetrical and divided laterally into a clearly marked dorsal and ventral epitheca, and finally those that are only slightly asymmetrical especially in regard to the position of plate 4'. I believe this is a sufficiently natural genotypic division to warrant the application of particular names. The names chosen are derived from both biological and palaeontological literature and include *Stelladinium* Bradford 1975, a name coined to apply to the unique stellate morphology of *P. compressum* cysts. Herein I shall treat them as separate sections such that:

1. *Protoperidinium (Archaeperidinium* sect. *Archaeperidinium* stat. nov.) includes *minutum*
2. *Protoperidinium (Archaeperidinium* sect. *Stelladinium* stat. nov.) includes *compressum*
3. *Protoperidinium (Archaeperidinium* sect. *Fuscusasphaeridium* nomen nov.) includes *avellana*, *denticulatum*, and *excentricum*

The only new name, *Fuscusasphaeridium*, is formally erected in the appendix together with the change of status of the other two taxa. This approach hopefully embodies the general ideas expressed by Wall and Dale (1968), Dale (1976 and 1978), and Reid and Harland (1977). An amalgamation of systems should be possible since we are dealing with common organisms, albeit at different stages of their life-cycle.

Some difficulties are still apparent, for instance *P. (P.) punctulatum* (Paulsen) also has brown spherical cysts with transversely elongate archeopyles but with a very different thecal tabulation. Possible differences in cyst archeopyle morphology, i.e. ? attached and an asymmetrical opercula (see later discussion) may serve to differentiate them from cysts of *P. punctulatum*.

Subgenus *Protopteridinium* (Bergh) Balech 1974

Type species. Protopteridinium (Protopteridinium) pellucidum Bergh 1881, S. D. by Loeblich, Jr. and Loeblich, III, 1966.

Remarks. The thecal tabulation of *P. (P.) pellucidum* has already been discussed, see text-fig. 3. Balech (1974) does, however, subdivide the subgenus into a number of units based upon the pattern of the first apical plate and its adjacent plates, and then again on the dorsal intercalary configuration. Since the type species has a para first apical plate that group will be discussed first.

A. Para-species

- i. Quadra. No fossilizable cysts attributable to dinoflagellates in this group are known.
- ii. Penta. No fossilizable cysts attributable to dinoflagellates in this group are known.
- iii. Hexa. Only one species within this unit is known to produce fossilizable cysts and that is described below. The type species, *P. (P.) pellucidum*, also belongs in this group.

Protopteridinium (Protopteridinium) latissimum (Kofoid) Balech 1974

Remarks. The thecal tabulation of this species clearly demonstrates the para first apical plate and the hexa dorsal intercalary arrangement and the symmetry of the pattern. The fossilizable cyst for this species has been described by Wall and Dale (1968) as large, pentagonal, and dorso-ventrally compressed. A paracingulum is represented by broad weakly excavated lateral lobes. The epitract is triangular in outline and large, while the hypotract is much smaller and has two small antapical horns. The archeopyle is intercalary, has a hexa shape but is asymmetrical (see Wall and Dale 1968, pl. 2, fig. 7), is large, taking up most of the dorsal surface of the cyst. The operculum is free. Incubation experiments (Wall and Dale 1968) have firmly linked this theca with this cyst.

The cyst genus *Leipokatium* Bradford 1975 was erected to accommodate cysts very similar to that described above. Since, however, the type species for the subgenus also is assigned to this group it might be prudent to suppress *Leipokatium* in favour of *Protopteridinium (Protopteridinium) sect.*

EXPLANATION OF PLATE 39

All figures are illustrated at a magnification of $\times 500$ and were photographed in plain transmitted light unless otherwise indicated.

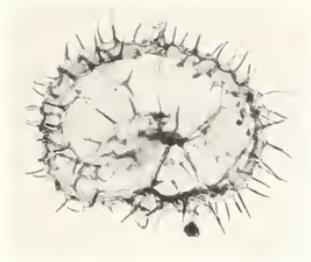
Figs. 1-3. *Protopteridinium (Protopteridinium) sect. Selenopemphix conicum* (Gran) Balech. 1, apical view to show the reniform ambitus and offset standard hexa archeopyle, specimen MPK 2770. 2, ditto, specimen MPK 2771. 3, ditto, specimen MPK 2772.

Figs. 4, 5. Indet. ?*Protopteridinium* cyst, *Xandarodinium xanthum* Reid. 4, ?apical view showing over-all morphology, Nomarski interference contrast, specimen MPK 1261. 5, ditto, specimen MPK 2773.

Fig. 6. *Protopteridinium (Protopteridinium) sect. Selenopemphix subinermis* (Paulsen) Loeblich, III, apical view showing broad paracingular zone, lack of ornament, and offset archeopyle with operculum, specimen MPK 1634.

Figs. 7-11. *Protopteridinium (Protopteridinium) sect. Trinovantedinium pentagonum* (Gran) Balech. 7, dorsal view showing the broad hexa archeopyle, hyaline nature of the cyst, and the paracingulum. 8, ventral view with parasulcus and planar paracingulum. 9, optical section illustrating the nature of the apical boss, specimen MPK 1240. 10, dorsal view with broad hexa operculum and nature of the parasutural and intratabular spines. 11, ventral view and deeply indented parasulcus, specimen MPK 2774, all figures with Nomarski interference contrast.

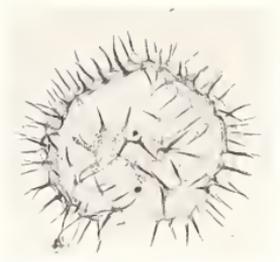
Fig. 12. *Protopteridinium (Archaepteridinium) sect. Stelladinium compressum* (Abé) Balech 1974, dorsal view showing stellate morphology and the 21 archeopyle with the two opercular paraplates attached laterally, Nomarski interference contrast, specimen MPK 1256.



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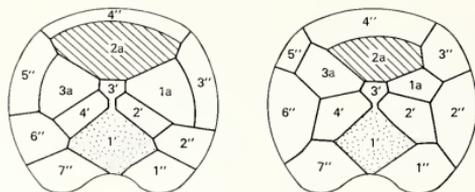
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TEXT-FIG. 12 (left). Epithecal tabulation of *Proto-peridinium* (*Protoperidinium*) *latissimum* (Kofoid) Balech (after Wall and Dale 1968).

TEXT-FIG. 13 (right). Epithecal tabulation of *Proto-peridinium* (*Protoperidinium*) *claudicans* (Paulsen) Balech (after Wall and Dale 1968).

Protoperidinium stat. nov.). However, no fossilizable cysts are known from the type species and therefore the thecal and cyst morphologies cannot be compared. In fact certain thecal tabulation details are different between *P. pellucidum* and *P. latissimum*, but it is difficult to know if these are taxonomically significant at this level (compare text-figs. 3 and 12).

B. Meta-species

Fossilizable cysts have not been described from Modern species attributable to the quadra, penta, or hexa subdivisions of this unit. However, it is of interest that a new species of *Phthanoperidinium* described by Edwards and Bebout (1981) has a meta configuration.

C. Ortho-species

This group contains the most numerous fossilizable *Protoperidinium* cysts and like those above can be subdivided as follows:

- i. Quadra. This includes the species *P. (P.) claudicans* (Paulsen) Balech 1974 and *P. (P.) oblongum* (Aurivillius) Balech 1974. Balech (1974) considers the latter to be a part of *P. (P.) oceanicum* Vanhöffen. Both species produce fossilizable cysts.

Protoperidinium (*Protoperidinium*) *claudicans* (Paulsen) Balech 1974

Text-fig. 13

Remarks. The roughly symmetrical thecal tabulation clearly shows the ortho first apical plate and a penta dorsal configuration. This perhaps indicates that the dorsal configuration is subject to some phenotypic variation as this species is usually placed in the quadra group (Balech 1974) although it is admitted that some possess the penta pattern. The cyst of this species has been described by Wall and Dale (1968) and Reid (1977). In dorsal view it is a chordate cyst that bears numerous short-pointed spines. Paratabulation not present but the parasulcus is deep and separates the two broad asymmetrical antapical lobes. Paracingulum not observed. Archeopyle formation is reported to be by loss of the 2a intercalary paraplate which is subapical in position and has a tendency to truncate the apex. Its shape tends to be pentagonal and if indeed only the one paraplate is involved then it is surely an enlarged archeopyle. Incubation experiments have confidently established the theca/cyst relationship in this species (Wall and Dale 1968). These cysts have in the past been included in Reid's (1977) genus *Votadinium*.

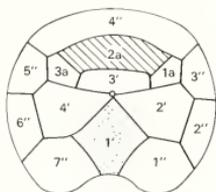
Protoperidinium (*Protoperidinium*) *oblongum* (Aurivillius) Balech 1974

Text-fig. 14; Plate 40, figs. 10-12

Remarks. The thecal tabulation as illustrated clearly demonstrates the ortho first apical plate and quadra 2a plate and the symmetrical nature of the over-all pattern. The cyst of this species has been

described by Wall and Dale (1968), Reid (1977), and Harland (1977), with the last two authors referring it to Reid's (1977) genus *Votadinium*. It may be that this species also exhibits variation in the dorsal thecal configuration, as in *P. claudicans*, since there appears to be some variation in cyst morphology (see Wall and Dale 1968, pl. 1, figs. 23-29). Incubation experiments have established the theca/cyst relationship within the species, but some experiments have shown that relationships exist with the varieties *latidorsale* Dangeard, *inaequale* Dangeard, and *symmetricum* Dangeard and this may in part explain some, if not all, of the cyst morphological variations.

TEXT-FIG. 14. Epithelial tabulation of *Protoperidinium* (*Protoperidinium*) *oblongum* (*Aurivillius*) Balech (after Wall and Dale 1968).



Cyst description. The cysts are chordate and smooth, formed of autophragm. They possess a clearly defined deeply indented parasulcus which effectively divides the two rounded antapical lobes. Faint traces of probable reflected flagellar pores may sometimes be seen in the sulcus. Paracingulum not seen. The archeopyle is broad and quite large and appears to reach the apex of the cyst on the dorsal surface, giving the cyst a truncated appearance similar to *P. claudicans*. Whether this archeopyle is an enlarged intercalary involving the loss of paraplate 2a or whether it includes paraplates 1a, 2a, 3a, and 3' is not known. Cyst diameters range from 54.0 to 75.0 μm .

Discussion of ortho quadra *Protoperidinium* species

The two species of this subdivision of the subgenus are clearly related in terms of both their thecal tabulation and cyst morphology. The cysts have in common their over-all chordate morphology and archeopyle style despite the uncertainty as to which paraplates may be involved. The use of a particular name to identify the condition is, therefore, clearly necessary. In this instance *Votadinium* is available for use as a section of the subgenus; hence *Protoperidinium* (*Protoperidinium* sect. *Votadinium* stat. nov.).

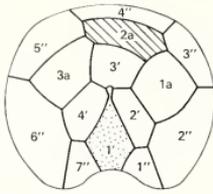
The variation in the dorsal tabulation of *P. claudicans* and the variation in the cysts of *P. oblongum* may point to a deficiency in the taxonomy of these species, with perhaps a lack of sufficient evidence on the varieties that exist and their respective cysts. Further incubation experiments are essential to more closely define the apparent variation.

- ii. Penta. Only one species *Protoperidinium* (*Protoperidinium*) *punctulatum* (Paulsen) Balech 1974 produces fossilizable cysts and is included here.

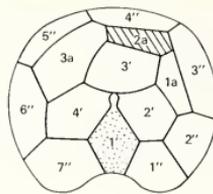
Protoperidinium (*Protoperidinium*) *punctulatum* (Paulsen) Balech 1974

Text-figs. 15-17; Plate 42, figs. 3-6

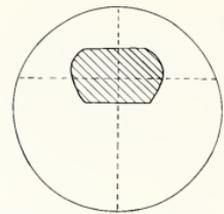
Remarks. This dinoflagellate, although usually penta, can have a hexa dorsal configuration as seen in the illustrations, and can appear slightly asymmetrical. The cyst has been described by Wall and Dale (1968) and is spherical, brown, with a large intercalary archeopyle formed by the loss of paraplate 2a. Operculum may be attached (Wall and Dale, pl. 2, fig. 27). The aperture is transversely elongate but is asymmetrical and this may be a significant difference compared with the cysts of *P. (A.) avellana* and *P. (A.) denticulatum* (compare text-figs. 7 and 17). Confusion between all these cysts can occur if well-preserved, three-dimensional orientated specimens are not available. However, the nature of the archeopyle and thecal tabulation does serve to distinguish this dinoflagellate from other species. Wall and Dale (1968) have established by incubation the link between this theca and cyst.



TEXT-FIG. 15 (left). Epithecal tabulation of a hexa *Protoperidinium* (*Protoperidinium punctulatum* (Paulsen) Balech (after Wall and Dale 1968).



TEXT-FIG. 16 (centre). Epithecal tabulation of a penta *Protoperidinium* (*Protoperidinium punctulatum* (Paulsen) Balech (after Lebour 1925).



TEXT-FIG. 17 (right). Apical view of the cyst of *Protoperidinium* (*Protoperidinium punctulatum* (Paulsen) Balech showing the laterally elongate, asymmetrical archeopyle.

A name is required to accommodate these dinoflagellates and to differentiate them from section *Fuscusasphaeridium* which is erected herein to hold the two *Archaeperidinium* species discussed previously. The name proposed is *Asymmetropedinium* nom. nov. (see appendix), hence *Protoperidinium* (*Protoperidinium* sect. *Asymmetropedinium*) *punctulatum* for this species.

Cyst description. Spheroidal brown cyst made up of autophragm or two closely adpressed wall layers. Surface smooth, shagreenate, or slightly granulate. Paratabulation only revealed by archeopyle formation. Archeopyle intercalary formed by the loss of paraplate 2a. Operculum large, transversely elongate but asymmetrical. Cyst diameter ranges from 40.0 to 60 μm .

iii. Hexa. This group contains the following species that produce fossilizable cysts.

Protoperidinium (*Protoperidinium*) *conicoides* (Paulsen) Balech 1974

Text-fig. 18; Plate 38, figs. 1-3

Remarks. The epithecal tabulation of this species illustrates the nature of the ortho first apical plate and the hexa dorsal intercalary arrangement together with the symmetry. The cyst of this species has

EXPLANATION OF PLATE 40

All figures are illustrated at a magnification of $\times 500$ and were photographed in plain transmitted light unless otherwise indicated.

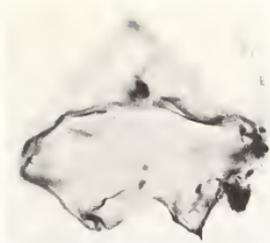
Figs. 1-8. *Protoperidinium* cyst, *Lejeunia paratenella* Benedek. 1, low-focus dorsal view with attenuated hexa archeopyle. 2, high-focus dorsal view showing the paracingulum and nature of acuminate antapical horns. 3, ventral view with slightly displaced paracingulum, specimen MPK 2775. 4, dorsal view with archeopyle and denticulate cingular parasutures. 5, ditto in phase contrast, specimen MPK 2776. 6, dorsal view showing attenuated hexa archeopyle with operculum in place, Nomarski interference contrast. 7, ventral view, Nomarski interference contrast, specimen MPK 1247. 8, dorsal view with attenuated hexa archeopyle, Nomarski interference contrast, specimen MPK 1245.

Fig. 9. *Protoperidinium* (*Protoperidinium* sect. *Quinqucuspis*) *leonis* (Pavillard) Balech, dorsal view with standard hexa archeopyle exhibiting slight tongue. Difference in archeopyle style between this and previous species is marked, specimen MPK 2777.

Figs. 10-12. *Protoperidinium* (*Protoperidinium* sect. *Votadinium*) *oblongum* (Aurivillius) Balech. 10, ventral view showing overall chordate morphology. 11, dorsal view with archeopyle truncating apex. 12, ditto, Nomarski interference contrast, specimen MPK 2778.



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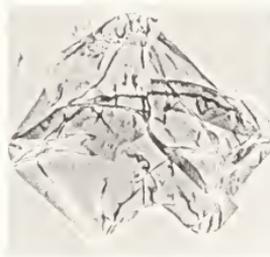
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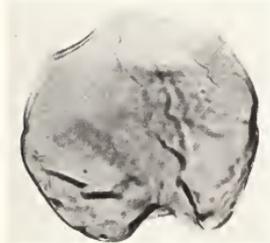
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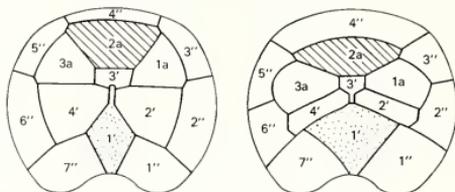


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been described by Wall and Dale (1968), Reid (1977), and Harland (1977), and was originally placed in the cyst genus *Chytroeisphaeridia* as *C. simplicia* by Wall (1965). More recently it has been chosen as the type species for the cyst genus *Brigantedinium* Reid which has been validated by Harland and Reid (1980) in Harland *et al.* (1980). The cyst morphology is, like many other *Protoperidinium* cysts, a simple brown ball. This cyst has not been successfully incubated but the link between theca and cyst is almost certain (Wall and Dale 1968).



TEXT-FIG. 18. (left) Epithecal tabulation of *Proto-peridinium* (*Proto-peridinium*) *conicoides* (Pausen) Balech (after Wall and Dale 1968).

TEXT-FIG. 19 (right). Epithecal tabulation of *Proto-peridinium* (*Proto-peridinium*) *conicum* (Gran) Balech (after Wall and Dale 1968).

Cyst description. A spherical brown cyst made up of autophragm which may be smooth, shagreenate, or loosely reticulate. May exhibit a slightly indented paracingular and parasulcal area, the latter possessing indications of the flagellar pores. Archeopyle formed by loss of a single intercalary paraplate (2a) of standard hexa shape which may show interesting detail around the margin (Pl. 38, fig. 1). This detail, especially, toward the apex, perhaps suggests the loss of more than just a single paraplate. Operculum free. Cyst diameters range from 30.0 to 50.0 μm .

This cyst can be distinguished from other similar cysts by the nature of its archeopyle (see earlier sections) but it is often difficult to recognize if the cysts are crushed.

Proto-peridinium (*Proto-peridinium*) *conicum* (Gran) Balech 1974

Text-fig. 19; Plate 39, figs. 1-3; Plate 42, figs. 1, 10

Remarks. The thecal epitabulation shows the main features of this group and is distinctly symmetrical. An interesting feature is, however, the almost rectangular shape of plates 2' and 4'. The cysts of this species have been described by Wall and Dale (1968), Bradford (1975), Reid (1977), and Harland (1977). The cyst genus *Multispinula* Bradford has been applied to them although this is a junior synonym of *Selenopemphix* Benedek which was originally erected for cysts showing polar compression and an offset archeopyle (Stover and Evitt 1978). Bujak (1980) formally emended *Selenopemphix* to draw attention to this offset archeopyle and also to include spinose forms. Wall and Dale (1968) established the theca/cyst link by incubation studies.

Cyst description. Ovoidal to reniform cysts probably made up of two wall layers, the outer making up the solid aciculate processes. Cyst usually has a polar compression due to its general cyst morphology of low epicystal and hypocystal cones (see Wall and Dale 1968, pl. 2, figs. 4, 5). This compression may also have the effect of slightly rotating the epicyst to accentuate the offset archeopyle. Pl. 39, figs. 1-3 demonstrates the variable amount of offset of the archeopyle. The sulcal area is exhibited as an indentation in the ventral side of the ambitus and the paracingulum is displayed as a circumferential band. Processes are generally most common at the apex and circumference although they also occur all over the cyst. Archeopyle intercalary formed by the loss of paraplate 2a which exhibits a standard hexa shape and is asymmetrically placed. Operculum free. The offset archeopyle may indicate the utilization of an additional paraplate to the 2a in archeopyle formation. Cyst diameter 40.0 to 60.0 μm .

There is some confusion between these cysts and those of *P. (P.) nudum* that have a similar morphology but are smaller. Bradford (1975) and Reid (1977) argued that a continuous size gradation existed between the two such that only the one cyst species can be recognized in the absence of knowledge of the thecal morphology.

Protoperidinium (Protoperidinium) leonis (Pavillard) Balech 1974

Text-fig. 20; Plate 41, figs. 1–14; Plate 42, figs. 7, 9.

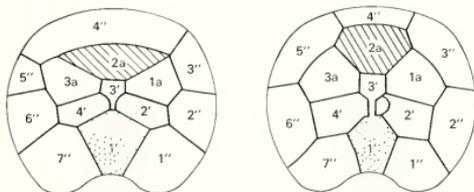
Remarks. The epithecal tabulation of this species indicates a possible assignment to the penta group and not to the hexa as Balech (1974) suggests, but Lebour (1925) has figured a specimen from Plymouth Sound with a clear hexa dorsal arrangement. Again some slight variation in the dorsal tabulation pattern is apparent. A symmetrical arrangement of plates on the epitheca is normal. The cysts of this species have been described by Evitt and Davidson (1964), Wall and Dale (1968), Bradford (1977), Reid (1977), and Harland (1977) using such generic taxa as *Lejeunia* Gerlach, *Trinovantedinium* Reid and *Quinquecuspis* Harland (see Harland 1977 for some synonymies). Wall and Dale (1968) established the theca/cyst link by incubation but had difficulty in distinguishing *P. leonis* from such species as *P. marielebournae* (Paulsen) and *P. obtusum* (Karsten). The range of cyst morphologies place within *P. (P.) leonis* reinforces the need for further study as it is perfectly possible that there are a number of separate species involved, including those represented in Pl. 40, fig. 9—species 1, Pl. 41, figs. 1, 2, 7, 8—species 2, Pl. 41, figs. 3–6—species 3, Pl. 41, figs. 9, 10—species 4 and Pl. 41, figs. 11–14—species 5.

All these forms can be attributed to the genus *Lejeunia* Gerlach emend Stover and Evitt 1978 now *Lejeunecysta* Artzner and Dörhöfer 1978 but I believe there is a justification in keeping them within a separate taxon, *Quinquecuspis*. This is based upon their brown colour, thick wall, deeply indented parasulcus, often discontinuous paracingulum, and the standard hexa archeopyle, and an archeopyle index of *c.* 0.35–0.45. By contrast, *Lejeunia* cysts are often paler in colour, thin walled, have a planar continuous paracingulum with an attenuated hexa archeopyle, and an archeopyle index of *c.* 0.2–0.3.

Cyst description. Peridinioid acavate brown cysts made up of autophragm which is often thickened at the apex and antapex. The cyst surface is generally smooth but may be somewhat shagreenate. Epittract may be conical or have shoulders, whilst the hypotract carries two asymmetrical horns. Paratabulation may be represented by distinctly indented paracingulum and sulcus, the former delimited by low discontinuous or continuous ridges. Archeopyle intercalary by loss of paraplate 2a. Archeopyle shape can vary from standard hexa (Pl. 41, figs. 3, 14) to standard hexa with an apical tongue (Pl. 41, fig. 1). The antapical margin of the archeopyle is often at, or very close to, the paracingulum. Operculum free. Cyst diameter varies from 60.0 to 75.0 μm .

Protoperidinium (Protoperidinium) nudum (Meunier) Balech 1974

Text-fig. 21



TEXT-FIG. 20 (left). Epithecal tabulation of *Protoperidinium (Protoperidinium) leonis* (Pavillard) Balech (after Wall and Dale 1968).

TEXT-FIG. 21 (right). Epithecal tabulation of *Protoperidinium (Protoperidinium) nudum* (Meunier) Balech (after Wall and Dale 1968).

Remarks. The epithecal tabulation pattern shows all the usual features of this group; the ortho first apical and the hexa dorsal intercalary arrangement. The cyst has been described by Wall and Dale (1968) as being similar to those of *P. (P.) conicum* but smaller (31.0 μm , excluding spines as compared to 50.0 μm for *P. (P.) conicum*), and possessing relatively longer spines with conical bases. The archeopyle is formed by the displacement of the dorsal intercalary paraplate (2a). The attached operculum carries two spines. The confusion in distinguishing this cyst from those of *conicum* in palynological preparations has already been noted. Wall and Dale (1968) incubated two thecae from cysts but some doubt in identification of the thecae is apparent from their ?*mudum* designation.

Protoperidinium (Protoperidinium) pentagonum (Gran) Balech 1974

Text-fig. 22; Plate 39, figs. 7-11; Plate 42, fig. 8

Remarks. This species fits well into this group by virtue of its epithecal tabulation whereas its cyst, described by Wall and Dale (1968), Bradford (1977), Reid (1977), and Harland (1977), is somewhat different from those described above. It has in fact been described under the names *Lejeunia applanata* by Bradford (1977) and *Trinovantedinium capitatum* by Reid (1977) and Harland (1977).

This cyst is quite distinct from others described within this group by virtue of its hyaline wall, possession of short sutural and intratabular spines, and a broad hexa archeopyle. The cyst of *P. (P.) pentagonum* was chosen by Reid (1977) as the type for his genus *Trinovantedinium*. This genus was used to accommodate other cysts, especially those having thick brown walls, a peridinioid outline, and standard hexa archeopyle. I prefer to restrict the genus *Trinovantedinium* to include the cyst of *P. (P.) pentagonum* and any similar forms (see Wall and Dale 1968, pl. 2, figs. 9-10 and 11-12 and Bradford 1977), but not to include brown cysts with standard hexa archeopyles. The cyst *Sumatradinium hispidum* (Drugg) Lentin and Williams could be related. Wall and Dale (1968) incubated a cyst to establish the cyst/theca relationship for *P. (P.) pentagonum*. However, other similar cysts produced thecae with minor differences such that a number of separate species or varieties may be involved.

Cyst description. Pentagonal peridinioid cyst made up of autophragm, epicyst with apical boss, and sometimes shoulders. Hypocyst has two slightly asymmetrical antapical horns or bulges. Paratabulation not easily recognized except for the planar non-indented paracingulum marked by sutural line of processes, the deeply indented parasulcus, and the pattern of intratabular processes defining paraplate areas. Processes are short, rigid with hollow bulbous bases, fine, aciculate with bifid, capitate, or infundibular solid tips. Processes are both sutural and intratabular but their dispositions are not sufficiently clear to reveal the paratabulation. Archeopyle intercalary formed by the loss of 2a paraplate, operculum free, archeopyle is a broad hexa style (Pl. 39, fig. 10). Cyst maximum length ranges from 65.0 to 70.0 μm .

EXPLANATION OF PLATE 41

All figures are illustrated at a magnification of $\times 500$ and were photographed in plain transmitted light unless otherwise indicated.

Figs. 1-14. *Protoperidinium (Protoperidinium* sect. *Quinquecuspis) leonis* (Pavillard) Balech. 1, dorsal view with archeopyle and operculum showing a clear apical tongue. 2, ventral view with deeply indented parasulcus and somewhat discontinuous paracingulum, specimen MPK 1230. 3, ventral view with standard hexa archeopyle, apical margin by transparency. 4, dorsal view, specimen MPK 2779. 5, ventral view with deeply indented parasulcus and discontinuous paracingulum. 6, dorsal view, specimen MPK 2780. 7, dorsal view showing posterior archeopyle margin almost affecting the paracingulum. 8, ventral view, specimen MPK 2781. 9, ventral view. 10, dorsal view, specimen MPK 2782. 11, ventral view with deep parasulcus and discontinuous paracingulum. 12, dorsal view, specimen MPK 2783. 13, ventral view with two flagellar parapores. 14, dorsal view showing standard hexa archeopyle with no apical tongue, specimen MPK 2784.



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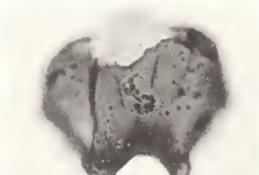
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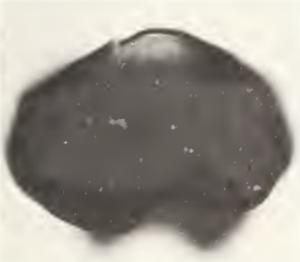
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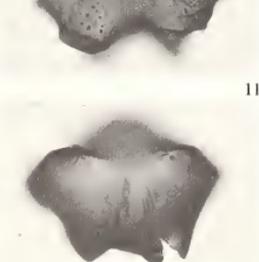
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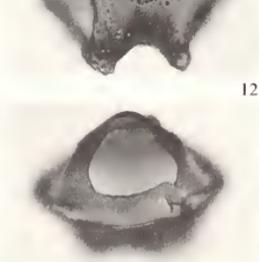
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14

Protoperidinium (Protoperidinium) subinermis (Paulsen) Loeblich, III, 1969

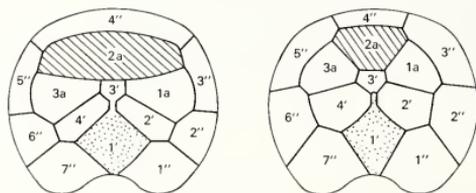
Text-fig. 23; Plate 39, fig. 6

Remarks. The thecal tabulation reveals the ortho first apical plate and the dorsal epithecal style. The cyst of this species has been described by Wall and Dale (1968) as being characterized by a relatively wide and deeply indented cingulum. The cyst illustrated here (Pl. 39, fig. 6) is believed to be attributable to *P. (P.) subinermis*. Wall and Dale (1968) established the theca/cyst relationship of this species although they recognized that the resultant theca from incubation was more elongate in the polar direction than other thecae of this species.

Cyst description. Ovoidal to reniform cysts, usually with a polar compression due to the low cone morphology of the epi- and hypocyst. Marked paracingular zone characterized by a broad circumferential band. Cyst smooth, light brown in colour, and possessing an offset standard hexa intercalary archeopyle formed by the displacement of ?2a paraplate. Operculum may be attached. Cyst diameter ranges from 45.0 to 60.0 μ m.

Discussion of the subgenus *Protoperidinium*

Within the para species of this subgenus the cyst morphology is of a peridinioid form with a reduced hypocyst and an intercalary standard hexa archeopyle. Unfortunately only one cyst type is known



TEXT-FIG. 22 (left). Epithecal tabulation of *Protoperidinium (Protoperidinium) pentagonum* (Gran) Balech (after Wall and Dale 1968).

TEXT-FIG. 23 (right). Epithecal tabulation of *Protoperidinium (Protoperidinium) subinermis* (Paulsen) Loeblich, III (after Wall and Dale 1968).

EXPLANATION OF PLATE 42

All figures, except the stereoscan photomicrographs, are illustrated at a magnification of $\times 500$ and were photographed in Nomarski interference contrast.

Fig. 1. *Protoperidinium (Protoperidinium) conicum* (Gran) Balech, specimen MPK 2949. A small specimen at the lower end of the size range that could be confused with *P. (P.) conicum* (Meunier) Balech.

Fig. 2. Indet. *Protoperidinium* cyst, specimen MPK 2950, with a well developed zigzag split archeopyle.

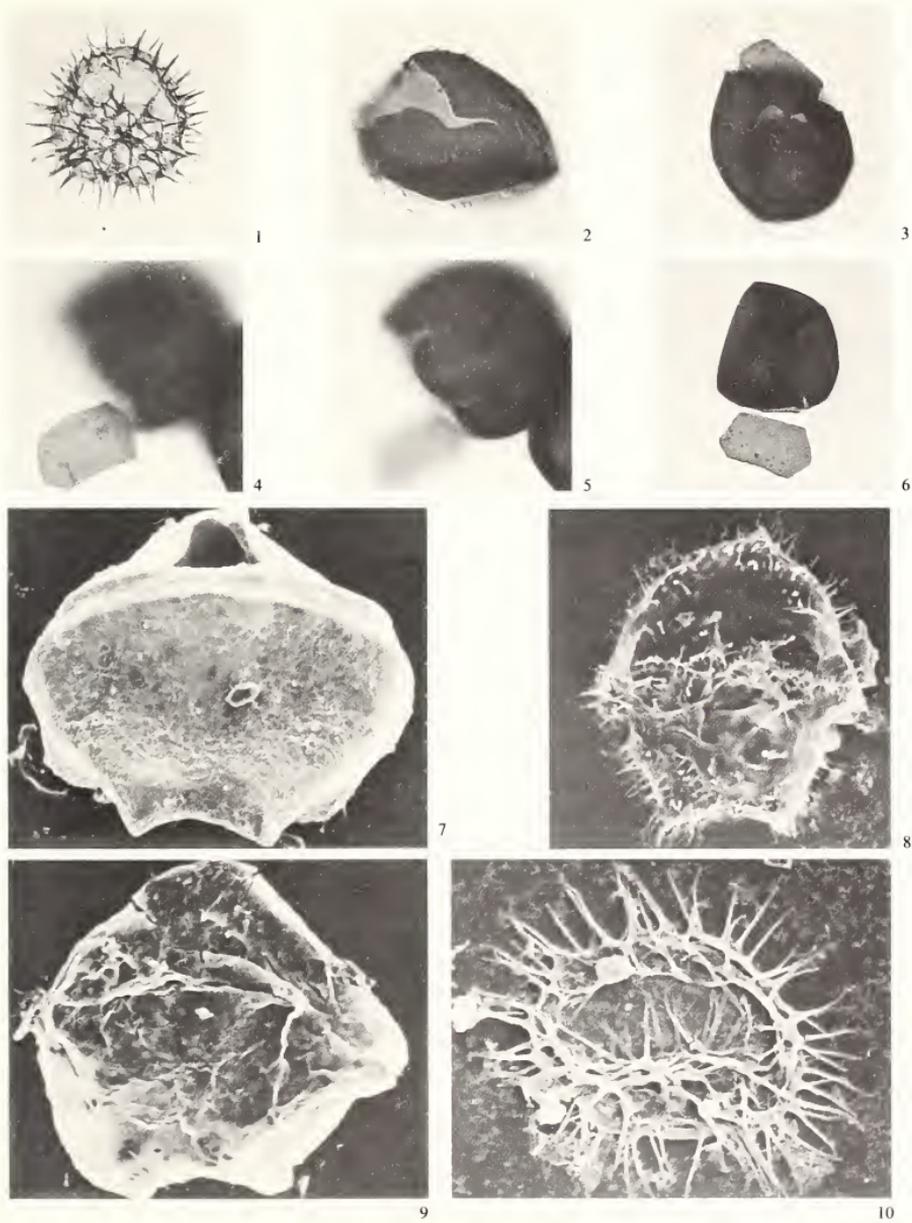
Figs. 3-6. *Protoperidinium (Protoperidinium) punctulatum* (Paulsen) Balech, specimen MPK 2951, 2952 and 2953) respectively. Specimens showing the over-all cyst morphology and nature of operculum, particularly its asymmetrical morphology.

Fig. 7. *Protoperidinium (Protoperidinium) leonis* (Pavillard) Balech, specimen MPK 2954 showing cyst morphology and archeopyle, together with a continuous paracingulum, $\times c.$ 1000.

Fig. 8. *Protoperidinium (Protoperidinium) pentagonum* (Gran) Balech, specimen MPK 2956, showing cyst morphology and the broad hexa archeopyle, $\times c.$ 1000.

Fig. 9. Indet. *Protoperidinium* cyst, specimen MPK 2957. Could be part of the cyst variation as currently attributed to *P. (P.) leonis* (Pavillard) Balech, $\times c.$ 1000.

Fig. 10. *Protoperidinium (Protoperidinium) conicum* (Gran) Balech, specimen MPK 2958, showing over-all cyst morphology, $\times c.$ 1000.



from this group at the present time. The designation *Protopteridinium* (*Protopteridinium* sect. *Protopteridinium*) may be used for thecae with a para first apical and hexa dorsal intercalary arrangement and for peridinioid cysts with reduced hypocysts. However, it must be admitted that the type species does not appear to have fossilizable cysts.

In the ortho species we have most of the living cyst species including, in the quadra subsection, the chordate cysts, with or without spines and having an archeopyle that truncates the apex, i.e. the species *P. (P.) claudicans* and *P. (P.) oblongum* respectively. The designation *Protopteridinium* (*Protopteridinium* sect. *Votadinium*) can be used for these ortho, quadra species.

Amongst the ortho penta species only the cyst of *P. (P.) punctulatum* is known, and like so many *Protopteridinium* cysts it is a brown sphere. It is, however, characterized by its archeopyle which is transversely elongate and asymmetrical. The name *Asymmetropedinium* is proposed at section level to accommodate this species.

In the ortho hexa species a fourfold division based upon cyst morphology is possible. The thecal tabulation does not in itself support this division but perhaps other factors need to be considered. The first division is represented by *P. (P.) conicoides* which has a spherical brown cyst with a standard hexa archeopyle; the second by *P. (P.) conicum*, *P. (P.) nudum*, and *P. (P.) subinermis* that have cysts commonly showing polar compression because of the low conate shape of the epi- and hypocyst, and an offset standard hexa archeopyle. A third type represented by *P. (P.) leonis* contains brown peridinioid cysts with standard hexa archeopyles and finally the fourth is characterized by *P. (P.) pentagonum* with a hyaline peridinioid cyst with a broad hexa archeopyle. The names *Brigantedinium* Reid, *Selenopemphix* Benedek, *Quinquecuspis* Harland, and *Trinovantedinium* Reid respectively are used here to designate these dinoflagellates at section level and are names that were first established in the palaeontological literature.

Unattributed ?*Protopteridinium* cysts

Remarks. There are many ?*Protopteridinium* cysts described in the literature that have been observed in palynological assemblages of Recent sediments, but whose attribution to the thecate stage is unknown. A number of such forms are illustrated and commented upon here. The first (Pl. 38, figs. 10–12, and Pl. 42, fig. 2) is in essence a brown spherical cyst that opens by means of a zigzag split. Reid (1972) described such cysts from intertidal sediments around the British coast. It is interesting to note that the brown spherical morphology is again apparent, but that the archeopyle morphology is sufficiently different to differentiate these cysts from the other forms described earlier. It is, however, quite possible that these cysts are from glenodiniacean dinoflagellates such as *Diplopsalis* (see Wall and Dale 1986, pl. 4, fig. 20).

A second type, that has been described under the name of *Xandarodinium xanthum* Reid 1977, is illustrated on Pl. 39, figs. 4–5. This cyst has a unique morphology with hollow processes carrying distal furcate and bifid tips. Reid (1977) describes these cysts as having a possible single paraplate intercalary archeopyle, but an archeopyle has not been seen by me. The morphology in regard to the ovoidal/reniform ambitus suggests a polar compression and hints at an attribution to sect. *Selenopemphix*, but confirmation and details of archeopyle formation must await further study. *Artemisiocysta cladodichotoma* Benedek may be related to the cyst form described here. This cyst might be a representative of a gymnodinialean dinoflagellate (see Wall and Dale 1968, pl. 4, fig. 29).

The final type (Pl. 40, figs. 1–8) has been referred to as *Lejeunia paratenella* Benedek 1972 by Harland (1977) and *Trinovantedinium olivum* Reid 1977 by Reid (1977). It is characterized by its peridinioid outline, pale brown colour, thickened apex and antapex, the latter often developed into acicular horns, planar paracingulum delimited by denticulate sutures, and an attenuated hexa archeopyle (Lentin and Williams 1975). This cyst differs, therefore, from those referred to as *Quinquecuspis*, and I prefer to see it accommodated in *Lejeunecysta* Artzner and Dörhöfer 1978. Lentin and Williams (1975) have attributed a standard hexa archeopyle to *Lejeunecysta* (as *Lejeunia*), but the nature of the archeopyle in the type species has not been clearly demonstrated. The specimen figured by Benedek (1972) does, however, appear to have a standard hexa archeopyle which may

indicate that *Lejeunecysta* is a senior of *Quinquecuspis* and that a new name needs to be erected for these cysts. Until the thecate form is identified further speculation is unwarranted.

GENERAL DISCUSSION

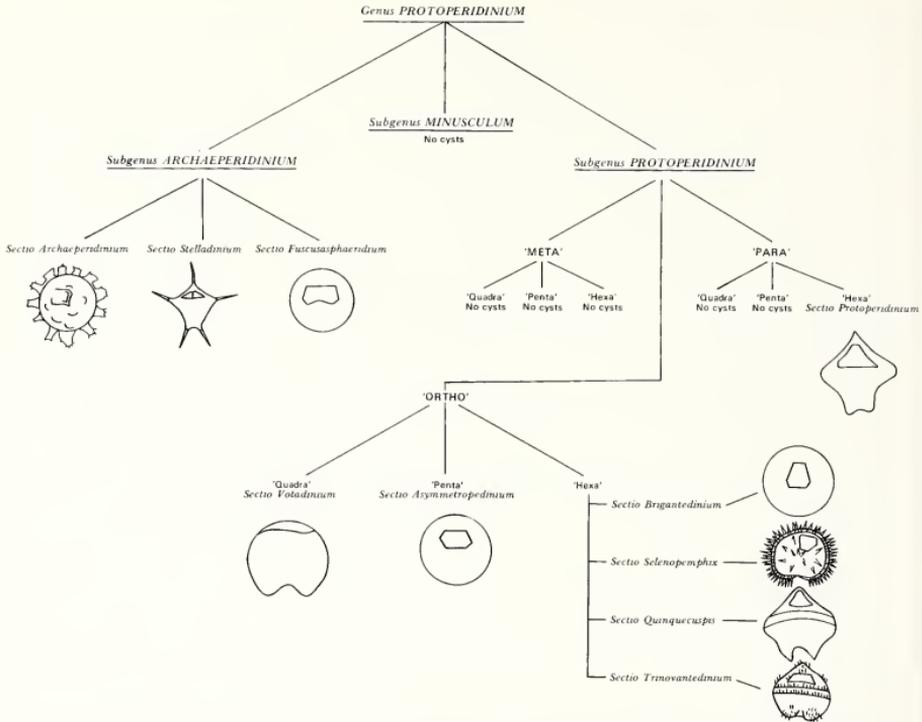
A taxonomic system capable of amalgamating both cyst and thecal data must be one of the aims of dinoflagellate research and would inevitably lead to a rationalization of much of our fossil data. The exercise, outlined above, tests that possibility and shows this, or a similar system, is practical. It is clear that both the major and minor divisions of the genus *Protoperidinium* Bergh are largely upheld by differing cyst morphologies (text-fig. 24). The genus is basically characterized by cysts of spherical to peridinioid shape, possessing an intercalary archeopyle. The subgenus *Archaeperidinium* is characterized by such unique cysts as those of *P. (A.) minutum*, *P. (A.) compressum*, and simple brown spherical cysts distinguished by broad hexa, transversely elongate, symmetrical archeopyles. Cyst morphology can also be used to further subdivide the subgenus at section level. These subdivisions need, however, further testing in relation to total dinoflagellate morphology.

Similarly the subdivisions of the subgenus *Protoperidinium* based upon thecal morphology appear to be largely substantiated by differences in cyst construction. The para species may have cysts with reduced hypocysts and no paracingulum (but the evidence is based upon one species only). The different divisions of the ortho forms have the following morphologies; the quadra cysts are chordate in shape with an archeopyle that is basically intercalary but truncates the apex and may involve additional paraplates; the penta cysts are brown and spherical, with a broad hexa archeopyle that is asymmetrical; and the hexa cysts are both spherical and peridinioid, with standard or broad hexa archeopyles. In this last case the cyst morphologies may serve to further subdivide the group.

Dale (1978) has pointed out that dinoflagellate cysts are often non-conservative, with large differences in cyst morphology being reflected by small 'minor' differences in thecae. This is supported by the present study; indeed in the ortho hexa cysts large differences in cyst morphology are seemingly not reflected in thecal morphology at all. In my view, major and minor differences in morphology are relative terms. What should be remembered is that the genetic information is common to both stages of the life cycle, and that all morphological differences must be critically evaluated. Dinoflagellate taxonomy should be based upon the holomorph where possible or on as much information as is available such that a common taxonomy can evolve. In this way it is necessary to evaluate both the cyst-based taxonomy, often 'overclassified' and the thecate-based taxonomy, often 'underclassified' (Dale 1978), in order to arrive at the best amalgamation. Whilst agreeing with Dale (1978) that new cyst-based nomenclature should not be created to artificially maintain the cyst-based taxonomy, much useful information can be derived from good taxonomic work based upon cysts, thecae, or on both.

From a review of this nature the major difference between the thecal-based taxonomy and the cyst-based system is one of hierarchy (see text-fig. 24). The palynologist would regard his cyst taxa as separate genera whereas the phycologist might be prepared to accept them at section level. Once this hierarchical difference is recognized, the conflict between the two systems largely vanishes and both theca and cyst data can point to areas where further study is needed to help resolve or enlarge upon taxonomic decisions. In addition, it should assist the palynologist to view his fossil taxa in a better perspective. It is clear, however, that the species is the common denominator, is constant, and should be the basis of all our mutual research.

This study has also highlighted the 'variation' in thecal and cyst morphologies, especially in the ortho quadra species, which appear to have both quadra and penta dorsal configurations as in *P. (P.) claudicans*, the ortho hexa species such as *P. (P.) leonis* with both penta and hexa configurations, and the ortho penta species such as *P. (P.) punctulatum* that have both penta and hexa dorsal epithelial patterns. In the ortho quadra group the data also suggest variation in cyst morphologies, from chordate cysts with archeopyles truncating the apex to cysts with a peridinioid shape and standard hexa archeopyles. Recent studies have tended to show that the dorsal epithelial and epicystal pattern



TEXT-FIG. 24. Recent and Quaternary *Protoperidinium* cyst types and their respective positions in the taxonomic subdivision of the genus.

is of considerable importance in dinoflagellate organization as both the keystone plate and overlap system, together with archeopyle position, all relate to that pattern, and suggest a common genetic control.

Some of the 'variation' discussed may in fact be more artificial than real, because much of it is inextricably linked to taxonomic difficulties. The examples of *P. (P.) oblongum* and *P. (P.) leonis* are cases in point. Much of these difficulties will need detailed research on both thecal and cyst morphologies, together with population studies, before any satisfactory conclusions can be reached.

There is a range of cyst types associated with a single living genus, i.e. from simple brown spheres to peridinioid and quite complex stellate morphologies. The cyst types are, however, dominated by two cyst morphologies—the simple brown spheres and the peridinioid cysts. The intercalary archeopyle is a common factor throughout, although its shape, style, and involvement of adjacent paraplates is different in the separate groups. The occurrence of the simple brown spherical cyst morphology in the subgenera *Archaeperidinium* and *Protoperidinium* (and in both ortho penta and ortho hexa groups) may be cited as a good example of the development of a common cyst form by different dinoflagellates (homoeomorphy). Indeed this morphology is also seen in cysts of unknown affinity (see Pl. 38, figs. 10–12) and in the glenodiniacean dinoflagellates (Reid 1977). There is difficulty in recognizing species among these brown spheres because of a usual lack of well-preserved and well-orientated specimens. In addition, brown peridinioid cysts also occur in more than one dinoflagellate group.

It is interesting to observe the lack of correspondence between some dorsal epithecal tabulations and the partial paratabulations revealed by archeopyle formation. In particular, the stellate cyst of *P. (A.) compressum* appears to have a symmetrically placed type 2I archeopyle but not a symmetrical dorsal epithecal tabulation pattern. Similarly *P. (P.) conicum*, *P. (P.) nudum*, and *P. (P.) subinerme* have symmetrically placed 2a thecal plates, but offset type I archeopyles. Although the over-all genetic control is apparent there does not seem to be a strict template mechanism. Whether or not additional paraplates are involved in these cases in archeopyle formation, there is an obvious need for caution. The mechanism and control of archeopyle formation is a fascinating question and is clearly more complex than at first appears.

Unfortunately there are still a number of cysts, described in the literature, of possible *Protopteridinium* affinity, whose 'parental' thecae are not known. One of these is the cyst referred to as *Lejeunia paratenella* Benedek by Harland (1977). It would be of special interest to know the thecal affinity of *L. paratenella* in order to compare it with other *Protopteridinium* species known to produce *Quinquecuspis* type cysts. This should serve to help in understanding the nature of *Lejeuncysta/Quinquecuspis* species in the fossil record.

Other fossil cysts may be underrepresented within this scheme because of their susceptibility to oxidation in nature, in the palynological preparation technique, and to treatment with strong acids (Dale 1976; Reid 1972). It is apparent from Lentini and Williams (1975) that the fossil record of the genus *Protopteridinium* includes only those cysts attributable to the subgenus *Protopteridinium*, including ortho forms, such as the fossil genera *Rhombodinium* Gocht and *Wetzeliella* Eisenack, which have a geological record from the Palaeocene, and ortho forms such as *Alterbia* Lentini and Williams and *Deflandrea* Eisenack, with records from at least the Albian. Other peridiniacean cysts with more complex compound archeopyles are not represented here. The cysts portrayed within the sections *Selenopemphix* and *Quinquecuspis/Lejeuncysta* have fossil records at least as far back as the Late Eocene and Late Cretaceous respectively.

CONCLUSIONS

This study should have demonstrated the feasibility of combining cyst and thecate morphological data into a sensible taxonomic scheme which might be of some application to both Quaternary and some Tertiary peridiniacean dinoflagellates. It is, of course, not complete, because much more thecal data are needed before a fully comprehensive taxonomy can be attempted. I hope it does suggest a possible way forward and one that could be equally applied to gonyaulacacean, glenodiniacean, ceratiacean, or pyrophacacean dinoflagellates where and when sufficient evidence is available. Notable points of interest have been the morphological range of cysts from a single living genus, and the hierarchical difference between the sections erected herein and what would be undoubtedly regarded as separate genera by palynologists. The species concept does, however, appear to be a mutually acceptable base.

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APPENDIX

The appendix is used here to indicate new names, and names whose status has been altered. The order adopted follows that presented in the main text.

Subgenus *Archaeperidinium* (Jørgensen) Balech 1974

Section *Archaeperidinium* Jørgensen stat. nov.

Type species. *Protoperidinium* (*Archaeperidinium* sect. *Archaeperidinium*) *minutum* (Kofoid) Loeblich, III, 1969

Remarks. This name has been used at generic level by Jørgensen (1913), at sub-generic level by Balech (1974), and here is used at section level as one of the sections of the subgenus *Archaeperidinium*. It is characterized by cysts with unique process structure and a symmetrical epithecal tabulation pattern.

Section *Stelladinium* Bradford 1975 ex Harland and Reid 1980 stat. nov.

Type species. *Stelladinium reidii* Bradford 1975 ≡ *Protoperidinium* (*Archaeperidinium* sect. *Stelladinium*) cf. *compressum* (Abé) Balech 1974.

Remarks. This name, originally erected as a genus, is altered in status to become a section of the subgenus *Archaeperidinium*. The type species *reidii* is based upon a cyst holotype and not a thecate form but the parent must be a species similar to *P. compressum*. It is characterized by stellate cysts and an asymmetrical thecal tabulation.

Section *Fuscusphaeridium* nom. nov.

Derivation of name. Latin: *fuscus*, brown, *sphaera*, ball.

Diagnosis. Spherical to spheroidal brown cyst of autophragm with a laterally elongate, symmetrical, archeopyle formed by the loss of a single intercalary paraplate (2a). Margin of archeopyle often shows its configuration with paraplates 3', 4', 1a, and 6''. Operculum free.

Cista autophragmatis aurea quae forman habet sphaericalem vel spheroidalem et latus elongatum, symmetricalis est. Archaeopyla facta est uno paraplato intercalari amisso (? 2a). Margo archaeopylae saepe configurationem suam ostendit cum paraplatis 3', 4' 1a et 6''. Operculum liberum est.

Type species. *Protoperidinium* (*Archaeperidinium* sect. *Fuscusphaeridium*) *avellana* (Meunier) Balech 1974 ≡ *Protoperidinium avellana* Meunier 1919, pp. 56, pl. 18, figs. 37-41. Recent.

Remarks. The new section erected here accommodates those dinoflagellates possessing brown spherical cysts with symmetrical, transversely elongate archeopyles and with slightly asymmetric dorsal epithecal tabulations.

Subgenus *Protoperidinium* (Bergh) Balech 1974

Section *Protoperidinium* Bergh 1881 stat. nov.

Type species. *Protoperidinium* (*Protoperidinium* sect. *Protoperidinium*) *pellucidum* Bergh 1881.

Remarks. *Protopteridinium* is used here at section level as a part of the subgenus *Protopteridinium*. It may be characterized by cysts with inflated epicysts but this is as yet unproven since the type species does not appear to have fossilizable cysts.

Section *Votadinium* Reid 1977 stat. nov.

Type species. *Votadinium calvum* Reid 1977 \equiv *Protopteridinium* (*Protopteridinium* sect. *Votadinium*) *oblongum* (Aurivillius) Balech 1974.

Remarks. This name is given the new status of section within the subgenus *Protopteridinium*, and is characterized by chordate cysts with large dorsal intercalary archeopyles that truncate the apex together with ortho quadra epithecal tabulation patterns.

Section *Asymmetropedinium* nov.

Derivation of name. Greek: *asymmetro*, without symmetry; *ope*, opening; and *dinium* of dinoflagellate affinity, with reference to the asymmetrical archeopyle.

Diagnosis. Spherical to spheroidal, brown cyst of autophragm that possesses a laterally elongate archeopyle which is asymmetrical about the dorso-ventral plane, formed by the loss of a single intercalary paraplate (?2a). Margin of archeopyle may show its configuration with adjacent paraplates. Operculum ?attached.

Cista aurea autophragmatis quae habet et formam sphericalem vel spheroidalem et latus elongatum asymmetricalis est. Archeopyla facta est uno paraplato amisso (?2a). Fieri potest ut margo archaeopylae ostendat configurationem cum paraplatis quae proximae sunt. Operculum ? adiunctum.

Type species. *Protopteridinium* (*Protopteridinium* sect. *Asymmetropedinium*) *punctulatum* (Paulsen) Balech 1974 \equiv *Peridinium punctulatum* Paulsen 1907, p. 19, fig. 28. Recent.

Remarks. *Asymmetropedinium* is used here for ortho penta dinoflagellates that have brown spherical cysts with transversely elongate archeopyles that are asymmetrical.

Section *Brigantedinium* Reid 1977 ex Harland and Reid 1980 stat. nov.

Type species. *Brigantedinium simplex* (Wall) Reid 1977 \equiv *Protopteridinium* (*Protopteridinium* sect. *Brigantedinium*) *conicoideis* (Paulsen) Balech 1974.

Remarks. This section is characterized by an ortho hexa epithecal configuration and brown spherical cysts with a standard hexa archeopyle. *Brigantedinium* was originally coined at generic level by Reid (1977) to accommodate all brown spherical cysts.

Section *Selenopemphix* Benedek 1972 stat. nov.

Type species. *Selenopemphix nephroides* Benedek 1972 \equiv ?*Protopteridinium* (*Protopteridinium* sect. *Selenopemphix*) *subinermis* (Paulsen) Loeblich, III, 1969.

Remarks. *Selenopemphix*, originally erected as a genus by Benedek (1972), is here altered in status to a section of the subgenus *Protopteridinium* to hold ortho hexa dinoflagellates whose cysts show polar compression and offset archeopyles. The type species, the fossil *S. nephroides* Benedek, is very similar, if not identical to the cyst of *P. (P.) subinermis* (Paulsen).

Section *Quinquecuspis* Harland ex et emend. Harland stat. nov.

Type species. *Quinquecuspis concretum* (Reid) Harland 1977 \equiv ?*Protopteridinium* (*Protopteridinium* sect. *Quinquecuspis*) *leonis* (Pavillard) Balech 1974.

Emended diagnosis. Pentagonal, peridinioid, acavate, brown cyst, made up of autophragm which thickens towards the apex and antapex. Epittract conical or with shoulders, hypottract with well or

poorly developed asymmetrical horns. Paratabulation absent, paracingulum conspicuous, planar, and delimited by low continuous or broken ridges. Deeply indented parasulcus sometimes with flagellar scars. Archeopyle intercalary, standard hexa, formed by the loss of paraplate 2a, with or without an apical tongue. Operculum free.

Cista aurea pentagonalis peridinoidalis et acavata, ex autophragmate facta quod densum fit versus apicem et antapicem. Epittractum habet vel formam conicalem vel humeros, hypottractum habet cornua asymmetricalia quae bene vel male formata sunt. Paratabulatio nulla est sed paracingulum et videri potest et planare finitum est rugis quae vel imae vel fractae sunt. Parasulcus alte dentatum cum cicatricibus flagellaribus. Archaeopyla intercalaris, hexa normalis quae facta est amisso paraplate 2a, cum vel sine lingua in apice. Operculum liberum.

Remarks. This name was originally erected at generic level (Harland 1977) but did not comply with Article 36 of the International Code of Botanical Nomenclature (Stafleu *et al.* 1978) which requires that Recent algal taxa be furnished with a Latin diagnosis. The type species had a Latin diagnosis in its original publication (Reid 1977) and was valid from that date. As a section of the subgenus *Protoperidinium* it is characterized by an ortho hexa epithecal tabulation and peridinoid brown cysts with a standard or modified standard hexa archeopyle.

These cysts are noted in particular for their thick brown walls, and archeopyles often having an apical tongue and deeply indented sulcal areas. During archeopyle formation a break often occurs down across the paracingulum (see Pl. 41, figs. 4, 7) from the posterior archeopyle margin.

Section *Trinovantedinium* Reid 1977 stat. nov.

Type species. *Trinovantedinium capitatum* Reid 1977 \equiv *Protoperidinium* (*Protoperidinium* sect. *Trinovantedinium*) *pentagonum* (Gran) Balech 1974.

Remarks. *Trinovantedinium*, a genus erected by Reid (1977), is herein given the new status of section within the subgenus *Protoperidinium*. It accommodates dinoflagellates with ortho hexa epithecal tabulations and hyaline peridinoid cysts with short spines and a broad hexa archeopyle.

A NEW GENUS OF SHARK FROM THE MIDDLE TRIASSIC OF MONTE SAN GIORGIO, SWITZERLAND

by O. RIEPPEL

ABSTRACT. Associated material from the Middle Triassic of Monte San Giorgio, Kt. Tessin, Switzerland, demonstrates that the sharks *Nemacanthus tuberculatus* and *Acrodus bicarinatus* constitute a single taxon that must be included in a new genus, *Acronemus tuberculatus*. Finspine structure of *Acronemus* is distinctly different from that of *Nemacanthus monilifer*, but does correspond to the general ctenacanthiform pattern. Other features of *A. tuberculatus* such as tooth structure and placoid scales have previously been reported for Triassic hybodontiform sharks only. A discussion of the orders Ctenacanthiformes and Hybodontiformes concludes the study.

THE *Grenzbitumenzone* of Monte San Giorgio, Kt. Tessin, Switzerland, has so far yielded four hybodontiform shark genera, viz. *Hybodus*, *Acrodus*, *Asteracanthus*, and *Palaeobates*. A fifth selachian taxon, the most frequently found one in the deposits at Monte San Giorgio, will be described in the present contribution. This shark is important as it highlights some problems in the distinction of the Mesozoic orders Hybodontiformes and Ctenacanthiformes as defined by Maisey (1975).

Kuhn (1945) first described the genus *Acrodus* from the Middle Triassic of Monte San Giorgio. Kuhn's (1945) specimen *d* was not fully prepared at the time. The radiograph showed, however, that the proportions of the finspines of this shark were very different from those of *Acrodus*, and that the palatoquadrate was cleaver-shaped (Kuhn, 1945, fig. 4), a feature which is otherwise not known in the genus *Acrodus*. Peyer (1957) mentioned an *Acrodus* from Monte San Giorgio with a tuberculate finspine ornamentation. *Acrodus* finspines always show a costate ornament.

The misidentifications by Kuhn (1945) and Peyer (1957) are based on the fact that in the specimens mentioned by these authors typical *Acrodus* teeth are associated with stout and tuberculate finspines. The teeth and the finspines have been named and referred to different genera by earlier authors. Bellotti, in an unpublished manuscript on the fossil fishes at the Museo Civico di Milano (1873), had named the teeth *Acrodus bicarinatus* and the spines *Nemacanthus tuberculatus*. The first author to use these names in a formal publication was Bassani (1886). He used the names in connection with a valid diagnosis, referring to Bellotti's specimens and manuscript. According to the kind information provided by Professor G. Pinna, Museo Civico di Storia Naturale Milano, the entire old collection on which Bellotti's research was based has been destroyed during the Second World War. No type material has been preserved. Likewise, Bellotti's (1873) manuscript can no longer be located. The only material still available is unpublished drawings by Bellotti including those of *N. tuberculatus*.

The associated material from Monte San Giorgio demonstrates that *A. bicarinatus* and *N. tuberculatus* are a single taxon. Since Bassani (1886) is the formal author of both names, and since in his publication *N. tuberculatus* has page priority, the correct species name for this shark must be *tuberculatus*. The description of the Monte San Giorgio material will make it clear that this shark species cannot be included in the genus *Nemacanthus*, nor in the genus *Acrodus*. A new genus must consequently be erected. Since no original type material is preserved, it is appropriate to select a neotype for that species.

SYSTEMATIC PALAEONTOLOGY

Class CHONDRICHTHYES

Subclass ELASMOBRANCHII

Order CTENACANTHIFORMES incertae familiae

Genus ACRONEMUS n.gen.

Type and only known species. Acronemus tuberculatus (Bassani 1886).

Revised diagnosis. Small (30–35 cm long) ctenacanthiform shark; teeth *Acrodus*-like, with a single and blunt main cusp, crown ornamented with prominent longitudinal and transverse carinae, root without lingual torus; palatoquadrate cleaver-shaped; finspines short and stout, heavily tuberculated with a longitudinal ridge along the leading edge of the crown, not or only slightly recurved, posterior wall concave without denticulate ornamentation, central cavity displaced posteriorly; placoid scales with a lanceolate crown ornamented with three or five longitudinal striae.

Acronemus tuberculatus (Bassani 1886)*Selected synonymy*

- 1886 *Nemacanthus tuberculatus*, Bassani, p. 30.
 1886 *Acrodus bicarinatus*, Bassani, p. 31.
 1891 *Nemacanthus tuberculatus*, Woodward, p. 117.
 1910 *Acrodus bicarenatus*, Alessandri, p. 34, pl. 7, figs. 6–9.
 1910 *Nemacanthus tuberculatus*, Alessandri, p. 36, pl. 7, fig. 10.

Neotype. Paläontologisches Institut und Museum der Universität Zürich T 1548, Monte San Giorgio, point 902, layer 118, collected 20.9.1957.

Diagnosis. Same as for genus.

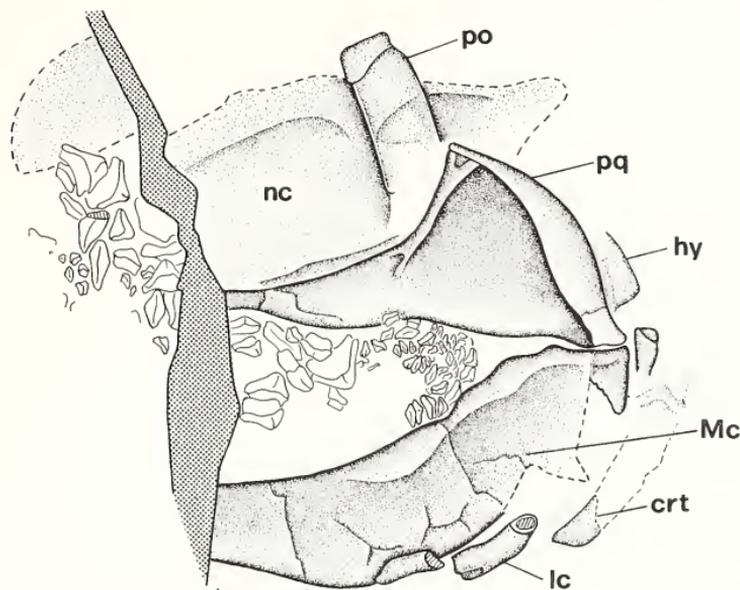
Referred material. All specimens with T-numbers belong to the Tessin collection, Paläontologisches Institut und Museum der Universität Zürich. T 1177, dentition and two finspines; T 1178, dentition, two finspines, skull fragments; T 1181, isolated tooth; T 1289, dentition, anterior finspine; T 1291, dentition, anterior finspine; T 1292, isolated tooth; T 1426, isolated tooth; T 1427, isolated tooth; T 1431, sectioned finspine; T 1434, isolated tooth; T 1448, dentition; T 1457, teeth, sectioned finspine; T 1487, dentition; T 1531, dentition and two finspines; T 1551, incomplete finspine; T 2465, dentition, upper and lower jaws, two finspines (see Kuhn 1945, fig. 4); T 3297, isolated tooth; T 3812, dentition; T 3818, two finspines; T 3819, dentition; T 3820, dentition; T 3821, dentition and jaw fragments; T 3822, dentition and anterior finspine; T 3827, dentition; T 3825, dentition and two finspines; T 3826, dentition; T 3828, posterior finspine; T 3829, dentition and anterior finspine; T 3831, dentition; T 3833, dentition; T 3834, dentition; T 3835, dentition and finspine; T 3836, dentition; T 3837, dentition; T 3840, sectioned finspine; T 3841, anterior finspine; T 3843, sectioned finspine; T 3844, finspine; T 3845, finspine; T 3846, sectioned finspine; T 3847, sectioned finspine; T 3849, fifty-two isolated teeth; British Museum (Natural History) P 19450, complete dentition.

Distribution. Middle Triassic of Southern Alps (Grenzbitumenzone of Monte San Giorgio, Kt. Tessin, Switzerland, and the same beds near Besano, Lombardy, Italy).

Description

Neurocranium and jaws. Virtually nothing is known of the neurocranium. Remains are observed in T 1548 (lateral view, text-fig. 1) and in T 2465 (dorsal view, text-fig. 2). There is a very prominent postorbital process which lies just in front of the otic process of the palatoquadrate. The rostrum appears to have been short and blunt, projecting little beyond the suborbital ramus of the palatoquadrate.

The palatoquadrate (text-figs. 1 and 2) shows a large postorbital ramus (slightly more than half the total length of the palatoquadrate) with a prominent otic process. The latter articulates with the postorbital process of the neurocranium. The anterior edge of the otic process is steeply inclined. The posterior edge is thickened and thus forms a rim which limits the area of origin of the m. adductor mandibulae externus. The lower end of the thickened posterior edge forms the articular condyle of the palatoquadrate which fits into a facet on the posterior end of Meckel's cartilage. The narrow, tapering suborbital ramus makes up slightly less than half of the total length of the palatoquadrate. A weak elevation of its dorsal edge in its anterior portion (text-fig. 2) forms the orbital process which articulates with the suborbital shelf of the neurocranium.



TEXT-FIG. 1. Skull remains in *Acronemus tuberculatus* T 1548. Abbreviations: crt, ceratohyal; hy, hyomandibula; lc, labial cartilages; Mc, Meckel's cartilage; nc, neurocranium; po, postorbital process; pq, palatoquadrate. Scale equals 10 mm.

Meckel's cartilages (text-figs. 1 and 2) are elongated and moderately deep. The ventral margin is convex and slightly thickened. The thickened ventral rim limits the site of insertion of the m. adductor mandibulae externus. The dorsal edge is concave except for the posterior portion where the dorsal edge is straight.

All the Monte San Giorgio material is strongly compressed, but from a thickening it appears that both the dorsal edge of Meckel's cartilage as well as the ventral edge of the palatoquadrate formed an outwardly turned shelf for the support of the teeth.

Labial cartilages. Only broken fragments are observed in T 1548 (text-fig. 1) along the ventral edge of Meckel's cartilage.

Hyoid arch. The articulation of the hyomandibula with the ceratohyal is preserved just posterior to the jaw articulation in T 1548 (text-fig. 1). The jaw suspension in a shark with a cleaver-shaped palatoquadrate may be assumed to have been amphistylic (Schaeffer 1967).

Cephalic spines. These are not recorded in any specimen.

Teeth. The teeth of *Acronemus tuberculatus* have long been known under the name of *Acrodus bicarinatus* (Bassani 1886; Alessandri 1910). The teeth are characterized by a single, blunt main cusp. No accessory lateral cusps are developed (Pl. 43, fig. 1). There is a marked longitudinal and a marked transverse ridge across the crown. The ridges meet at right angles on the apex of the main cusp (text-fig. 3 and Pl. 43, fig. 3). From the longitudinal and transverse ridges fine striae radiate towards the edges of the crown. The main cusp forms a bulbous lingual projection which overlaps the next inner tooth of the same tooth family. This results in a supporting mechanism for the outer functional tooth very similar to the one observed in *A. lateralis*.

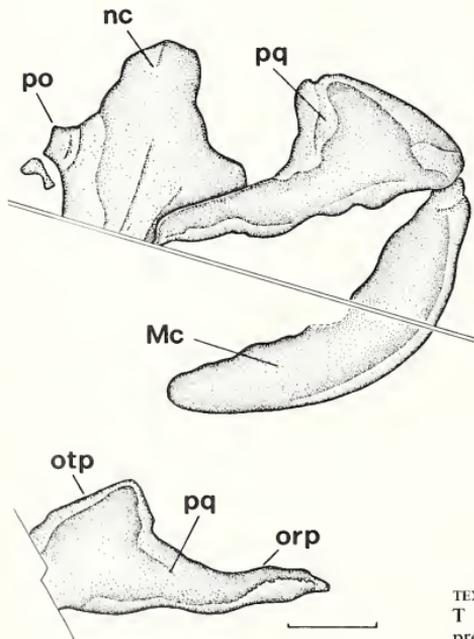
The enameloid layer covering the crown is of the single-crystallite type (Pl. 43, fig. 4) as defined by Reif (1973), without a superficial shiny layer. The root bears no expanded lingual torus. Root foramina were very difficult to observe because the bituminous matrix does not allow chemical preparation to expose these foramina.

The large lateral teeth are symmetrical, with the main cusp in a fairly central position. The crown is high and the lower edge of the root is distinctly concave (text-fig. 3). Towards the symphysis the teeth become progressively smaller and the crown lower and asymmetrical in that the main cusp is shifted towards the distal side of the crown. The lower edge of the root becomes less concave or even straight (text-fig. 3). Distal to the large lateral teeth there is a series of very low but very elongated and distinctly asymmetrical teeth (text-fig. 3) with the main cusp displaced towards the mesial side of the tooth. The lower edge of the crown is almost straight. Again, the teeth diminish in size towards the distal end of the jaw.

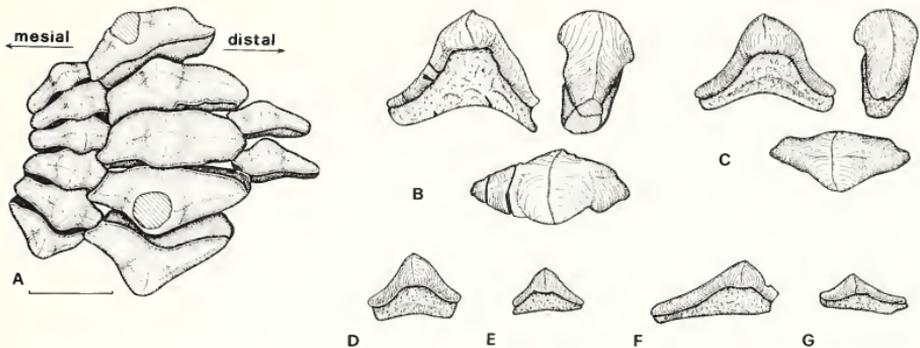
Pectoral girdle. The left pectoral girdle is preserved in T 1548 (text-fig. 4). Its structure clearly resembles that of *Acrodus* and *Hybodius* (Koken 1907). The suprascapular portion is an elongated, spinous structure curved in an anterior direction. The scapulocoracoid and the ventral coracoid bar are poorly preserved. Below the pectoral girdle, a single basal element of the pectoral fin is preserved (text-fig. 4). The incompleteness of the specimen does not allow the reconstruction of the basal skeleton of the pectoral fin.

Finspines. The finspines of *Acronemus* (syn. *Nemacanthus tuberculatus*) are relatively short and broad which results in characteristic stout proportions. The anterior finspines are relatively longer and relatively broader than the posterior finspines (text-fig. 5; Pl. 43, figs. 6, 7). The crown of the anterior finspine is frequently of a broad-based, upright triangular shape (text-fig. 6A). However, it may become somewhat elongated and recurved to a variable degree (text-fig. 5; Pl. 43, figs. 6, 8). The posterior finspines are relatively smaller and narrower with an upright crown that is never distinctly curved in a posterior direction.

The most characteristic feature of the spines is their conspicuous tuberculation. Large and rounded tubercles are arranged in a regular pattern on which it is possible to superimpose straight longitudinal lines. It is equally possible to superimpose on the pattern of tuberculation curved and obliquely oriented lines which run in a posterodorsal direction across the lateral surface of the crown (text-fig. 6A). There is in some spines the tendency of the tubercles to fuse into segments of ridges running in a curved posterodorsal direction across the lateral surface of the crown (text-fig. 6; Pl. 43, figs. 6, 7). The arrangement of the tubercles along curved, obliquely



TEXT-FIG. 2. Skull remains in *Acronemus tuberculatus* T 2465. Abbreviations: orp, orbital process; otp, otic process; others as in Text-fig. 1. Scale equals 20 mm.



TEXT-FIG. 3. The teeth of *Acronemus tuberculatus*. A: T 3821, articulated part of dentition (surface abraded). Scale equals 5 mm. B-G: T 3849, isolated teeth. B-C, large lateral teeth in lingual, lateral, and occlusal views; D-E, successive mesial teeth in lingual view; F-G, successive distal teeth in lingual view.

oriented lines reflects the growth pattern of the spine. The completely closed enameloid mantle of euselachian finspines frequently shows similarly oriented growth lines (Maisey 1977).

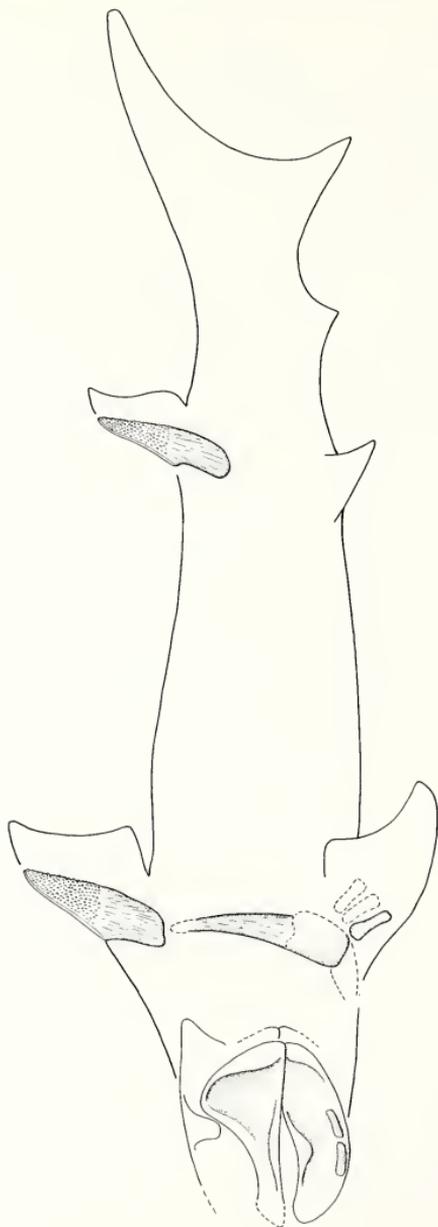
In some specimens the tubercles are small and scattered irregularly (text-fig. 6b). The scattered arrangement is probably due to wear, but the smaller size of the tubercles results in a larger number of longitudinal rows counted across the base of the crown. Also, the anterior finspines have a larger number of longitudinal rows of tubercles than the posterior finspines since the anterior spines are relatively broader. On the anterior finspines there are from 10 to 23 longitudinal rows of tubercles counted at the base of the crown, the average ranging from 13 to 15 rows. On the posterior finspines there are usually 13 rows of tubercles, variation ranging from 9 to 13 rows.

Along the leading edge of the crown the finspines bear a more or less conspicuously developed longitudinal ridge. In T 1289 this ridge, as far as preserved, retains an enameloid covering. The anterior ridge results from the fusion of a single anteromesial row of tubercles. This is demonstrated by the finspines of T 3825 in which this fusion is incomplete. The anterior ridge usually extends ventrally along the leading edge of the finspine beyond the lowermost anterior tubercles up to close to an anterior projection formed by the upper part of the root. This anterior projection indicates the level to which the finspine was inserted in the epaxial trunk musculature.

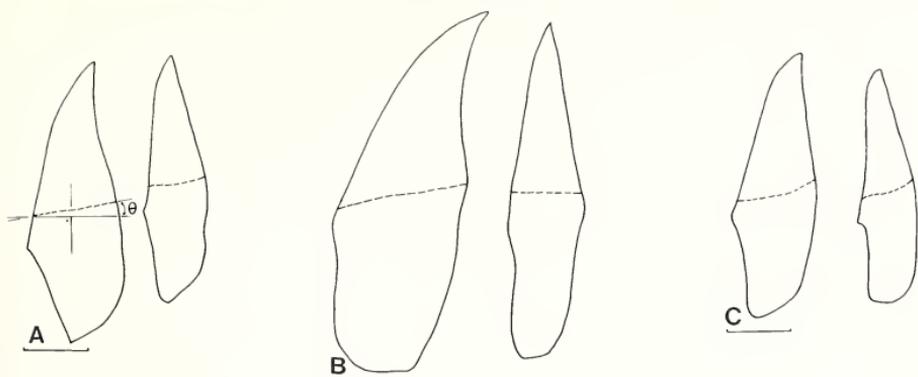
The posterior wall of the finspine is concave. The posterior opening of the central cavity extends upwards to the level of the lowermost posterior tubercles. A longitudinal row of tubercles runs along the posterolateral edge of the crown, but these tubercles do not differ in size or shape from those covering the lateral surface of the crown.

The line which connects the lowermost tubercles along the anterior and posterior edges of the finspine is chosen to represent the base of the crown. The angle θ between the base of the crown and the normal on the longitudinal axis of the finspine (text-fig. 5) ranges from 8 to 24° in the available spines.

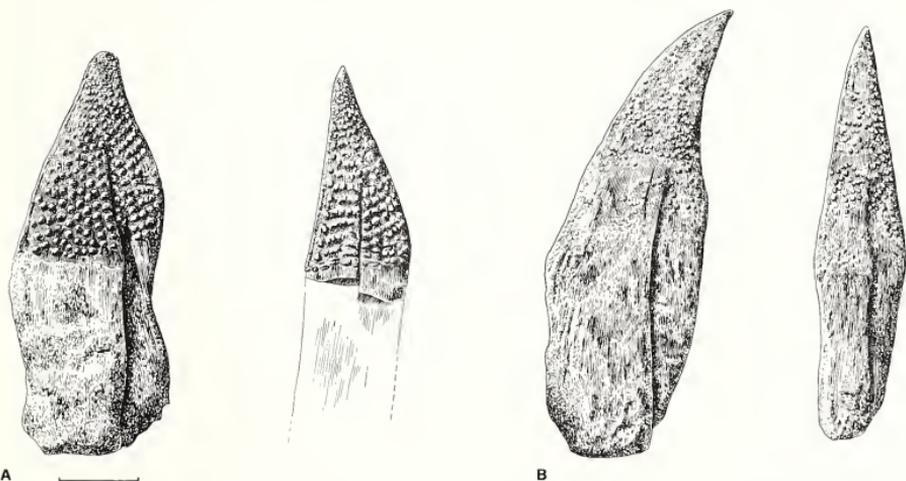
Five finspines of *Acronemus* were sectioned at successive levels along their long axis. A composite and slightly diagrammatic representation of finspine histology shown in text-fig. 7A may be compared to the section figured in text-fig. 7B. There is a lamellar inner trunk layer which is only apically distributed, above the posterior opening of the central cavity. The central cavity is generally small at this level, sometimes even (ontogenetically?) reduced to the size of an ordinary vascular canal (T 1431, section Nr. 8). The lamellar inner trunk layer is surrounded by a well vascularized outer trunk layer which also forms the entire root of the finspine. The central cavity is displaced backwards which results in a thick anterior wall largely made up by the vascularized outer trunk layer. The vascular canals and their surrounding denteons are rather small and widely spaced which gives the outer trunk layer a relatively compact appearance. Towards the leading edge of the spine a distinctly larger, longitudinally running vascular canal is observed lying straight in front of the central cavity (text-fig. 7). The tubercles are formed by the mantle component, but no clearcut boundary separates the mantle component from the outer trunk layer (for the terminology of finspine histology see Maisey 1979).



TEXT-FIG. 4. Tentative reconstruction of *Acronemus tuberculatus*, based on T 1548. Approx. $\times 0.4$.



TEXT-FIG. 5. Variation in size and shape of the anterior (left) and posterior (right) finspines of *Acronemus tuberculatus*. A, T 1178; B, T 2465; C, T 1548. Scale equals 10 mm. For further explanations see text.

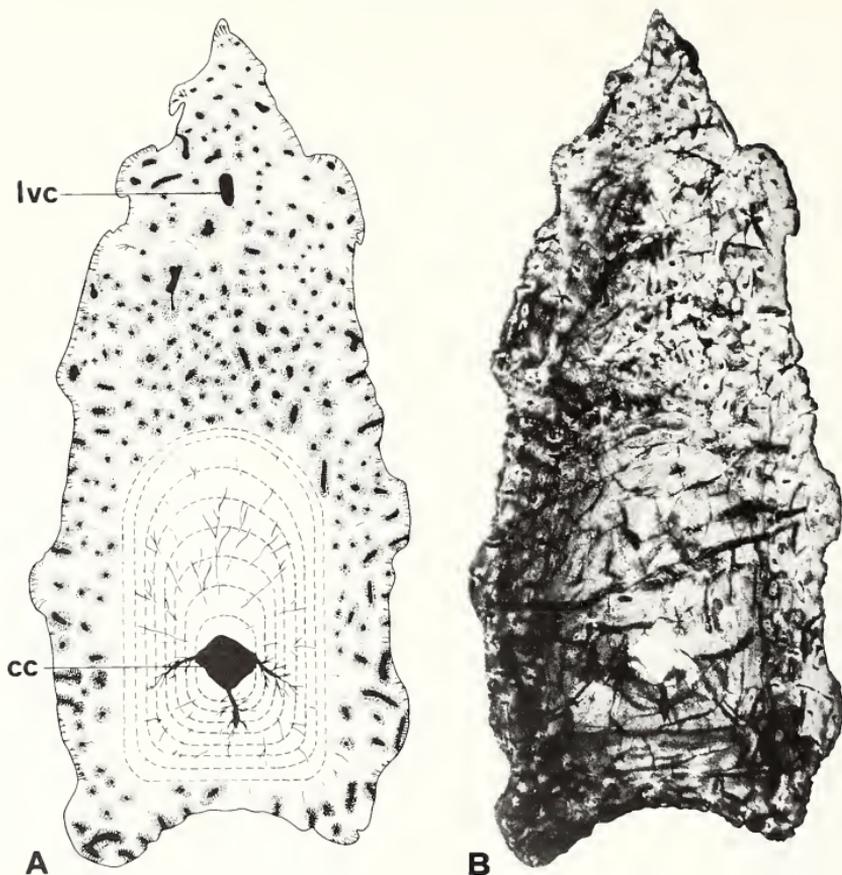


TEXT-FIG. 6. Ornamentation of the anterior (left) and posterior (right) finspines of *Acronemus tuberculatus*. A, T 3818; B, T 2465. Scale equals 10 mm.

Scales. Flank scales of the specimen T 1548 are shown on Pl. 43, fig. 5. They are of the non-growing, placoid type. They bear a recurved, lanceolate crown which is ornamented with three or five widely spaced longitudinal striae.

COMPARISON WITH THE GENUS *NEMACANTHUS*

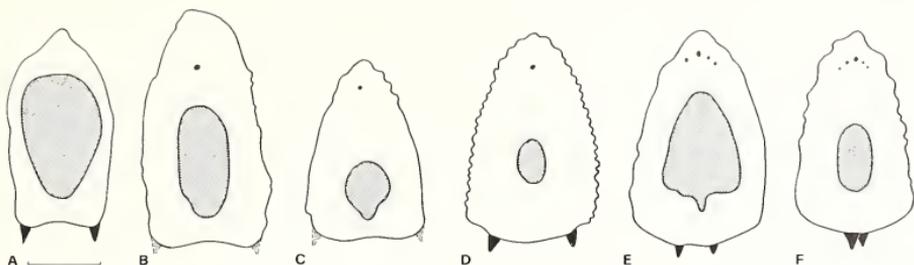
The finspines of *Acronemus tuberculatus* were originally referred to the genus *Nemacanthus* Ag. (Bellotti 1873, in Bassani 1886). Type species of the latter genus is *Nemacanthus monilifer* Ag., with which comparison thus must proceed. *N. monilifer* is represented by finspines from the Rhaetic of England which differ in several respects from those of *A. tuberculatus*. Assuming a relatively



TEXT-FIG. 7. Finspine histology of *Acronemus tuberculatus*. A. Semidiagrammatic representation of a transverse section through the crown of a finspine, based mainly on section T 3847/7. Abbreviations: cc, central cavity; lvc, longitudinal vascular canal. B. Ground section Nr. T 3847/7. Approx. $\times 30$.

constant structure of the finspines within shark genera, this justifies the erection of a new genus to include the spines of *tuberculatus* (Maisey, pers. comm.).

The finspines of *N. monilifer* (comparative material used for this study is housed in the British Museum (Natural History) and is listed in the Appendix) are long and slender in comparison to *Acronemus*. They are regularly curved in a posterior direction. If the total height of the finspines is divided by their maximum width, the values obtained for two complete specimens of *N. monilifer* are 8.56 (BM(NH) P.8328) and 9.3 (BM(NH) P.46830). Nine anterior finspines of *A. tuberculatus* have a corresponding mean value of 3.15, while six posterior finspines have a mean value of 4.1. In both genera the finspines bear an anterior enamelled ridge as well as a tuberculate mantle ornament, but the tubercles are fewer in number in *N. monilifer*. In the latter genus one usually



TEXT-FIG. 8. Semidiagrammatic sections through the finspines of chimaeroids and selachians. A, *Leptacanthus longissimus*, BM(NH) Egerton coll.; B, *Ctenacanthus angustus*, BM(NH) P.9581; C, *Nemacanthus monilifer*, BM(NH) P.15497, section 10; D, *Palaeobates keuperinus*, BM(NH) P.7604; E, *Hybodus lawsoni*, BM(NH) P.2174a; F, *Hybodus acutus*, BM(NH) P.6157. Scale equals 5 mm.

counts less than ten rows of tubercles across the base of the crown, variation ranging from 7 rows in BM(NH) P.46830 to 11 rows in BM(NH) P.2852, whereas in *A. tuberculatus* one usually counts more than 10 rows (9–23) of tubercles across the base of the crown. The connection of the lowermost tubercles at the anterior and posterior margins of the finspine results in a line which slants much more steeply in a posterodorsal direction in *Nemacanthus* as compared to *Acronemus*. This line intersects the normal on the long axis of the spine at an angle θ (text-fig. 5) which in *N. monilifer* ranges from 60° (BM(NH) P.46830) to 78° (BM(NH) P.51433), but from $8-24^\circ$ in *Acronemus*. A function of this angle is the fact that the tubercles approach the posterior edge of the spine only towards its apex in *N. monilifer*. The extent of tuberculation in *N. monilifer* may either be due to ontogenetic changes or to wear. In the specimen BM(NH) P.8328 isolated rudiments of a few worn or resorbed tubercles can be observed on the posteroventral part of the lateral surface of the crown, an area which lies well below the regularly tuberculated part of the crown but above the ventral end of the enamelled anterior ridge. The angle θ might be an indication of the degree of posterior inclination of the finspine insertion relative to the long axis of the body. Specimen BM(NH) P.8328 suggests that the degree of posterior inclination of finspine insertion increased during ontogeny in *N. monilifer*.

In both genera the posterior wall of the finspine is concave. In *Acronemus* longitudinal rows of unmodified tubercles run along the posterolateral edges of the crown. In some specimens of *N. monilifer* rows of small but pointed denticles are observed running along the posterolateral edges of the crown (Maisey 1977, Pl. 1. fig. D, and specimens BM(NH) P.1882, P.51433). Such posterolateral rows of denticles are also observed in some specimens of the genus *Ctenacanthus* (BM(NH) P.2525, P.2529).

The histology of the finspine is basically similar in *Acronemus* and *Nemacanthus*, except for the detailed histology of the thick anterior wall. In *N. monilifer* the vascular canals are large and closely juxtaposed, which results in the characteristic open spongy texture of the anterior wall (Maisey 1977, pl. 2, fig. C; Stromer 1927, text-fig. 12). This contrasts with the much more compact texture of the anterior finspine wall in *Acronemus*.

DISCUSSION: THE CLASSIFICATION OF *ACRONEMUS*

Maisey (1975) subdivided the phalacanthous sharks (*sensu* Zangerl 1973) into three groups of ordinal rank, the Hybodontiformes, the Ctenacanthiformes, and the Euselachiformes. The distinction of these three groups is based mainly on a detailed study of finspine structure. On the basis of finspine structure alone, *Acronemus* clearly has to be classified with the Ctenacanthiformes as defined by Maisey (1975). The structure of the palatoquadrate ties in well with such a conclusion.

It is cleaver-shaped in *Acronemus* as in some Palaeozoic ctenacanthiformes such as *Goodrichthys* (Moy-Thomas 1936), whereas *Hybodus* and its allies show a reduction of the otic process. The cleaver-shaped palatoquadrate probably is a primitive feature, however (Schaeffer 1967). Cephalic spines are not reported in ctenacanthiform sharks or in *Acronemus*.

However, other features do not support the classification of *Acronemus* with the Ctenacanthiformes. The teeth of *Acronemus* are very similar to those of *Acrodus*, and they lack an expanded lingual torus on the root. The teeth of Palaeozoic ctenacanthiforms are of the multicuspid cladodont type with a lingual torus on the root (Maisey 1975). Which type of tooth was possessed by the Lower Triassic (Stensiö 1921, 1932) or Rhaetic *Nemacanthus* is controversial (Maisey 1977). No associated *Nemacanthus* specimen has yet been found.

All Palaeozoic ctenacanthiform sharks have scales of a composite, growing type (Reif 1978). *Acronemus* has placoid scales which are typical of pre-Rhaetic hybodontids (Reif 1978, p. 126), as well as of euselachians.

These latter features of *Acronemus* might indicate that the ctenacanthiform and hybodontiform sharks can only be recognized by their finspine structure. However, they might also indicate that the distinction between the two orders is not as clearcut as it would appear (Schaeffer and Williams 1977). In fact, some mixture of hybodontiform and ctenacanthiform features was noted by Dick (1978) in his description of *Tristychius*.

Among all those finspines examined by me (see Appendix) there is enough variability to substantiate this point. The only ctenacanthiform features which are really constant throughout the material examined are a flat or concave posterior wall and a posteriorly displaced central cavity which results in a relatively thick anterior wall. In hybodontiform finspines the posterior wall may be flat or convex to a variable degree, and the anterior wall of the finspine is never much thicker than the posterior wall. This latter feature is a function of the posteriorly displaced central cavity of ctenacanthiform spines, but the position of the central cavity may again be correlated at least to some extent with the degree of convexity of concavity of the posterior wall. If the central cavity is held at a constant distance from the leading edge of the spine it will appear in a central position if the posterior wall is strongly convex, but it will appear in a posteriorly displaced position if the posterior wall is strongly concave. The crown of the *Hybodus* finspine BM(NH) P.57794 is broken at successive levels. Examination of the four levels of breakage showed that the anterior wall gets relatively thicker towards the apex of the spine as the diameter of the central cavity diminishes. A finspine of *Nemacanthus monilifer* (BM(NH) P.15497) which was sectioned at successive levels from top to bottom shows that the relative thickness of the anterior wall remains constant throughout the length of the spine.

The anterior wall of the ctenacanthiform finspine is said frequently to be of an open spongy texture (Maisey 1975). This in fact is only true for *N. monilifer* (and for the euselachian genus *Breviacanthus* Maisey 1976). The anterior wall of the *Ctenacanthus* finspine has exactly the same

EXPLANATION OF PLATE 43

Acronemus tuberculatus

Fig. 1. Tooth T 3849 in lingual view, $\times 10$.

Fig. 2. Tooth T 3849 in lateral view, $\times 10$.

Fig. 3. Tooth T 3849 in occlusal view, $\times 10$.

Fig. 4. Tooth T 3849, cross-section etched with 2n-HCl for 5 sec. to show the single-cristallite enamel, approx. $\times 150$.

Fig. 5. Placoid scale from specimen T 1548, approx. $\times 130$.

Fig. 6. Anterior finspine from specimen T 3818, $\times 1.8$.

Fig. 7. Posterior finspine from specimen T 3818, $\times 1.8$.

Fig. 8. Anterior finspine T 1289, $\times 1.25$.



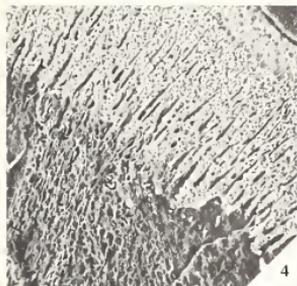
1



2



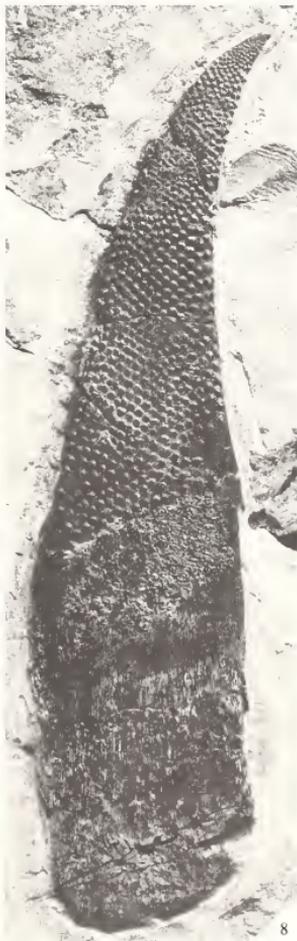
3



4



5



8



6



7

RIEPEL, Middle Triassic shark

vermiculate texture produced by relatively small vascular canals as is observed in typical hybodontiform finspines. *Acronemus* has an even more compact finspine histology.

Hybodontiform finspines are said to show a concentric ring of longitudinally running vascular canals around the central cavity (Maisey 1975, 1978). This is not always very clearly differentiated. In addition, a comparison with chimaeroid finspines (see Appendix) as well as with acanthodian finspines (Krebs 1960) indicates that concentrically arranged vascular canals are a primitive character-state in selachians. However, in all the hybodontiform and ctenacanthiform finspines examined by me there is a conspicuously larger longitudinal vascular canal which lies straight in front of the central cavity.

An important difference between hybodontiform and ctenacanthiform finspines is the ornamentation of the posterior wall in hybodontiforms, with one or two longitudinal rows of denticles, said to be absent in ctenacanthiforms (Maisey 1975). Hybodontiform finspines typically carry a double or a single row of rather large denticles close to, or on, the midline of the posterior wall. Such denticles indeed are absent in ctenacanthiforms. But in genera such as *Ctenacanthus* and *Nemacanthus* (Maisey 1977, Pl. 1, fig. D, and quotations above) rows of small denticles are arranged along the posterolateral edges of the crown which has a concave posterior wall. Maisey (1975) considers the denticles on the posterior wall of hybodontiform finspines as either highly modified mantle components or as specialized scales secondarily fused to the finspine. The posterolateral denticles of ctenacanthiform finspines are merely considered to represent 'posterolateral rows of pointed tubercles' (Maisey 1977, p. 265). This distinction appears meaningless since it is impossible to determine the morphogenetic status of the hybodontiform versus the ctenacanthiform denticles. If the denticles are considered homologous, it is possible to claim that posterolaterally placed denticles are a primitive character state while denticles which have shifted to a posteromesial position represent an advanced character state. Outgroup comparison with chimaeroid finspines (see Appendix) demonstrates that in this group there are usually two longitudinal rows of posterolaterally placed denticles, arranged along the edges of a concave posterior wall (text-fig. 8A). One undescribed chimaeroid finspine (BM(NH) P.2850) shows a single row of denticles along the midline of the concave posterior wall. This single row of denticles may well have originated from double rows of posterolaterally placed denticles that have shifted towards the midline of the posterior wall. A similar phenomenon has been noted for *Hybodus* finspines (Maisey 1978). A single row of posteromesially arranged denticles appears to originate from the superposition of two collateral rows of denticles on the midline of the posterior wall (text-fig. 8E-F). This point is further corroborated by a consideration of the finspines of *Palaeobates keuperinus* (text-fig. 8D). In fact, the structure of these finspines is perfectly intermediate between the ctenacanthiform and hybodontiform types and thus illustrates the potential difficulties in recognizing the two orders. In *P. keuperinus* the posterior wall of the finspine is weakly convex (as in some *Hybodus* finspines), but it carries two posterolaterally placed rows of denticles (as in ctenacanthiforms). The central cavity is small and somewhat displaced backwards as in ctenacanthiforms, but the posterior wall still retains a considerable thickness although it is thinner than the anterior wall.

In summary it can be stated that hybodontiform and ctenacanthiform sharks together form a group of selachians with a finspine structure involving an apically distributed inner trunk layer surrounded by a trabecular outer trunk layer. The details of the histology of the outer trunk layer are quite variable and only characteristic at the generic level. There is no clearcut boundary between the outer trunk layer and the mantle component. The mantle ornamentation may be tuberculate or costate. As evidenced by the genus *Acronemus*, the orders Hybodontiformes and Ctenacanthiformes can at present be recognized on the basis of finspine structure alone. Ctenacanthiform finspines show a flat or concave posterior wall with two rows of posterolaterally placed denticles (primitive) and a posteriorly displaced central cavity. Hybodontiform finspines show a flat or convex posterior wall with one or two rows of denticles close to or on the midline of the posterior wall (derived). The central cavity is rather centrally positioned. However, intermediate forms such as *P. keuperinus* and *Tristychius* (Dick 1978) do occur.

On the basis of finspine structure, *Acronemus* can be classified as a ctenacanthiform shark. The

posterior wall of the fin spine is concave, and the central cavity displaced backwards. If such an arrangement is accepted it must be concluded that neither the 'hybodontiform' tooth structure nor the presence of placoid scales can be used to distinguish hybodontiform and ctenacanthiform sharks from the Triassic.

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APPENDIX

All the comparative material used to study finspine structure is housed in the British Museum (Natural History). The specimen numbers are as follows.

Sharks: *Hybodus* sp., P.47145, P.57794; *acutus*, P.6157; *ensatus*, P.2162; *lawsoni*, P.2174a; *minor*, P.51443; *reticulatus*, one uncatalogued specimen; *Ctenacanthus* sp., P.2525, P.28928-9, P.34865; *angustus*, P.9581, P.9262; *pustulatus*, P.2529; *Nemacanthus monilifer*, P.1882, P.2852, P.2854, P.8328, P.15497, P.46830, P.51433; *Palaebates keuperinus*, P.2767, P.7604.

Chimaeroids: *Edaphodon* sp., P.3097; *Leptacanthus longissimus*, Egerton coll.; *Myriacanthus paradoxus*, P.1736a, one uncatalogued specimen; undescribed genus, P.2850.

Ground sections—Sharks: *Breviacanthus brevis*, P.2851; *Ctenacanthus angustus*, P.9581; *Lonchidion* sp., CP.12.9.64; *Nemacanthus monilifer*, P.2217, P.15497; ?*Oracanthus*, P.45768.1.

Chimaeroids: *Callorhynchus callorhynchus*, Zool. Dept. 1935.4.23.17; *Deptoptychius armigurus*, P.11358; *Edaphodon* sp., P.11807; ?*Erismacanthus* sp., P.6257; *Metopacanthus granulatus*, P.43065; *Myriacanthus paradoxus*, P.1736.

A NEW SPECIES OF THE FISH *AMIA* FROM THE MIDDLE EOCENE OF BRITISH COLUMBIA

by MARK V. H. WILSON

ABSTRACT. A new species of amiid fish is described from a semi-articulated skeleton found in Middle Eocene freshwater shales of the Allenby Formation, Princeton Group, south-central British Columbia. The new species is assigned to *Amia* because it lacks *Kindleia* specializations such as styliiform teeth, and it shares skull specializations with *A. calva*, *A. scutata*, and *A. uitaensis*. The new species is reconstructed as a deep-bodied piscivore with large jaws and strong, sharp teeth. The holotype is the first identifiable skeleton to be found among many amiid scales recovered from numerous fossil-fish assemblages in southern British Columbia and northern Washington State.

THIS paper presents a description and partial reconstruction of a new species of amiid fish, based on a single partially articulated skeleton and several disarticulated skull bones from Middle Eocene freshwater shales in British Columbia. The significance of the discovery lies in the relatively complete information obtainable about the anatomy of this fish, and the resulting implications for the taxonomy of fossils of *Amia* elsewhere in North America.

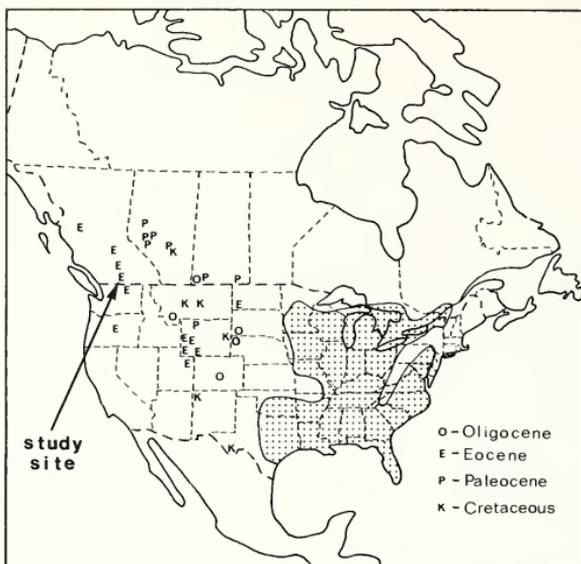
Amia calva, the only living species of amiid, is confined to the fresh waters of south-eastern North America, but Late Cretaceous and Tertiary records of amiids are widespread in central and western parts of the continent (text-fig. 1), as well as in Europe and Asia. North American fossil amiids were reviewed by Boreske (1974), who recognized three valid fossil species in a single genus from the twenty-three species and seven genera previously described. Many of the rejected names were based on poorly preserved material or on single vertebrae, and were considered to be junior synonyms or *nomina dubia*. The three fossil species considered valid by Boreske are the Late Cretaceous to Middle Eocene *Kindleia fragosa*, the Palaeocene to Early Oligocene *A. uitaensis*, and the Oligocene *A. scutata*.

None of the previously known Eocene occurrences of *Amia* from British Columbia, Washington, and Oregon had been identified to species, because they consisted primarily of undiagnostic scales (Cavender 1968; Wilson 1977a, 1978a, 1979, 1980) which were nevertheless very common fossils. These westernmost records seemed to reflect habitats similar to those preferred by other *Amia* species including *A. calva* (Scott and Crossman 1973): warm, shallow, swampy conditions, as evidenced by lithology and the associated fishes, insects, and plants (Wilson 1980).

The discovery of the *Amia* specimens described here resulted from work by palaeobotanists on silicified plant fossils, preserved in an outcrop of alternating chert and coal layers in the Allenby Formation (Boneham 1968; Miller 1973; Robison and Person 1973; Basinger 1976; Basinger and Rothwell 1977). James Basinger discovered a trionychid turtle in shales immediately overlying the chert. When I revisited the site in 1977 and 1978, I obtained the fish specimens described here, along with coprolites containing fish bones, and disarticulated remains of small suckers (Catostomidae: *Amyzon* sp.), and trout-perches (Percopsidae: *Libotomius* sp.). The fish occur in the shales with carbonized plant fossils which include stems and twigs, dicotyledonous leaves, taxodiaceous leafy shoots, seeds, ferns, and amber (Wilson 1980).

GEOLOGY AND AGE

The specimens were found in a hard black siliceous shale immediately overlying a 10-m-thick outcrop of interbedded carbonaceous chert and coal which extends into the Similkameen River



TEXT-FIG. 1. Map of North America showing the fossil locality. Also shown are Late Cretaceous through Oligocene sites from which remains of *Amia* and/or *Kindleia* have been reported (modified after Boreške 1974), together with the distribution of Recent *Amia calva* (stipple, after Scott and Crossman 1973).

from its east bank, 8.4 km south of Princeton, British Columbia (text-fig. 1). According to Boneham (1968) the fossiliferous layers are 550 m above the Princeton-Black Coal of the Allenby Formation, Princeton Group. The Allenby Formation consists of sedimentary rocks, deposited in fresh water, and yields an abundant assemblage of fishes and insects at several localities in the Princeton Basin (Wilson 1977a, 1977b, 1978b, 1980).

The age of the fossils is Middle Eocene, based on potassium-argon ages of approximately 47-50 million years for the Allenby Formation (Hills and Baadsgaard 1967), and on the occurrence of the mammalian genus *Trogosus* elsewhere in the formation (Russell 1935). Other occurrences of fossil amiid scales in British Columbia and in the Klondike Mountain Formation of Washington State are of a similar geologic age (Wilson 1977a, 1978a, 1979).

MATERIALS AND METHODS

The *Amia* fossils occur as fractured bone, spread parallel to bedding planes. The hard and tough matrix contains a faithful imprint of the original shape and ornamentation of the bones and, therefore, the specimens were prepared by removing the fossilized bone with mechanical tools and an ultrasonic probe. Casts of the resulting impressions were made in black latex. Measurements were taken from the original shale moulds. For photographic purposes the black-latex casts were coated with ammonium chloride. The reconstructions were made by drawing the outlines of the bones at uniform scale, using a camera lucida attached to a Wild M8 stereomicroscope, and then graphically assembling the bone outlines with regard to perspective distortions and suture outlines. For dermal roofing bones of the skull, the external surfaces of the bones correspond to their

ornamented portions. Osteological terminology follows Boreske (1974) except that, following Janot (1967), the term 'posttemporal' is used in place of 'suprascapular' (Table 1). The abbreviation UAVP designates that specimens are deposited in the Vertebrate Paleontology Collections, Department of Geology, The University of Alberta.

TABLE 1. Abbreviations used in the figures

a	angular	es	extrascapular	p	pectoral fin	sc	supracleithrum
ao	antorbital	fr	frontal	pa	parietal	sm	supramaxilla
br	branchiostegal	h	hyomandibular	pop	preopercle	so	subopercle
c	cleithrum	io	infraorbital	ps	parasphenoid	sy	symplectic
ch	ceratohyal	la	lachrymal	pst	parasphenoid teeth	v	vomer
cod	coronoid teeth	m	maxilla	pt	(dermo)pterotic	vt	vomerine teeth
d	dentary	mc	metacleithrum	r	rostral	vtb	vomerine tooth base
ds	dermosphenotic	n	nasal	s	posttemporal		
e	endopterygoid	op	opercle	sa	surangular		

SYSTEMATIC DESCRIPTION

Class OSTEICHTHYES

Order AMIIFORMES

Family AMIIDAE Bonaparte, 1837

Genus *AMIA* Linnaeus, 1766

Type species. *Amia calva* Linnaeus, 1766.

Amia hesperia sp. nov.

Text-figs. 2-6

Diagnosis. Deep-bodied *Amia* having square parietals; long frontals with shallow orbital excavation; large nasals without anterior notch; large fourth infraorbital; deep maxilla, mandible, and opercle; dentary with large teeth; lachrymal with posterior notch; parasphenoid with long posterior ramus and short tooth patch; vomers with short tooth patch; vomers and coronoids with sharp, conical teeth; and cleithrum with arms at obtuse angle.

Holotype. UAVP 14758 (text-figs. 2-5 and 6A, B), an almost complete, partially articulated fish in part and counterpart with estimated total length about 55 cm, preserved as a mould in hard siliceous shale, and collected by the author's party in 1977.

Etymology. The specific epithet is from the Latin *hesperius* meaning 'western'.

Locality and age. Ashnola chert site, 8.4 km S of Princeton, British Columbia (U.T.M. Grid Reference IOUFGK783724), from the Middle Eocene Allenby Formation, Princeton Group.

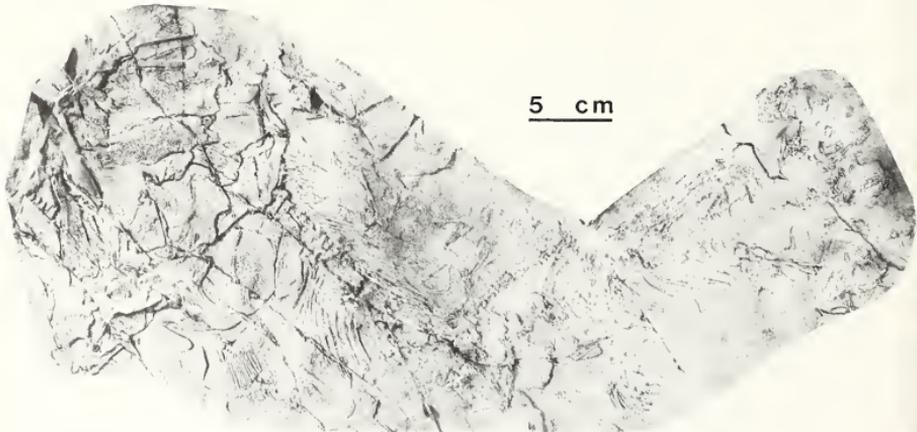
Non-type material. UAVP 13801, a patch of scales and two branchial tooth plates; UAVP 13804 (text-fig. 6C), a right dentary and maxilla; UAVP 13805, a right extrascapular (text-fig. 6E), right fourth infraorbital, and left fifth infraorbital; UAVP 13806 (text-fig. 6D), a branchial toothplate; and UAVP 13812 (text-fig. 6E), a right opercle. All of the above specimens were collected at the type locality in 1977, within a few centimetres of the holotype.

Description. Unless otherwise indicated, the following description is based on the holotype, which shows the dermal investing bones of the skull in the part (text-fig. 3) and many ventral and internal bones of the skull in the counterpart (text-fig. 4). The postcranial skeleton is present but not well preserved (text-fig. 2). Non-type material is limited, but corroborates conclusions based on the holotype.

Parietals are approximately square (text-fig. 3), and frontals are relatively long and narrow (width to length ratio 0.41), with shallow orbital excavations ('orbital concavity ratio' of Boreske 1974 is 0.117; 'dermosphenotic angle' is 136°). The 'parietal/frontal' ratio is 0.37. Extrascapulars are decidedly wider laterally than medially

(text-figs. 3, 6F), dermopterotics substantially overlap the frontals laterally, and are tapered both anteriorly and posteriorly. Nasals are large, not notched anteriorly, and fit the anterior outline of the frontals posteriorly. The rostral is stout, and the ornamented area of the antorbitals is small.

Laterally, the lachrymal has a prominent posterior notch which fits the anterior end of the small second infraorbital (text-fig. 3). The large fourth infraorbital is deep posteriorly, where it has an angular margin. It tapers to the orbit, but forms less of the orbital rim than does the fifth infraorbital. The latter is about as deep anteriorly as posteriorly, and is considerably smaller than the fourth infraorbital.



TEXT-FIG. 2. *Amia hesperia* sp. nov., holotype, part, UAVP 14758a, latex peel of whole fish.

The premaxilla is not preserved. The maxilla is a stout, deep bone with a marginal row of numerous, very small teeth (text-figs. 3, 4). The posterodorsal margin of the maxilla has an elongate excavation which fits a long, deep supramaxilla.

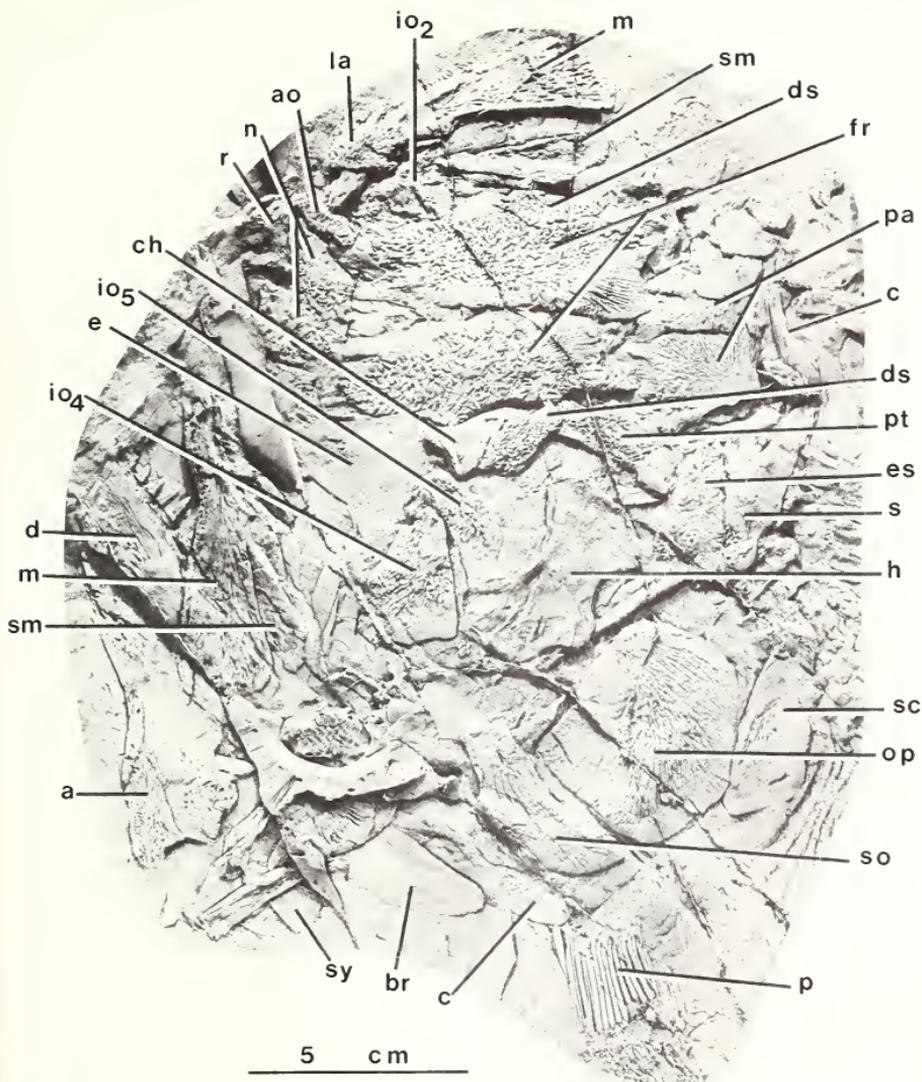
The mandible is deep and stout, with a steeply inclined posterior border formed by the angular and surangular (text-figs. 3, 4), a broad coronoid process, and a dentary with a long row of large, pointed teeth (text-figs. 3, 4, 6B). Proportions and shape of the dentary are more clearly shown in UAVP 13804 (text-fig. 6C), where, toward the front of the bone, the ventral margin is apparently angled ventrally. This is interpreted as a medial deflection of the mandibular ramus as seen most noticeably in *Kindleia fragosa* (Boreske 1974, figs. 16B, 18). The coronoids are not visible, but small, sharp teeth located internal to the dentary teeth, where coronoid teeth would be expected, are visible in the holotype (text-fig. 6B).

The parasphenoid (text-fig. 4) is partially obscured by a branchiostegal, a ceratohyal, an angular, and the vomers, but its proportions are evident. It has a relatively long posterior ramus, 0.84 times the length of its anterior ramus. The ascending process of the right side is partially covered in the holotype by an angular, but is approximately perpendicular to the long axis of the parasphenoid. The posterior portion of the parasphenoid tooth patch consists of many tiny denticles. Where it is not obscured by the ceratohyal (text-fig. 4), the anterior ramus of the parasphenoid appears devoid of denticles.

Vomers are elongate (text-fig. 4) but have short-toothed portions. Most teeth are broken, but unbroken teeth together with some broken tooth tips indicate that the vomerine teeth are conical and sharply pointed (text-fig. 6A). The endopterygoid (text-figs. 3, 4) is plate-like and bears numerous tiny denticles.

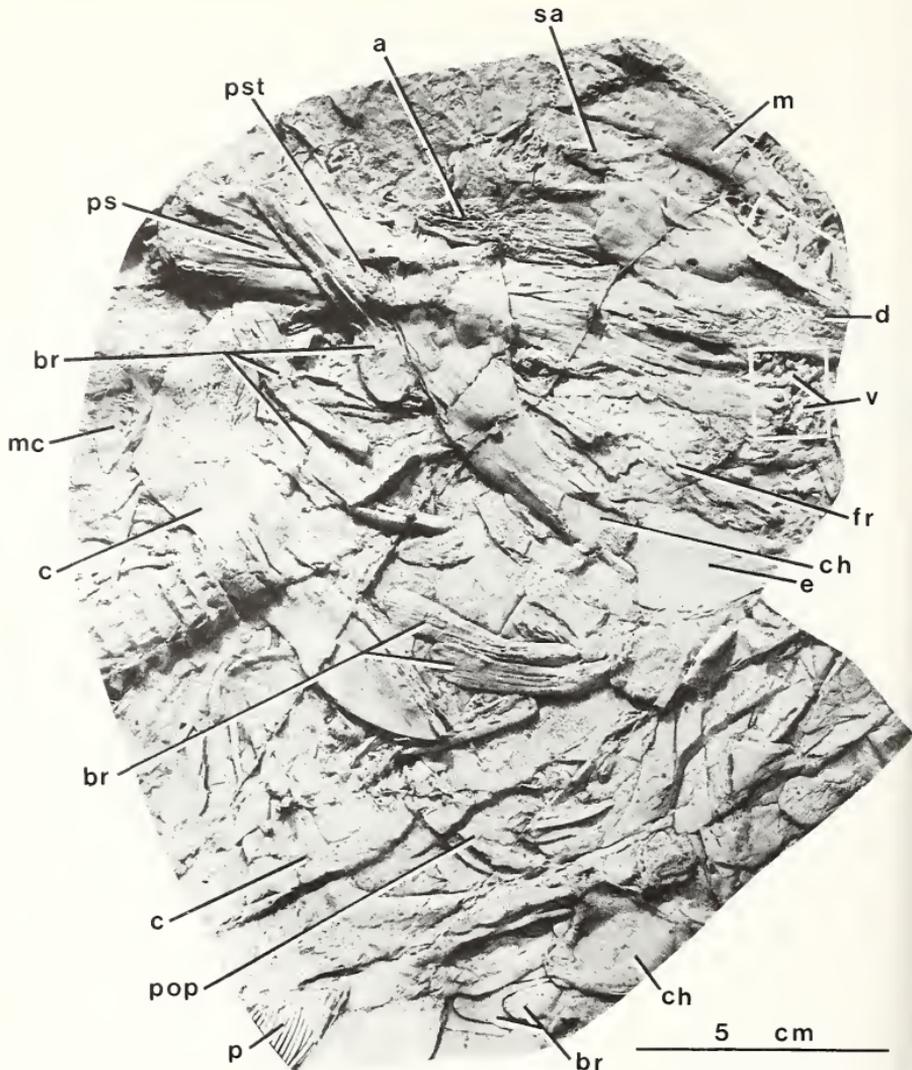
The opercular bones are deep relative to their length. The opercle in the holotype has a length to height ratio of 0.90, and these proportions are also seen in UAVP 13812 (text-fig. 6E). The subopercle has an elongate anterodorsal ramus. The preopercle is not well preserved (text-fig. 4), but seems similar to those of other species of *Amia*.

The hyomandibular, preserved in lateral view (text-fig. 3), has a posteroventrally directed opercular process and a moderately developed posterodorsal notch. The symplectic is partially visible in the holotype (text-fig.



TEXT-FIG. 3. *Amia hesperia* sp. nov., holotype, part, UAVP 14758a, latex peel of skull. Abbreviations Table 1.

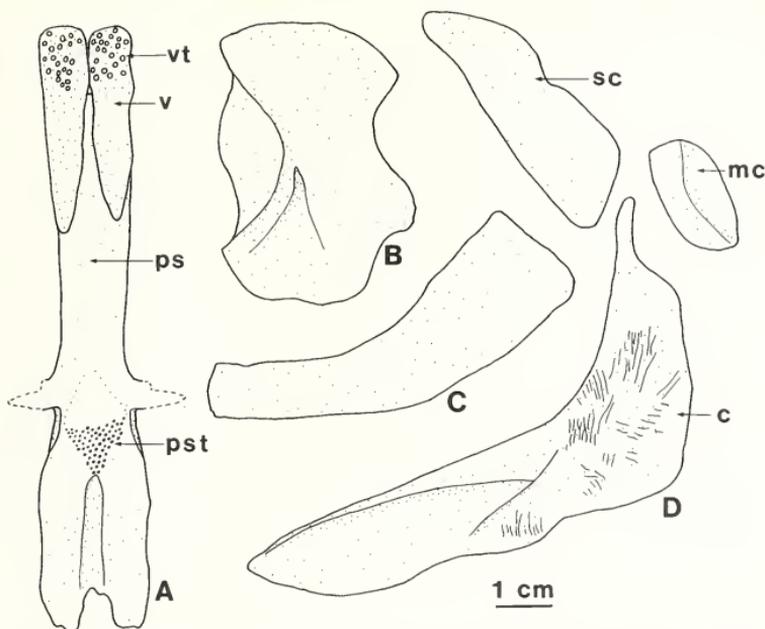
3). The ceratohyal (text-fig. 4) is typical of the genus, and bears branchiostegals which vary from narrow to broad. Branchiostegal ornamentation is extensive and posterior margins of preserved branchiostegals are rounded. Branchial arches are not preserved, but several tiny bones bearing numerous sharp, hollow, conical, and slightly curved teeth (text-fig. 6b) were found in the shales close to the holotype. In view of the similarity



TEXT-FIG. 4. *Amia hesperia* sp. nov., holotype, counterpart, UAVP 14758b, latex peel of skull. Abbreviations Table 1. The two areas outlined in white are enlarged in text-fig. 6A, B.

of teeth of these bones to teeth of the holotype, the bones are interpreted as branchial tooth plates of the same species.

The dermal pectoral girdle is well preserved in the holotype (text-figs. 3-5). The cleithrum is like that of other *Amia* species, but the ornamented area is more extensive than in *A. calva*. As well, the posterodorsal



TEXT-FIG. 5. *Amia hesperia* sp. nov., holotype UAVP 14758. A. Reconstruction of parasphenoid and vomers in central view. B. Left hyomandibular, lateral view. C. Left ceratohyal. D. Left dermal pectoral girdle in lateral view. Abbreviations Table 1.

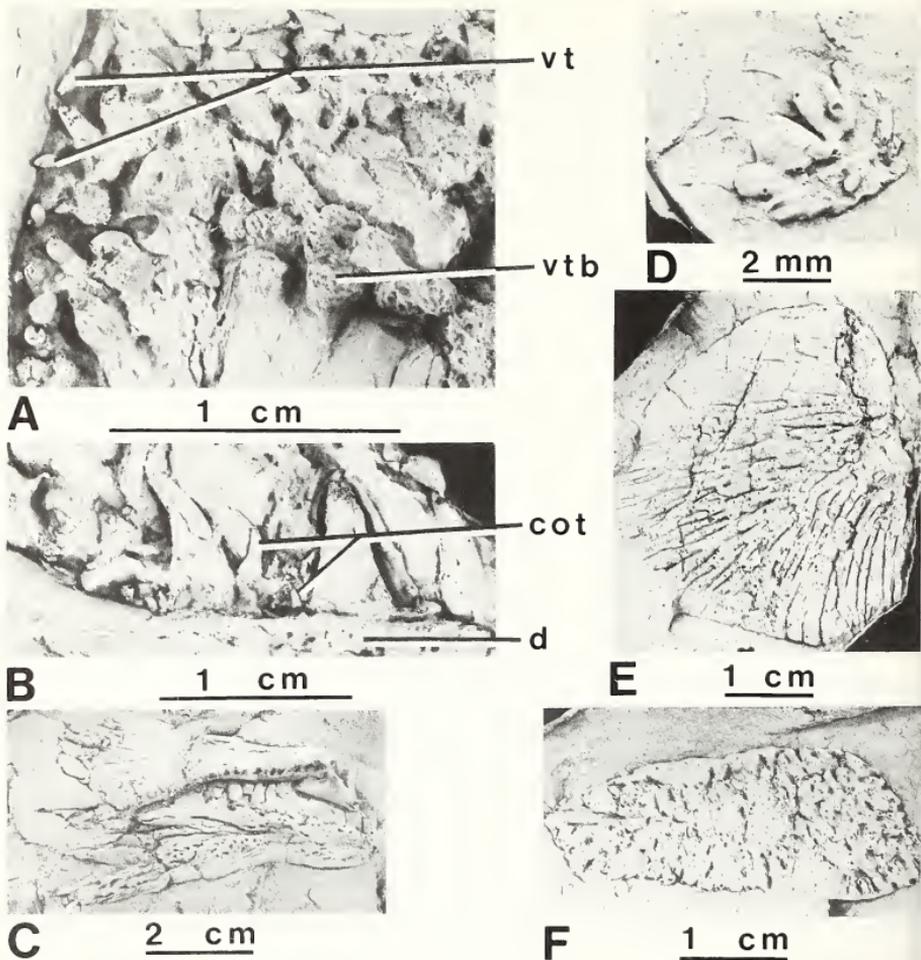
ramus of the cleithrum forms an obtuse angle of about 120° with the anteroventral ramus, as in *K. fragosa* but not in *A. calva* or *A. uintaensis* where the rami are at right angles to each other (Boreske 1974, fig. 21). The plate-like posterior portion of the cleithrum is broadly rounded. The posttemporal (text-fig. 3) is elongate, and the posterolateral portion is ornamented. The pectoral fin has about sixteen rays and originates medial to the posteroventral angle of the cleithrum (text-fig. 3). Only the general position of the pelvic fin is apparent in the holotype.

The postcranial portion of the axial skeleton is poorly preserved (text-fig. 2), but a few general statements are possible. Anterior trunk vertebrae are about four times as broad as they are long, and bear dorsal neural facets and ventral aortal facets as in other *Amia* species (Boreske 1974, fig. 11). Ribs, neural and haemal spines, hypurals, and pterygiophores are all slender, rod-like elements. Posterior caudal vertebrae are diplospondylous. The dorsal fin originates approximately above the seventeenth trunk centrum, and the anal fin consists of about nine rays.

Scales are thinner than those of Cretaceous and Palaeocene *K. fragosa* from Alberta (O'Brien 1969), thicker than scales of *A. calva*, but similar to other Eocene *Amia* scales from British Columbia (Wilson 1977a). They are mostly rounded apically and truncate basally, about two-thirds as wide as long, with an apical (posterior) focus, a thick, horseshoe-shaped rim of smooth lamellar bone around the lateral and apical margins, and a central area of somewhat thinner bone ornamented on the internal surface by small bumps. Externally the circuli or ridges radiate to the margins from the focus, which is approximately triangular and has its apex directed basally (anteriorly). In the focal area the circuli form a vermiculate pattern.

Reconstruction

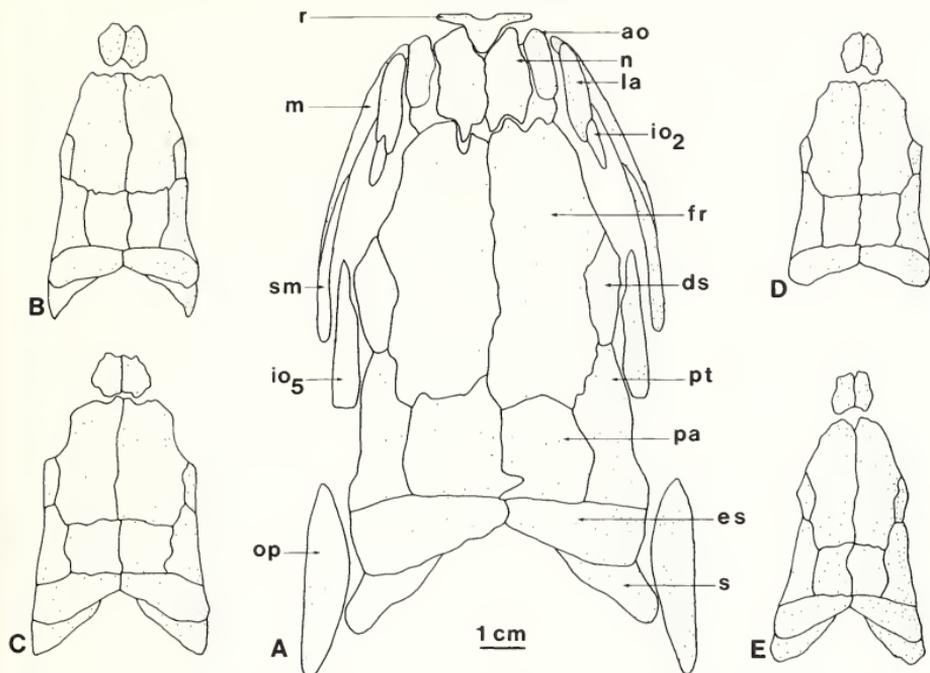
The parasphenoid and vomers of *A. hesperia* are reconstructed in text-fig. 5A. Notable features are the inferred short parasphenoid tooth patch, the ascending processes perpendicular to the



TEXT-FIG. 6. *Amia hesperia* sp. nov. A. Detail of anterior portion of vomers of holotype, UAVP 14758b, showing pointed vomerine teeth. B. Detail of dentary tooth row of holotype, UAVP 14758b, showing pointed coronoid teeth. C. Right dentary and maxilla, lateral view, UAVP 13804. D. Branchial tooth plate, UAVP 13806. E. Right opercle, lateral view, UAVP 13812b. F. Right extrascapular, dorsal view, UAVP 13805c. Abbreviations Table 1.

long axis of the parasphenoid, and the elongate vomers with their anterior one-third occupied by sharp teeth.

Text-fig. 7 shows the skull, reconstructed in dorsal view, compared with partial reconstructions of the skulls of *A. calva*, *K. fragosa*, *A. scutata*, and *A. uintaensis*. Notable are the elongate frontals with shallow orbital excavations, relatively short parietals, tapered extrascapulars, long



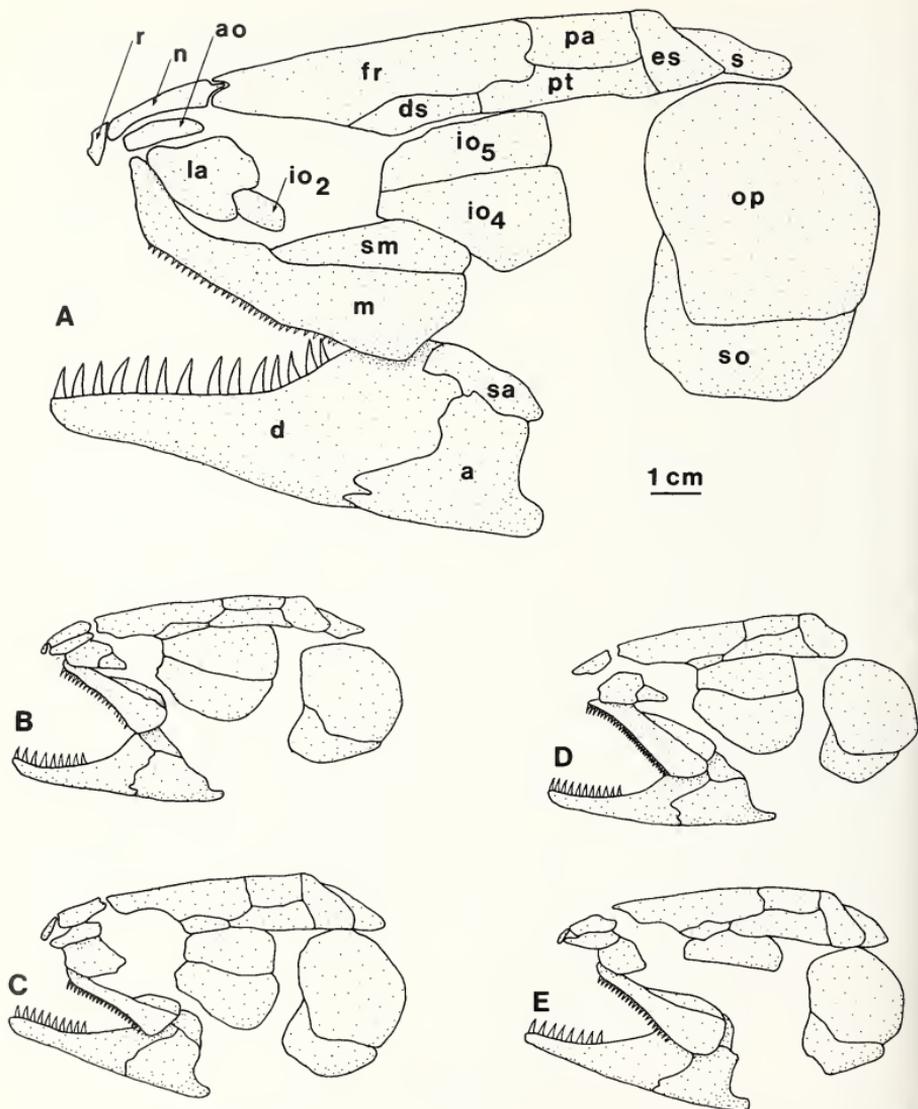
TEXT-FIG. 7. Comparison of dorsal skull reconstructions of North American amiids. A. *Amia hesperia*, sp. nov., based on the holotype, UAVP 14758. B. *A. calva*. C. *Kindleia fragosa*. D. *A. scutata*. E. *A. uintaensis*. B-E after Boreske (1974), not to uniform scale. Abbreviations Table 1.

dermopterotics, large nasals shown interdigitating with the frontals, and the over-all shape of the skull roof, which is elongate but only slightly narrower at the rear of the orbit than it is at the rear of the extrascapulars.

The skull of *A. hesperia* is reconstructed in lateral view in text-fig. 8. In this view the skull appears relatively deep and large-jawed. Features that contribute to the impression of skull depth are the large lachrymal, deep opercle and subopercle, deep maxilla and supramaxilla, deep mandible, and large teeth in the dentary. The obtusely angled cleithrum is additional evidence of a deep body. In view of the poor preservation of the postcranial skeleton, a reconstruction of the entire fish is not presented here. However, the evidence of the dorsal fin apparently originating over the seventeenth trunk centrum suggests that *A. hesperia* was long-bodied, rather than short and stout as was *K. fragosa* (Boreske 1974, fig. 21).

DISCUSSION

In addition to the one Recent and three fossil species of *Amia* from North America that were recognized by Boreske (1974), there are a number of nominal European and Asian fossil species (Boreske 1974; Janot 1967). Fairly complete information is available about several of these, including some which are most similar to the North American *K. fragosa* (*A. kehleri* Andreae, *A. valenciennesi* Agassiz, *A. munieri* Priem, and *A. russelli* Janot), and others which are similar to *A. uintaensis* (*A. robusta* Priem and possibly *A. mongoliensis* Hussakof). Janot (1967), Estes and Berberian (1969),



TEXT-FIG. 8. Comparison of lateral skull reconstructions of North American amiids. A. *Amia hesperia*, sp. nov., based on the holotype, UAVP 14758. B. *A. calva*. C. *Kindleia fragosa*. D. *A. scutata*. E. *A. uintaensis*. B-E after Boreske (1974), not to uniform scale. Abbreviations Table 1.

Boreske (1974), and Gaudant (1980) advocate synonymizing *Kindleia* Jordan with *Amia* Linnaeus. The main distinguishing features of *Kindleia* are the presence of styliform teeth on the coronoids, dermopalatines, and vomers; differences in proportions of some skull bones; and a shorter body with less separation between the skull and the origin of the dorsal fin and between the insertion of the dorsal fin and the caudal fin, and about twelve fewer trunk centra and eight fewer monospondylous caudal centra (Boreske 1974). These authors cited intra- and interspecific variability in *Amia*, and found the above differences insufficient grounds for separation into two genera, especially considering that Estes and Berberian (1969) believe most features of *Kindleia* to be primitive. Gaudant (1980), however, treats *Kindleia* as a subgenus of *Amia*, and cites several derived features shared by *K. fragosa* and *A. kehleri* in support of this view. Gaudant's list of shared derived characters is very similar to the list of features (above) that Estes and Berberian (1969) interpreted as mostly primitive. For example, Gaudant cites a relatively short, deep body; an enlarged fourth infraorbital; short parietals; and styliform coronoid, palatal, and vomerine teeth.

I agree with Gaudant that these characters are mostly derived, but go further in favouring the recognition of *Kindleia* as a genus distinct from *Amia*. To Gaudant's list of shared derived characters can probably be added the relatively short, wide frontal: the frontals of the geologically older but closely related genera *Urocles* (Lange 1968) and *Enneles* (Santos 1960) are long and narrow. An enlarged fourth infraorbital found also in *A. hesperia* and in *Enneles* (Santos 1960) should probably be removed from the list of derived features of *Kindleia*.

Retention of *Kindleia* as a separate genus is also useful because most species share a number of other similarities, some or all of which might be primitive. These include the deep orbital notch in the frontal; the short vomers; the small supramaxilla; the narrow maxilla and mandible; the short, truncated gular plate; and fewer than seventy-five vertebrae.

Boreske (1974) suggested that molluscs were a more important part of the diet for *Kindleia* than for *Amia*. At some localities in the Palaeocene Paskapoo Formation of Alberta, *Kindleia* remains are found with finely crushed mollusc shells concentrated in patches on bedding planes. To my knowledge gut contents have not been observed in *Kindleia* specimens, but the explanation of the styliform teeth as an adaptation to molluscivorous habits is a reasonable one. Perhaps the fish did not completely swallow the shells with their contents, or perhaps the patches of broken shells represent regurgitated gastric residues.

The new species described here clearly belongs with *Amia*. *A. hesperia* has none of the *Kindleia* specializations listed above. It shares with some or all of the other well-known species of *Amia* derived features such as a shallow orbital excavation in the frontal, a deep maxilla with elongate supramaxilla, the lack of an anterior notch in the nasal, the presence of a posterior notch in the lachrymal, and a tooth patch restricted to the front end of the vomer.

A. hesperia differs from valid North American species of *Amia* (Boreske 1974) in the following features. Compared with *A. uintaensis* it has slightly shorter frontals, shorter parietals, unnotched nasals, interdigitating nasals and frontals, posteriorly notched lachrymals, more angular fourth infraorbitals, a relatively longer posterior parasphenoid ramus, parasphenoid ascending processes more nearly at right angles to the long axis, shorter parasphenoid and vomerine tooth patches, and more obtusely angled cleithra. Compared with *A. scutata* and *A. calva* it has longer frontals, shorter parietals, interdigitating nasals and frontals, a shorter parasphenoid tooth patch, more rectangular opercles, and more obtusely angled cleithra. It differs further from *A. calva* in having longer pterotics, larger fourth infraorbitals, a relatively shorter posterior parasphenoid ramus, ascending processes more nearly at right angles to the long axis, and more extensive ornament on the cleithra.

A. robusta, a Palaeocene to Oligocene European species, is very similar to *A. uintaensis*. Compared with *A. hesperia* it has more elongate frontals, more rectangular parietals, a longer parasphenoid tooth patch, and more right-angled cleithra, judging by bones illustrated in Janot (1967).

Piscivorous habits for *A. hesperia* are implied by the large mouth and the large, sharp teeth. This supports previous conclusions (Wilson 1980) based on association of amid scales with coprolites containing fish bones at many Eocene localities in British Columbia and Washington

State. I would predict that the amiid(s) occurring at these other localities will prove to be closely related to or conspecific with *A. hesperia*. The geographic distribution of Eocene amiid species in North America, with *A. hesperia* in the extreme west and *A. uintaensis* and *K. fragosa* in the mid-west, is suggestive of geographic ranges separated by a north-south barrier such as a continental divide similar to the one separating western and eastern species of fishes today.

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A FUSED CLUSTER OF CONIFORM CONODONT ELEMENTS FROM THE LATE ORDOVICIAN OF WASHINGTON LAND, WESTERN NORTH GREENLAND

by R. J. ALDRIDGE

ABSTRACT. A fused conodont cluster, comprising six distacodontiform elements and one oistodontiform element, from upper Ordovician limestones of the Aleqatsiaq Fjord Formation of Washington Land, north Greenland, is described. A notable microstructural feature of all the elements is the presence of oblique striations along the anterior margins of the lateral faces. The distacodontiform elements are similar to elements included in *Acodus? mutatus* (Branson and Mehl) and *Dapsilodus obliquicostatus* (Branson and Mehl), but the apparatus structure appears to be different and the cluster is assigned to *Besselodus arcticus* gen. et sp. nov.

CONODONT elements are normally found as isolated, discrete specimens, and until the mid 1960s conodont taxonomy and nomenclature were almost entirely based on the morphology of single elements. A multielement concept of conodont species was first proposed over a hundred years ago, by Hinde (1879), and the discovery of 'natural assemblages' of conodonts on shale bedding surfaces by Schmidt (1934) and Scott (1934) provided direct evidence that each animal possessed a skeletal apparatus consisting of different element types. Subsequently, several hundred similar associations, each representing the skeletal remains of an individual animal, have been found, mostly in Carboniferous shales (e.g. Scott 1942; DuBois 1943; Rhodes 1952). Descriptions of many of these naturally occurring apparatuses have yet to be published. Additional evidence of apparatus structures is provided by fused conodont clusters recovered from acid-insoluble residues (e.g. Rexroad and Nicoll 1964; Austin and Rhodes 1969; Pollock 1969; Ramovs 1977, 1978), most of which represent complete or partial apparatuses.

Once the multielement structure of conodont apparatuses was appreciated it was only a matter of time before workers began to reconstruct apparatuses from collections of isolated specimens. Walliser (1964), for example, suggested reconstructions of nine Silurian conodont apparatuses (informally named 'Conodonten-Apparat' A-J), although no naturally occurring apparatuses or clusters were at that time known from the Silurian. A transition of emphasis in conodont taxonomy from a single element to a multielement basis has followed as more and more reconstructions, based on statistical, distributional, and morphological evidence, have been published. Huddle (1972) has documented the development of the early phases of this transition. Of importance in this taxonomic revolution was the realization that apparatuses conform to a limited number of basic plans (Klapper and Philip 1971; Barnes, Kennedy, McCracken, Nowlan, and Tarrant 1979). Hence, the structures exhibited by naturally occurring apparatuses and clusters, together with those of well-established reconstructions, can serve as models in the analysis of new collections.

Naturally occurring apparatuses and clusters are rare, and it is probable that the apparatuses of most species will be recognized entirely from collections of isolated elements. However, the direct evidence furnished by natural associations is of paramount importance to multielement taxonomy; not only do they provide templates for reconstructions, but new finds allow testing and evaluation of current hypotheses. Additionally, it is only from these associations that we can confidently assess the relative numbers and dispositions of the component elements.

The only natural associations of late Ordovician conodonts recorded to date are three clusters

of *Belodina compressa* (Branson and Mehl) from Canada (Barnes 1967; Nowlan 1979). Another cluster, also of coniform elements, has recently been isolated from late Ordovician limestones of northern Greenland. Although the material is limited, the apparatus differs in structure from those reconstructed for similar Ordovician and Silurian elements, and the cluster is assigned to a new taxon, *Besselodus arcticus*.

SAMPLE LOCALITY AND HORIZON

The cluster was recovered from Geological Survey of Greenland sample no. GGU 242821, collected by Dr. J. M. Hurst from the Aleqatsiaq Fjord Formation of Aleqatsiaq Fjord, Washington Land, western North Greenland (see Peel and Hurst 1980; Hurst 1980). The sample of fissile, argillaceous calcilitite is from 132 m above the base of the formation and approximately 140 m below the top. The conodont fauna includes *Amorphognathus* aff. *ordovicianus* Branson and Mehl, which is also present in samples GGU 242820 and GGU 242822, from 20 m below and above the horizon. A late Ordovician, Ashgill, age is indicated.

THE CONODONT FAUNA

The 730 gm sample available for processing yielded only a small number of conodont specimens. Some of these are fragmentary, but the following are identifiable:

<i>Amorphognathus</i> aff. <i>ordovicianus</i> (Branson and Mehl)		
	Pa element	1
	Sa element	2
<i>Belodina compressa</i> (Branson and Mehl)		
	compressed rastrate element	1
	eobelodiniiform element	1?
<i>Besselodus arcticus</i> gen. et sp. nov.		
in cluster:	distacodontiform element	6
	oistodontiform element	1
isolated:	distacodontiform elements	8?
	oistodontiform elements	5?
<i>Coelocerosodontus trigonius</i> Ethington		1
<i>Oulodus?</i> sp.	Sc element	4
<i>Panderodus</i> sp.		2
<i>Pseudobelodina?</i> sp.	rastrate element	1
<i>Pseudooneotodus</i> sp.		1

Isolated specimens similar to those of *Besselodus arcticus* occur sporadically and in small numbers throughout the lower and middle Aleqatsiaq Fjord Formation. Small acodontiform elements are occasionally found in the same samples, but it is not at present possible to ascertain whether these specimens belong in *Besselodus* or represent another apparatus.

SYSTEMATIC DESCRIPTION

Genus BESSELODUS gen. nov.

Type species. *Besselodus arcticus* sp. nov.; from the Aleqatsiaq Fjord Formation of Washington Land.

Diagnosis. The apparatus contains at least two members, distacodontiform and oistodontiform. All known elements are laterally compressed with sharp anterior and posterior edges.

EXPLANATION OF PLATE 44

Figs. 1-8. *Besselodus arcticus* gen. et sp. nov. 1-2, lateral views of sub-cluster 'a', partial holotype, MGUH 15071, $\times 250$. 3-4, lateral views of sub-cluster 'b', partial holotype, MGUH 15072, $\times 250$. 5-6, lateral views of isolated specimen, MGUH 15073, $\times 250$. 7, detail of partial holotype MGUH 15071, $\times 660$. 8, detail of partial holotype MGUH 15072, $\times 660$.



1



2



5



3



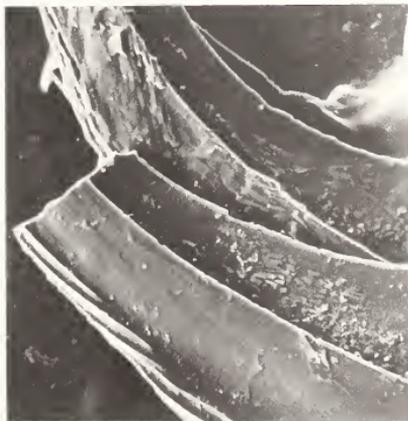
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6



7



8

ALDRIDGE, fused conodont cluster

Discussion. Distacodontiform (=acodontiform) elements similar to those of *Besselodus* are included in the reconstructions of the Silurian genus *Dapsilodus* (Cooper 1976, p. 211) and of the Ordovician species *Acodus? mutatus* (Branson and Mehl). The generic assignment of *A.? mutatus* was discussed fully by Löfgren (1978, pp. 43–45), who pointed out that the apparatuses of the type species of *Acodus*, *Distacodus*, and *Acontiodus* are all unknown.

Dapsilodus has an apparatus of distacodontiform, modified distacodontiform and acodontiform elements (Barrick 1977, p. 50); no oistodontiform element is included, nor are there any oistodontiform or modified oistodontiform elements known from the Silurian that might be considered as homologous to the oistodontiform of *Besselodus*. *A.? mutatus* also has an apparatus that includes distacodontiform and acodontiform elements (Bergström and Sweet 1966, pp. 303–305), although there have been suggestions that an oistodontiform element should also be included here (Barnes and Poplawski 1973, p. 779; Sweet, in Cooper 1976, p. 211). This has been contested by Löfgren (1978, pp. 45, 57), who found no distributional relationship between oistodontiforms and elements of *A.? mutatus* in her early Ordovician samples from northern Sweden. The oistodontiform included by Barnes and Poplawski (1973) is *Oistodus venustus* Stauffer, which is not closely similar to the element in the cluster of *Besselodus*.

There is currently little evidence for the inclusion of an acodontiform element in *Besselodus*. None occurs in the cluster, nor are there any isolated specimens in the remainder of the, admittedly small, sample from the same horizon.

Besselodus arcticus sp. nov.

Plate 44, figs. 1–8

Diagnosis. The apparatus contains at least two members, distacodontiform and oistodontiform. All known elements are laterally compressed with sharp anterior and posterior edges; at the anterior margins, the lateral faces of all elements display prominent oblique striations.

Description. The material to hand comprises a cluster and a few isolated specimens, all from the same sample. The cluster consists of very small, delicate coniform elements, all of which are broken at the tips. The elements are all very thin and translucent and white matter cannot be distinguished. Unfortunately, the cluster fell apart into two sub-clusters on initial picking, and subsequent handling has been kept to a minimum.

Sub-cluster 'a' (Pl. 44, figs. 1, 2, 7) is 0.25 mm in maximum dimension and consists of four distacodontiform elements in subparallel orientation. Each component measures about 0.2 mm from base to broken tip and is laterally compressed with sharp anterior and posterior edges. The basal outline is a highly compressed ellipse. Each lateral face bears a longitudinal costa, slightly to the posterior of the mid-line; on those specimens where the basal portion is visible, the costae terminate sharply a short distance from the basal margin. The posterior edge of each element is gently curved; the anterior edge is more sharply curved near the basal margin, producing a slight geniculation. As far as can be ascertained all the elements are bilaterally symmetrical, or very nearly so, and there is no apparent gradation in size or curvature. Each element displays well-developed fine, parallel striae on the lateral faces at the anterior margin; at the broken tips these striae are at an angle of less than 10° to the anterior edge, towards the base this angle steadily increases to greater than 20°. The striae fade towards the base and terminate at the point of geniculation (Pl. 44, fig. 7).

Eight isolated distacodontiform specimens from the same sample show similar features, with some variation in curvature apparent. Preservation is variable; the best-preserved is illustrated in Pl. 44, figs. 5, 6. This specimen differs from those in the cluster in lacking the geniculation of the anterior edge, producing a more triangular outline for the basal portion of the unit.

Sub-cluster 'b' (Pl. 44, figs. 3, 4, 8) is 0.24 mm in maximum dimension. Two distacodontiform elements comparable with those in sub-cluster 'a' are fused in subparallel orientation; a third, broken and cracked, oistodontiform element is orientated so that its cusp is parallel to those of the distacodontiform elements. The strong geniculation of the oistodontiform results in the basal margin of the unit lying at an angle of 30° to the basal margins of the distacodontiforms. The visible lateral face of the oistodontiform shows a longitudinal costa on the posterior portion of the cusp; oblique striae at the anterior margin of the cusp are also apparent, ranging in angle from 12° at the broken tip to 20° near the geniculation, where they terminate. These striae compare closely with those displayed by the distacodontiform elements.

There are five small, isolated oistodontiform specimens in the sample, but those examined under the scanning

electron microscope do not exhibit clear oblique marginal striations; they may or may not be referable to the same species as the cluster.

Holotype. MGUH 15071 and MGUH 15072, separated portions of a single cluster from sample GGU 242821; deposited in the type collection of the Geologisk Museum, Copenhagen.

Discussion. The cluster probably represents a partial, rather than a complete, apparatus. The presence of a single oistodontiform may indicate that it is a partial or complete half-apparatus. In addition to the general similarity of the morphology of the distacoodontiform elements, the oblique striae on the anterior margins of the elements may indicate a relationship to *Dapsilodus*. Similar striae are apparent on specimens of *D. obliquicostatus* figured by Serpagli (1970, pl. 23, figs. 1–10, pl. 24, figs. 1–6), Cooper (1976, pl. 2, figs. 11–12, 18–20), and Barrick (1977, pl. 2, figs. 6, 10). Serpagli (1970) noted the absence of similar striations on specimens referred to the older, possibly ancestral, species *Acodus? mutatus*. In the material referred to that species by Löfgren (1978, p. 44, pl. 2, figs. 9–21) longitudinal striations are developed and a single specimen (pl. 2, fig. 11A, B) also possesses anterior striae at an angle of 5–10° to the anterior margin. The presence of anterior striae may not be an important character in determining relationships, as they are displayed by other specimens, and are apparent in the clusters of *Belodina compressa* figured by Nowlan (1979, especially fig. 35.2).

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A NEW CALCAREOUS GREEN ALGA FROM THE MIDDLE JURASSIC OF ENGLAND: ITS RELATIONSHIPS AND EVOLUTIONARY POSITION

by GRAHAM F. ELLIOTT

ABSTRACT. *Leckhamptonella llewellyae* gen. et sp. nov., is described from the Middle Jurassic (Inferior Oolite; Aalenian) of the Cotswold district, England. Although known only from fragmentary material, it is recognizable as the remains of a new serial-segmented member of the Udoteaceae (Chlorophyta). It is compared with *Boueiina* and *Arabicodium* (both Mesozoic) and *Halimeda* (Cretaceous-Recent), and shows certain affinities with the latter especially. The evolution of serial-segmented Udoteaceae from Lower Palaeozoic to Recent is briefly reviewed.

THE fossil described below occurs as pieces and fragments of original small calcareous-walled hollow ovoids, near-circular in transverse section and curved-elongate in vertical section. The walls show a very distinctive structure formed by irregular but characteristic branching pores, with possible vestiges of a structure interior to the wall. The material studied occurs in an oomicrite with subordinate echinoderm, molluscan, brachiopod, and other organic fragments, often worn and encrusted and presumed current-swept and not on the site of growth.

The new fossil does not show the optical extinction of echinoderm-calcite pieces, nor the laminar structure of molluscs or brachiopods. The wall-structure is not that of stromatoporoids or hydrozoa, and has not the spicular mesh of any known sponge. It does, however, have the characteristics of certain green calcareous algae, notably the Order Dasycladales and the family Udoteaceae of the Order Caulerpales. The resemblance is very much with the cortical structure of the 'serial-segmented' members of the Udoteaceae (*Halimeda*, and various extinct genera discussed below). It possesses the marked irregularity in detail which is so characteristic, and the general pore-plan is that of yet another variant of the branching utricles of the family. It does not, in most specimens, show clearly the longitudinal medullary threads appropriate to this interpretation, but two well-preserved pieces show traces of this structure, which has to be carefully distinguished from peripheral diagenesis and staining of the clasts. The absence is probably due to the rolled state of the fragments and the usual originally weak medullary calcification in the Udoteaceae. In the Permian *Tauridium*, normally found fragmented, very much more abundant material than is available with the present fossil still leaves reconstruction a difficult task.

If comparison is made with the Udoteacean *Ovulites* (Cretaceous, Cenozoic), the external dimensions and shape of the Cotswold fossil as so far known are comparable with those of *O. margaritula* (Lmk.) Munier-Chalmas (cf. Massieux 1966). In these, however, and other *Ovulites* spp., the calcareous wall is thinner, the pores near-uniformly straight, thin, and radial, and no trace survives of medullary structures. *Ovulites* is usually regarded as remains of a plant comparable with the living *Penicillus*, the 'Neptune's Shaving Brush', where the thallus is of different morphology to that of *Halimeda*. *Ovulites* and *Halimeda* both appear in the Cretaceous, and it is interesting that the new Jurassic fossil brings both to mind, even if apparently much more similar to the latter in structure.

If the present remains are envisaged as those of a dasycladalean, they are anomalous in showing udoteacean irregularity and not a verticillate arrangement. The thin calcification of the swollen heads of the Jurassic *Petrascula* and *Contoporella* belongs to very much larger individuals.

It would thus seem that the fragments can be interpreted as those of ovoid serial-segments of a new udoteacean, the medullary part originally weakly calcified and now largely missing in the worn fragments available.

SYSTEMATIC PALAEOLOGY

Division CHLOROPHYTA (Green Algae)

Order CAULERPALES Feldmann 1946

Family UDOTACEAE Feldmann 1946

Genus LECKHAMPTONELLA gen. nov.

Udoteacean segments with calcified cortical zone showing swollen branching utricles each dividing into several thinner outer parallel utricles which again divide peripherally. Type-species *Leckhamptonella llewellyae* sp. nov., dedicated to Dr. Llewellya Hillis-Colinvaux in recognition of her extensive studies of the living *Halimeda*.

Leckhamptonella llewellyae sp. nov.

Plate 45, figs. 1-6

Description. *Leckhamptonella* with presumed ovoid segments of observed length up to 2.70 mm and estimated matching diameter of approximately 1.80 mm (but a section of 2.40 diameter may indicate larger segments). Medullary zone mostly missing in fossil pieces: thickness of presumed medullary filaments where preserved about 0.030 mm. Thickness of calcified cortical zone about 0.36 mm; inner half of this occupied by a zone of outwardly directed waisted and swollen branching utricles of 0.030-0.090 mm diameter. These each divide into several straight, thin, near-parallel outer utricles of about 0.015 mm diameter. These are at right angles to the longitudinal axis of the segment, and divide again just below the segment-surface, to short adjacent peripheral utricles of 0.010 mm or less diameter, which expand up to 0.020 mm terminal diameter, almost touching.

Holotype. The specimen figured in Pl. 45, fig. 1; British Museum (Natural History), Dept. Palaeontology registered number V.60703. Middle Jurassic, Lower Inferior Oolite (Aalenian *bradfordensis* subzone); Upper Freestone facies of Scotsquar Hill Limestone (Mudge 1978); Leckhampton, Cheltenham, Gloucestershire.

Paratypes. The specimens figured in Pl. 45, figs. 2-6; registered numbers V.60704-60708 incl.; same locality and horizon.

Other material. About thirty-five fragments in thin-sections: same locality and horizon.

THE EVOLUTION OF THE 'SERIAL-SEGMENTED' UDOTACEAE

The members of the Udoteaceae, to which *Leckhamptonella* is referred, show a structure of repeatedly branching threads, much intertangled and interwoven. In *Udotea* itself the whole thallus is a single

EXPLANATION OF PLATE 45

Figs. 1-6. *Leckhamptonella llewellyae* gen. et sp. nov. All pieces in thin-section from the Middle Jurassic, Aalenian *bradfordensis* subzone, Lower Inferior Oolite; Leckhampton, Gloucestershire, England. 1, portion of vertical section of calcareous wall, showing presumed medullary thread at base, swollen branching cortical utricles, radial utricles, and terminal peripheral utricles (shown a little left of top centre); $\times 80$; Holotype, British Museum (Natural History), Department of Palaeontology, registered number V.60703. 2, portion of transverse section of large unit, with external dark crust, $\times 30$; V.60704. 3, portion of vertical section, showing two presumed medullary threads (bottom right), swollen utricles and radial utricles, $\times 80$; V.60705. 4, tangential subsurface section, showing close-set peripheral utricles, $\times 80$; V.60706. 5, slightly oblique vertical section of whole side of unit, $\times 40$; V.60707. 6, tangential-longitudinal section of wall showing swollen and radial utricles, heavy dark crusting externally, $\times 40$; V.60708.

Fig. 7. Oblique cut, piece of *Tauridium* sp. for comparison; Upper Permian, Southern Tunisia, $\times 40$; V.54052.



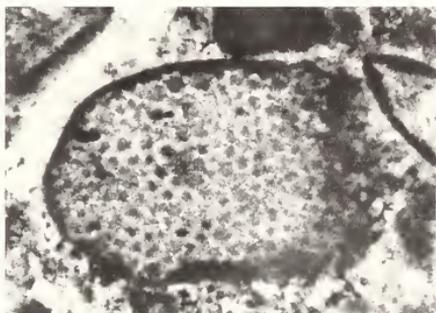
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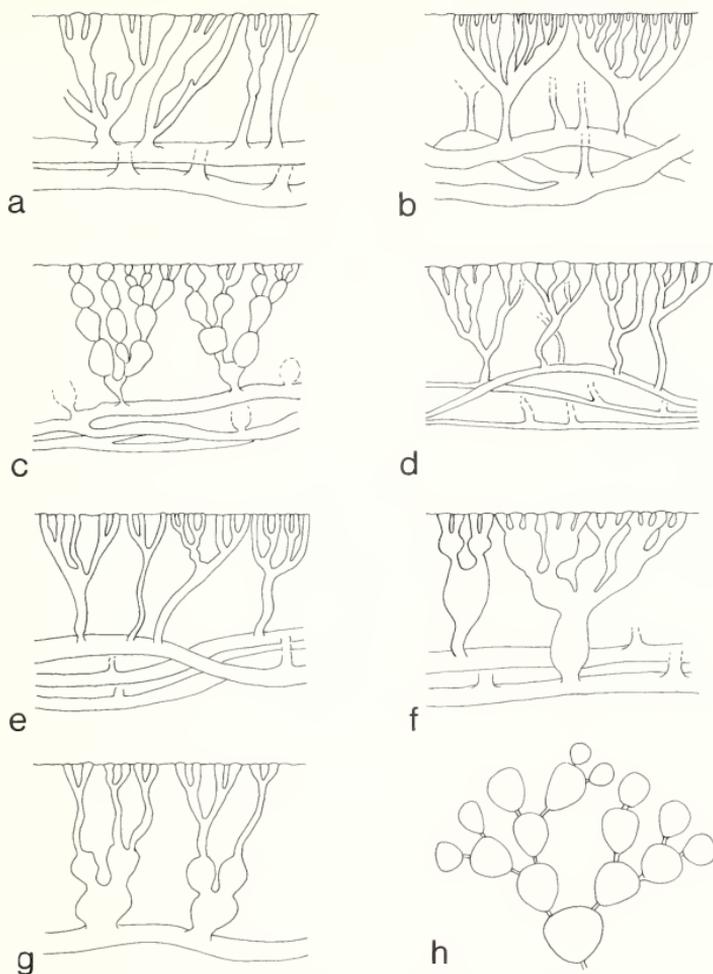
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fan-shaped structure, but another common growth-form, of which *Halimeda* is the modern representative, is shown by what may be termed 'the serial-segmented udoteaceans'. In these, known since the Lower Palaeozoic, the plant is (or is presumed to have been) a clump of branching successions of numerous individual calcified segments, connected by uncalcified threads or filaments. Each segment shows internal coarse longitudinal medullary filaments from end to end, and an outer cortical zone of lateral, branching, and often swollen utricles which terminate in a surface layer of closely packed peripheral utricles. The medullary filaments give rise distally during growth to new segments beyond the old, the connecting filaments being either separate or partially or completely fused at the nodes, so uniting the whole segmented plant as a flexible structure. The peripheral utricles are concerned with the assimilatory functions, and the swollen inner cortical utricles with eventual transference of their content to deciduous reproductive outgrowths (gametangia) at the times of sexual reproduction (Hillis-Colinvaux 1980). These last are only really known in the living *Halimeda* (one fossil record in Pfender 1940, p. 245) and our knowledge is incomplete.

Calcification of the segments is usually heavy cortically (interutricular), but much less so in the medullary zone. In the fossils the segments occur dissociated, mixed, and often broken. They are preserved because of the calcification. The behaviour of the medullary filaments at the nodes, so important in classification of the living *Halimeda* (Hillis-Colinvaux 1980) is thus not normally known in the extinct genera. A solitary example in the collections of the British Museum (Natural History) of an undescribed udoteacean from the Upper Permian of Tunisia, reg. no. V.54065, shows the nodal filaments parallel and in contact along their length, but apparently not fused (if this is the correct interpretation of their slightly different mineralizations). The variation in detail and degree of structure and calcification between older and younger segments of individual plants, between those of different individuals of the same species, and between those typical of different species, as known in living *Halimeda* (Hillis 1959; Hillis-Colinvaux 1980) can make precise specific evaluation of the fragmentary resorted fossil remains difficult, though often occurrences seem to be of a single species. Ideally, one should have a real abundance of material to describe (Conard and Rioult 1977), but this is not always available. The state of geological preservation may add to these difficulties, explaining such records as *Boueina*/*Arabicodium*, *Boueina*/*Halimeda* (Bismuth, Bonnefous, and Dufaure 1967).

The evolution of serial-segmented udoteaceans, as preserved fossil, appears to have consisted of variation and different combinations of the basic structures outlined above, from the Lower Palaeozoic onwards (text-fig. 1). Thus *Dimorphosiphon* (Ordovician) shows a coarse thread-structure and *Palaeoporella* (Ordovician-Devonian) a fine one, while *Maslovina* (Silurian) has the dense layer of small peripheral utricles typical of some later genera (Obrhel 1968), but not present in the other two. Text-fig. 1 shows a selection of patterns in different genera from *Dimorphosiphon* to *Halimeda*. Is this evolution more or less random, or does it show some progression in time with the surviving *Halimeda* as the most advanced as well as the latest of its kind? And does the new Jurassic *Leckhamptonella* throw any light on this problem?

It can be seen from text-fig. 1 that the central medullary filaments can be thick or thin, straight or tangled in varying degree in different genera. Similarly, the cortical utricles, while often branching, vary much in spacing or crowding, and in degree of swelling between genera. The examples figured show various combinations, typical of those genera. On mechanical grounds, strong straight medullary filaments, with some fusion and flexibility at the nodes, would equip such a plant to withstand a moderate degree of water-movement and enable it to colonize moderate-energy environments, other conditions being suitable. In addition, swollen cortical utricles and a layer of close-set peripheral utricles would provide for quick segment-growth and eventually for rapid production of gametangia at times of sexual reproduction. This combination, familiar in *Halimeda*, is apparently first achieved in the Permian *Tauridium*, though with different proportions in the utricles, but these were extremely fragile plants post-mortem, almost invariably found as debris or comminuted. Apparently calcification was thin and mostly outer-cortical, and in life the plant was probably confined to quiet waters. In *Halimeda*, however, calcification is heavy, and its success as witnessed by abundance, wide distribution, and occurrence in a range of low to moderate energy-environments (Hillis-Colinvaux 1980) is well known.



TEXT-FIG. 1. Diagrammatic representations of filament and utricle structure in various udoteacean genera, mostly based on materials in the collections of the British Museum (Natural History): (a) *Dimorphosiphon* (Ordovician); (b) *Aphroditicodium* (Permian; BM(NH) Dept. Palaeont. reg. no. V.59461); (c) *Tauridium* (Permian); (d) *Arabicotidium* (Jurassic-Cretaceous); (e) *Boucina* (Triassic-Cretaceous); (f) *Halimeda incrassata* (Ellis) Lamx (Recent) (Hillis 1959); (g) *Leckhamptonella llewellyae* Elliott (Jurassic); (h) diagrammatic growth-plan of serial-segmented udoteacean. See also comparisons for some other Palaeozoic genera in Obrhel (1968, fig. 1) and Guilbault and Mamet (1976, fig. 2).

Leckhamptonella llewellyae shows similarities in cortical utricle-structure to typical modern *Halimeda* spp. It differs in that the third layer of cortical branches are straight, thin, and parallel before dividing into peripheral utricles, whereas in the modern *Halimeda* spp. swollen branches and branchlets usually continue outwards to the peripheral utricles. In the light of the functional reasoning above this difference would be a primitive character is *Leckhamptonella*. The general appearance of the medullary zone is not known, and so cannot be compared with those of other genera.

Halimeda is itself known rarely from the Lower Cretaceous (Dragastan and Bucur 1979; possibly Wells 1944), becomes more common in the Upper Cretaceous, and is abundant throughout the Cenozoic to the present day. It has been considered as arising by hybridization from the earlier Mesozoic *Boueina* and *Arabicodium* (Elliott 1965) or as more closely related to *Boueina* as evidenced by comparable intrageneric species groupings (Conard and Rioult 1977). The fragmentary condition of the Middle Jurassic *Leckhamptonella*, as described above, precludes a detailed comparison of these four genera, but the cortical structure of *Leckhamptonella* appears closer to that of the later *Halimeda* than to those of the earlier genera.

Arabicodium, *Boueina*, and *Halimeda* were all Tethyan in origin: *Boueina* appears in the Upper Triassic of Central Europe and of Thailand (Flügel 1975; Kemper, Maronde, and Stoppel 1976) and its pan-tropical distribution in the Lower Cretaceous has been plotted by Elliott (1981). *Halimeda* may have appeared in the Lower Cretaceous of both hemispheres (Dragastan and Bucur 1979; Wells 1944) and was certainly widely distributed in the Upper Cretaceous (Elliott 1981). *Arabicodium* from the Jurassic-Cretaceous of the western Tethys (Mediterranean-Middle East) had a Jurassic straggler as far north as southern England (Elliott 1975) in the same area where *Leckhamptonella* occurs.

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ADDENDUM

AFTER completion of this paper, I read the memoir of Dr. D. Vachard (Doc. Trav. IGAL Paris no. 2, dated 1980, issued 1981) in which he suggests that various genera, including *Aphroditicodium* Elliott and *Tauridium* Guvenç should be considered as synonyms of *Permocalculus* (Vachard 1981, 382). *Aphroditicodium* he considers to be a well-preserved *Permocalculus fragilis*. The point is of some importance because it would transfer these two genera from Udoteaceae (green algae) to Gymnocodiaceae (red algae). I have examined material from Burma, much better preserved than the type of *Aphroditicodium*, and more extensive material of *Tauridium* from north Italy, in both of which the medullary structures and their relations to the cortical structures are well shown, better than in the types. However, in none of these specimens are reproductive structures to be seen (an absence to be expected in Udoteaceae), whereas in *Permocalculus* they are conspicuous in many individuals, even when preservation is poor. Whilst agreeing with Dr. Vachard as to the similarities of structural plan in these fossil genera, and as to the various changes in taxonomic allocation (to which I contributed) in the past, I consider that *Aphroditicodium* and *Tauridium* are Udoteacean genera, however wide a variation the Gymnocodiacean *Permocalculus* shows.

A RARE LYTOCERATID AMMONITE FROM THE LOWER LIAS OF RADSTOCK

by D. T. DONOVAN and M. K. HOWARTH

ABSTRACT. A single lytoceratid ammonite from the Jamesoni or IbeX Zone of the Lower Lias of Clandown Colliery Quarry, Radstock, Avon, is made the holotype of *Derolytoceras* (*D.*) *radstockense* sp. nov. It is the first record in Britain of a genus that is largely restricted to Tethyan areas of south and central Europe.

THE partial or complete restriction of certain groups of ammonites to the Tethys has long been known, and was documented in some detail by Donovan (1967) for the Lower Jurassic. At this time, the Suborders Phylloceratina and Lytoceratina are so restricted except for certain limited spans of time when certain genera are found in northern Europe. Thus, Phylloceratina are represented in Britain by *Tragophylloceras* in the Pliensbachian and *Phylloceras* in the Upper Pliensbachian and the Toarcian, and Lytoceratina by *Lytoceras* in the Upper Pliensbachian and the Toarcian and by genera of the Allocyloceratinae in the Upper Toarcian. A second class of occurrence comprises rare finds, usually made from a single horizon. The following fall into this category:

? a member of Juraphyllitidae from the Planorbis Zone of the Stowell Park Borehole, Gloucestershire (Spath 1956, p. 158). One of us (DTD) has re-examined this specimen, which was preserved in soft mudstone, but it is now in such an abraded state that further comment is not possible.

Galaticeras jacksoni Howarth and Donovan, a member of Juraphyllitidae, known from nine examples from the Flatstones (Obtusum Subzone) of the Dorset coast; *Galaticeras* sp. has been recorded from two boreholes in southern England (Howarth and Donovan 1964).

Meneghiniceras lariense (Meneghini), another juraphyllitid, a single specimen from the Grey Shales (Semicelatum Subzone) in the Toarcian near Whitby, Yorkshire (Howarth 1976).

Aegolytoceras rotundicosta (Tutcher and Trueman) from the Jamesoni Limestone of Radstock, discussed in detail below.

The present paper records an example of a lytoceratid genus new to Britain, from the Lower Lias of Radstock, collected sixty years ago but only recently recognized for what it is.

SYSTEMATIC PALAEOLOGY

Superfamily LYTOCERATACEAE Neumayr 1875

Family DEROLYTOCERATIDAE Spath 1927

Genus DEROLYTOCERAS Rosenberg 1909

Type species. *Ammonites lineatus tortus* Quenstedt 1885, subsequently designated by Spath 1924 (p. 4).

Subgenus DEROLYTOCERAS

Derolytoceras (*Derolytoceras*) *radstockense* sp. nov.

TEXT-fig. 1

Diagnosis. *Derolytoceras* attaining at least 80 mm diameter, with evolute, slowly expanding whorls, and an evenly rounded elliptical whorl section. Regular radial ribs are strong from 13 mm diameter.



TEXT-FIG. 1. *Derolytoceras (D.) radstockense* sp. nov. Holotype. Jamesoni Limestone, Lower Pliensbachian, Jamesoni or Ibex Zones, Clandown Colliery Quarry, Radstock, Avon. Bristol University Geology Museum no. 2877, $\times 0.95$.

and curve forwards to the middle of the venter. Three or four constrictions per whorl are similar in shape to the ribs, and are accentuated by an enlarged rib immediately in front. The suture-line is *Lytoceratid* with highly indented and undercut saddles.

Material. The holotype only, Bristol University Geology Museum no. 2877, from the Jamesoni Limestone, Lower Lias (Lower Pliensbachian: Jamesoni or Ibex Zone) at Clandown Colliery Quarry (ST 679 558), near Radstock, Avon. For the section at this quarry see Tutchter and Trueman 1925, p. 600. Collected in 1922 or 1923 by Mr. T. R. Fry.

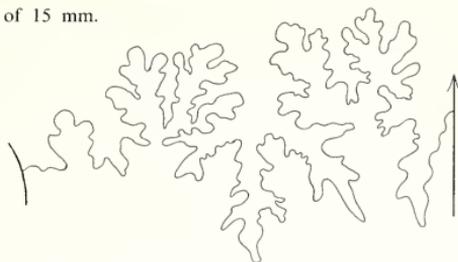
Measurements. Maximum diameter 80.5 mm. At 78.1 mm diameter, whorl height = 23.8 mm (0.30), whorl breadth = 18.1 mm (0.23), umbilical width = 38.0 mm (0.49). There are thirty-three ribs and four constrictions on the outer whorl ending at 80 mm diameter.

Description. The specimen consists of about four visible whorls ending at a diameter of 80 mm. The mouth border is not present, for at least the final one-eighth of a whorl is missing. Suture-lines can be clearly seen just over half a whorl behind the aperture at a diameter of 57 mm. From the rough state of preservation it is not possible to see whether there are more suture-lines at a larger size, but the phragmocone may have extended about one-eighth of a whorl further forwards. This makes the length of the body chamber that is preserved between three-eighths and half a whorl in length. The whorls are evolute but not completely so, for each whorl overlaps about 20% of the next inner whorl. The whorl section is compressed elliptical and has an evenly rounded venter and umbilical wall. Capricorn ribs are well developed on all visible whorls from the smallest size seen, about 13 mm diameter, up to the aperture, though they diminish in strength on the last half whorl. They are approximately radial on the side of the whorl, then curve forwards towards the middle of the venter. There are four well-marked constrictions on the outer whorl that follow the line of the ribs exactly. They are made more prominent by an enlarged rib immediately in front of each one. Three constrictions can be seen on the next inner whorl, but at smaller sizes the preservation is not good enough for constrictions to be visible.

The suture-line (text-fig. 2) is typically *Lytoceratid*. The large first and second lateral saddles are deeply indented and undercut, and have complicated moss-like endings. The large first lateral lobe is divided into three prongs.

Remarks. Ammonites of the superfamily *Lytocerataceae*, other than *Lytoceras* itself, are almost unknown in the Sinemurian and Pliensbachian in Britain. The only one known previously is the

TEXT-FIG. 2. Suture-line at whorl height of 15 mm.
Approx. $\times 5$.



single specimen from the Jamesoni Limestone at Radstock that was the holotype and sole basis of the name '*Peripleuroceras* *rotundicosta* Tutchter and Trueman (1925, p. 646, pl. 41, fig. 1) (BM(NH) C.41760). That specimen is smooth up to about 30 mm diameter, and then develops capricorn ribs mainly on the venter, that have become fairly strong by its maximum size of 49 mm diameter. It is wholly septate. It belongs to the Derolyoceratidae genus *Aegolytoceras* Spath 1924, of which *Peripleuroceras* Tutchter and Trueman 1925 is a junior synonym. Other species of *Aegolytoceras* develop the characteristic coarse capricorn ribs immediately behind constrictions, reverting to fine ribbing in front of constrictions. *Derolytoceras* (*D.*) *radstockensis* differs in having regularly strong capricorn ribs that develop at an earlier growth stage, and the only irregularity on the phragmocone is the single slightly stronger rib that follows in front of each constriction. It is difficult to tell whether the decrease in rib strength on the last half whorl is due to poor preservation or is the onset of adult ornamentation. These are features of the genus *Derolytoceras*, of which, at 80 mm diameter, it is one of the largest known examples. The subgenus *D.* (*Derolytoceras*) has ribs from an early growth stage, certainly by 13 mm diameter which is the smallest size visible in this Radstock specimen, while the subgenus *D.* (*Tragolytoceras*) remains smooth up to about 25 mm diameter. So the Radstock specimen belongs to the nominal subgenus. The type species is *D.* (*D.*) *torium* (Quenstedt), of which the lectotype (Quenstedt, 1885, p. 309, pl. 39, fig. 15), refigured by Wiedmann (1970, p. 995, text-fig. 8e, pl. 6, fig. 3), is from the Upper Pliensbachian of south-west Germany. It has quickly expanding whorls and very strong ribs commence at about 11 mm diameter. Another Sinemurian or Pliensbachian species is *D.* (*D.*) *haueri* Rosenberg (1909, p. 251, pl. 11, figs. 31, 32), which is based on specimens of up to 15 mm diameter that have slowly expanding and finely ribbed evolute whorls. Though it is difficult to compare the much larger Radstock specimen with either of these species, it appears to differ from both of them in its slowly expanding whorls and coarse ribs.

At first sight the Radstock specimen seems to have considerable resemblances to the Polymorphitid genus *Platypleuroceras*, and many examples of *P. brevispina* (J. de C. Sowerby) or closely allied species have been found in the Jamesoni Limestone at Radstock (e.g. Tutchter and Trueman 1925, p. 650, pl. 39, fig. 3; pl. 40, fig. 2). The *Derolytoceras* differs, however, in lacking the ventro-lateral tubercle that occurs in all the specimens of *Platypleuroceras*, and in having more strongly projected ribs on the venter. It also has constrictions that are only rarely present in Radstock *Platypleuroceras* (though constrictions are better developed in similar Polymorphitidae from Germany, e.g. Quenstedt 1885, pl. 32, fig. 6; pl. 33, figs. 11, 12). Finally, the suture-line of the Derolytoceratid is distinctively Lytoceratid, and suture-lines in *Platypleuroceras* do not have such deeply indented or undercut saddles.

The family and generic classification used here is that of the *Treatise* (Arkell, 1957, p. L194). Two more recently proposed generic names are *Adnethiceras* Wiedmann (1970, p. 997) for species that have ventro-lateral tubercles, and *Lytoconites* Wiedmann (1970, p. 1004) which is considered here to be a synonym of *Aegolytoceras*. *Peripleuroceras* Tutchter and Trueman 1925, is also a synonym of the latter genus. Wiedmann (1970, p. 988) did not admit a separate family Derolytoceratidae, but placed it and its included genera in the Lytoceratidae. The distinctive

capricorn ornament of Derolytoceratidae seems to us, however, to be sufficiently different from the ornament of normal Lytoceratidae to warrant separation of this Sinemurian to Toarcian group as a family. Most genera of Derolytoceratidae were also discussed by Fantini Sestini (1973) who reinterpreted the genus *Audaxlytocer* Fucini 1923 (type species *Ammonites audax* Meneghini 1881 (non Oppel, 1863)) on the basis of specimens that were larger than the very small originals, and concluded that it was the oldest name for the group of species that have usually been referred to *Aegolytocer* Spath 1924.

The best collection of Derolytoceratidae, which was not discussed by either Wiedmann (1970) or Fantini Sestini (1973), comes from the Pliensbachian at Monte di Cetona, central Italy. Nine species of '*Deroceras*' were described by Fucini (1903, pp. 166–185): all of them have Lytoceratid suture-lines, and amongst them are the largest known Derolytoceratidae, some specimens attaining 165 mm diameter. Several develop ventro-lateral tubercles and belong to *Adnethiceras* (e.g. *A. olenoptychum* Fucini, *A. mutans* Fucini and *A. instabile* Fucini), and about eight examples were figured of *Aegolytocer* *pecchiolii* (Meneghini), which is the most highly developed species of its genus. Nothing in the collection is exactly like the Radstock specimen, though the rather poorly preserved examples of *Derolytocer* *connexum* Fucini (1903, p. 176, pl. 26, figs. 7, 8) are the nearest, differing mainly in lacking clear constrictions.

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